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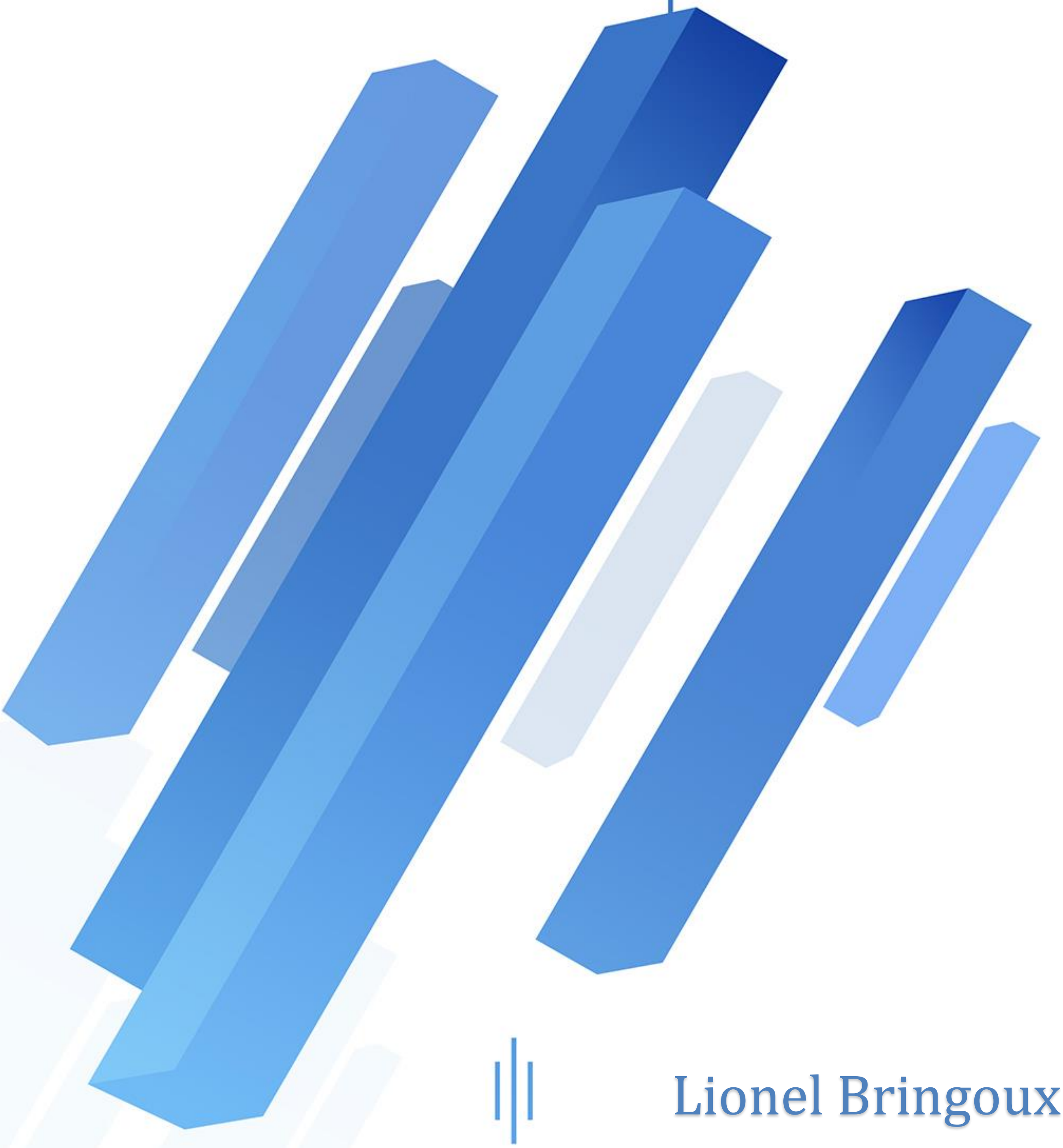

Lionel Bringoux

Perception de l’espace géocentré

Effet de l’ancrage des indices visuels sur l’orientation de tête

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RECHERCHES EMPIRIQUES
EMPIRICAL STUDIES

PERCEPTION DE LA VERTICALE AVEC UN CADRE VISUEL SOLIDAIRE DE LA TETE : IMPLICATIONS POUR L'UTILISATION DES VISIOCASQUES

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SUMMARY

PERCEPTION OF THE VERTICAL WITH A HEAD-FIXED VISUAL FRAME: IMPLICATIONS FOR USING HEAD-MOUNTED DISPLAYS

Head-mounted displays are now extensively developed and tested to be used in enhanced reality environments. The technique consists in transmitting synthetic visual information to the user's eyes in such a way that virtual objects are superimposed on the real world. Some displays give the feeling of viewing a rectangular head-fixed virtual screen with clearly visible contours. In addition, head-mounted displays allow for the presentation of head-fixed visual information to the user and this may be an advantage in some applications, military aeronautics for instance. Presenting head-fixed visual information may not be trivial with regard to actual models of spatial orientation. This study addressed the question of potential disorienting effects associated with head-mounted displays by investigating the influence of a head-fixed visual frame on the perception of the vertical when the head or the whole body was tilted in the frontal plane. In a first experiment, subjects were instructed to indicate the vertical by rotating a visual rod that appeared at the centre of the frame whilst tilting the head in various positions. This performance was compared with the effect on the subjective vertical of a tilted earth-based visual frame without head tilts as well as with the effect of tilting the head without a frame. With the tilted frames, subjects set the rod in an intermediate direction between the gravitational vertical and the orientation of the frame. Errors were substantially larger with a head-fixed visual frame during head tilt than with a tilted earth-based frame. This difference cannot be attributed to the addition of a postural effect caused by the head being tilted. Moreover, continuous vision of the frame when its orientation changed improved performance only when the head and the frame were dissociated, i.e. with an earth-based frame. A second experiment investigated the effects of a head-fixed frame on the subjective vertical and on the voluntary control of head orientation when the whole body was tilted. The effect of a head-fixed frame was contrasted with the effect of a trunk-fixed frame. Results show that the head-fixed frame modified the head behaviour when subjects were instructed to align the head with the trunk. These errors contributed to an increase in the visual frame influence on the subjective vertical. Results of both experiments suggest that integrating visual information in the head-centric reference frame is crucial for spatial orientation. This property of the perceptual system may be relevant for the design and use of head-mounted displays.

Key words: Reference Frames, Spatial Orientation, Subjective Vertical, Head-Mounted Displays, Sensory Integration, Vision, Enhanced Reality

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I. INTRODUCTION

Depuis l'avènement des ordinateurs à haute vitesse de calcul, la réalité augmentée (RA) s'est développée à une vitesse considérable et son utilisation dans le monde du travail donne lieu à de nombreuses recherches. Contrairement à la réalité virtuelle qui vise à immerger un individu dans un environnement artificiel en le coupant du monde extérieur, la RA permet à l'utilisateur de voir le monde réel, dont on modifie certaines caractéristiques en y surimposant des objets virtuels (Azuma, 1997). Autrement dit, la RA vise à enrichir le monde réel d'objets synthétiques qui coexistent avec le monde réel. Cette technique offre de nouvelles perspectives dans de nombreux domaines d'application : entraînement et aide à la visualisation en chirurgie (Fuchs *et al.*, 1998), conception et entretien de machines complexes (Curtis, Mizell, Gruenbaum, & Janin, 1998), architecture (Webster, Feiner, MacIntyre, Massie, & Krueger, 1996), téléopération (Tharp, Hayati, & Phan, 1995), divertissement (Maes, 1995) et aviation (Cohen, Otakeno, Previc, & Ercoline, 2001).

Au cœur de nombreux système de RA, on trouve des dispositifs appelés visiocasques (head-mounted display, selon la terminologie anglophone) dont le principe général est de présenter une image à chaque œil par l'intermédiaire de deux écrans miniatures (cathodiques ou à cristaux liquides). Pour obtenir une RA, deux solutions existent. La scène visuelle peut être filmée et présentée à l'utilisateur sous forme de vidéo que l'on enrichit d'images synthétiques. L'utilisateur est dans ce cas coupé du monde extérieur, même si l'image qui lui est présentée est en grande partie une copie du monde réel. Une autre solution consiste à utiliser des casques semi-transparents (see-through) qui permettent de projeter des objets virtuels en surimposition au monde réel. Si l'on souhaite présenter les objets virtuels de façon à ce qu'ils soient stables dans l'environnement, il est nécessaire de prendre en compte la position et l'orientation de tête dans l'espace. Les visiocasques sont par conséquent couplés à des systèmes de mesure qui permettent de compenser les mouvements de tête afin de stabiliser l'image dans le référentiel terrestre. Cependant, il est possible que l'utilisation de visiocasques mettent l'utilisateur face à des informations visuelles qui restent fixes dans le référentiel de la tête.

Des informations visuelles solidaires de la tête peuvent être induites par les limites intrinsèques du visiocasque. En effet, ces dispositifs disposent d'un champ visuel limité qui varie selon les modèles (entre 25° et 100° d'angle). Certains systèmes offrent une fenêtre de visualisation en dehors de laquelle il n'est pas possible de voir. D'autres donnent la sensation de voir un moniteur informatique semi-transparent qui reste fixe par rapport à la tête. Or, les contours qui délimitent le champ de vision ou le moniteur virtuel sont souvent visibles et forment un cadre visuel fixe dans le référentiel tête. Un tel cas de figure est observé, par exemple, dans le prototype MARS (Mobile Augmented Reality System : Feiner, MacIntyre, Höllerer, & Webster, 1997 ; Höllerer, Feiner, Terauchi, Rashid, & Hallaway, 1999). Ce système permet de surimposer à un environnement connu, en l'occurrence le campus de l'Université de Columbia, des éléments hypermédias (noms des bâtiments, icônes qui peuvent être sélectionnées pour faire apparaître un historique du bâtiment sur une tablette graphique portée à la main, représentations virtuelles de bâtiments disparus…). Ces éléments sont stabilisés dans le référentiel terrestre. Dans le visiocasque apparaissent également des éléments fixes dans le référentiel tête : une barre de menu horizontale, un pointeur de direction, mais aussi les contours de l'écran virtuel.

Inclure des informations visuelles céphalocentrées peut également avoir des avantages dans certaines applications. C'est le cas dans le domaine de l'aéronautique militaire où les concepteurs ont intégré, dans les visiocasques des pilotes, des éléments de symbologie qui sont solidaires des mouvements de la tête. De cette façon, le pilote n'a plus besoin de quitter des yeux l'environnement externe pour se référer aux instruments de bord. L'apport principal des visiocasques concerne à l'heure actuelle le système de visée et la perception de la situation tactique, mais les progrès technologiques font envisager aux concepteurs d'inclure d'autres indicateurs, y compris des indicateurs de l'attitude de l'avion (Cohen *et al.*, 2001 ; Ercoline, Self, & Matthews, 2002 ; Liggett & Gallimore, 2002). Ces indicateurs, puisque leur orientation est stable dans le référentiel géocentré, donneraient aux visiocasques le potentiel d'améliorer les capacités du pilote à s'orienter dans l'espace. Considérons maintenant l'exemple d'un concepteur de visiocasque qui désirerait fournir au pilote, dans la visière du dispositif, une série d'indications qui peuvent être utiles lorsque le pilote quitte des yeux les instruments du cockpit pour explorer l'environnement extérieur. Une façon de présenter ces indications sans obstruer le champ de vision du pilote pourrait consister à les fixer dans le référentiel céphalocentré et à les disposer parallèlement à l'axe vertical de la tête, de chaque côté de la visière. Les éléments visuels pourraient alors former un cadre visuel subjectif, présenté en vision périphérique et solidaire des mouvements de la tête.

Quelle que soit l'application envisagée, inclure un cadre visuel attaché à la tête n'est pas neutre au regard des modèles théoriques de l'orientation spatiale. En effet, il est connu qu'un cadre visuel incliné peut influencer les comportements d'orientation, qu'il s'agisse du maintien de l'équilibre (Isableu, Ohlmann, Cremieux, & Amblard, 1997) ou d'une tâche d'estimation de la verticalité (Witkin & Asch, 1948), ce qu'on appelle classiquement des effets cadre. La déviation posturale ou l'effet sur l'estimation de la verticale est commise dans la direction de l'inclinaison du cadre visuel. Il a également été démontré que la désorientation induite par le cadre est susceptible d'être potentialisée par l'inclinaison de la tête (DiLorenzo & Rock, 1982). De plus, de nombreux auteurs s'accordent à dire que s'orienter dans le référentiel gravitaire implique une chaîne de transformation de coordonnées impliquant des sources variées d'informations (Howard, 1986). La projection de l'image sur la rétine doit être encodée et mise en rapport avec l'orientation des yeux dans leur orbite, ce qui implique la prise en compte des signaux de position des yeux. Les informations vestibulaires doivent également être considérées, puisqu'elles renseignent sur l'orientation et les déplacements de la tête. Enfin, l'information proprioceptive utilisée pour réguler la posture fournit le lien entre la position de la tête dans l'espace et les forces de contact du corps au sol (Mergner & Rosemeier, 1998). En d'autres termes, l'orientation d'un objet visuel par rapport à la gravité est obtenue par la transposition des coordonnées rétinocentrées dans un référentiel géocentré en passant par des étapes intermédiaires, définies dans des référentiels centrés sur la tête ou sur le tronc. Au regard de ces considérations sur la construction des référentiels spatiaux, la présentation d'informations visuelles solidaires des mouvements de la tête met l'utilisateur d'un visiocasque face à une situation inhabituelle. En effet, lorsqu'il bouge la tête, les informations visuelles ajoutées bougent dans l'espace extra-personnel tout en restant fixes dans le référentiel de la tête. Cette configuration d'informations n'a pas d'équivalent dans des conditions naturelles, puisque les coordonnées relatives d'un objet visuel par rapport à la tête varient habituellement dès lors que la tête (ou l'objet observé) bouge dans l'espace. Cela implique que le système nerveux central n'a probablement pas évolué pour traiter des références visuelles solidaires des mouvements de la tête et pourrait donc être amené à résoudre un conflit informationnel.

Le but du travail rapporté ici est de déterminer si des références visuelles fixes dans le référentiel tête peuvent influencer la perception de l'orientation spatiale et, le cas échéant, d'éclaircir les mécanismes sous-jacents. Pour cela, deux expériences ont étudié l'influence sur la verticale subjective d'un cadre visuel solidaire des mouvements de la tête. Indiquer la verticale subjective consiste à aligner un objet, en général une barre lumineuse, sur la direction perçue de la gravité. L'étude de la verticale subjective a été privilégiée dans la mesure où il s'agit d'un indicateur des processus d'intégration multisensorielle pour la perception dans l'espace. En effet, la verticale subjective est influencée par l'ensemble des informations impliquées dans l'orientation spatiale (pour une revue, voir Howard, 1986). Cette tâche peut être considérée comme une lecture cognitive d'un modèle interne de la gravité, élaboré par le système nerveux pour l'orientation dans l'espace.

L'obtention d'un cadre incliné d'une amplitude identique à celle de la tête a été rendue possible par l'utilisation d'un visiocasque qui donne la sensation de voir un écran céphalocentré rectangulaire dont les contours sont clairement visibles. Ainsi, quelle que soit l'orientation de la tête du sujet, l'axe vertical de symétrie du cadre reste constamment aligné avec l'axe vertical de la tête. La première expérience s'intéresse tout d'abord à l'influence du port d'un tel dispositif sur la verticale subjective lors d'inclinaisons de la tête, chez des sujets assis. La seconde expérience étudie quant à elle les effets du même type de cadre visuel sur le comportement de réorientation de la tête des sujets et sur leur perception de verticalité lorsque le corps entier est incliné.

II. EXPERIENCE 1 : EFFETS D'UN CADRE VISUEL CEPHALOCENTRE SUR LA VERTICALE SUBJECTIVE LORS D'INCLINAISONS DE LA TETE

II.1. OBJECTIFS

Le premier objectif de l'expérience 1 vise à décrire les effets d'un cadre visuel céphalocentré sur la verticale visuelle, et ceci pour l'ensemble des inclinaisons possibles de la tête. L'influence de l'inclinaison de la tête en l'absence de référence visuelle, ainsi que l'influence d'un cadre visuel incliné, fixe dans l'espace et sans inclinaison de tête, sont également évaluées dans des conditions très similaires. La méthode utilisée se distingue de celles employées dans les études antérieures en ce qu'elle permet un positionnement libre de la tête à des inclinaisons variées en amplitudes. L'orientation de la tête et son maintien ne dépendent donc pas des dispositifs assez contraignants habituellement utilisés. De plus, la verticale visuelle est estimée pour un grand nombre d'amplitudes d'inclinaisons du cadre et/ou de la tête. Les analyses de régression effectuées sur ces valeurs permettent d'obtenir des fonctions psychométriques précises. Dans ces conditions, il est possible de déterminer si les effets d'un cadre fixe par rapport à la tête lors d'inclinaisons de la tête peuvent s'expliquer par l'addition d'un effet cadre et d'un effet postural ou, dans le cas contraire, de préciser quelle est la nature des pondérations sensorielles mises en jeu dans ces conditions. Afin d'évaluer l'influence potentielle de la commande motrice associée à la production volontaire d'inclinaisons de la tête, l'expérience compare également les estimations de la verticale à la suite de mouvements actifs et passifs de la tête.

Le second objectif de l'expérience consiste à évaluer l'influence de la vision continue ou discontinue des cadres visuels lors de leurs changements d'orientation. L'orientation du cadre solidaire de la tête ne peut être évaluée que sur la base des signaux de position de la tête, puisque son orientation ne change jamais par rapport au segment céphalique. En d'autres termes, les transformations de coordonnées visuelles dans le référentiel céphalocentré sont inexistantes. Au contraire, lorsque l'orientation du cadre est dissociée de celle de la tête, toute rotation peut être évaluée dans le référentiel de la tête. Ainsi, quand le sujet a la possibilité de garder les yeux ouverts pendant la rotation, les variations d'orientation du cadre par rapport à la tête peuvent être prises en compte en conjonction avec les signaux vestibulaires et proprioceptifs qui renseignent sur l'orientation de la tête dans l'espace. Nous faisons donc l'hypothèse que la vision du cadre lors de ses rotations dans l'espace ne diminue les effets observés sur la verticale visuelle que lorsque l'orientation du cadre est dissociée de celle de la tête.

II.2. METHODES

Douze sujets (9 hommes et 3 femmes, âgés de 23 à 41 ans) se sont portés volontaires pour cette expérience. Aucun sujet n'a déclaré souffrir ou avoir souffert de troubles vestibulaires. Leur vision était normale ou normalement corrigée.

L'expérience a été réalisée dans l'obscurité. Tous les sujets ont participé à 8 conditions expérimentales. Dans chacune d'elles, la tâche était de placer une baguette lumineuse à la verticale. La baguette visuelle, de couleur blanche, était de forme oblongue, d'une longueur de 10° d'angle et d'une largeur de 2° en son milieu. La baguette pouvait tourner autour de son axe central en agissant sur une manette de jeux placée sur l'accoudoir droit du siège. Aucune limite temporelle n'était fixée pour estimer la verticale. Cependant, les consignes insistant sur la nécessité d'effectuer la tâche en première impression, rares ont été les ajustements excédant 5 secondes. A chaque nouvel essai, l'orientation initiale de la baguette était déterminée de façon aléatoire. Chaque condition expérimentale comportait 40 essais.

La baguette lumineuse utilisée pour les estimations de la verticale était générée soit sur un moniteur informatique de 17", soit sur un casque vidéo (Glasstron PLM-S700 commercialisé par Sony) selon les conditions expérimentales (Fig. 1).

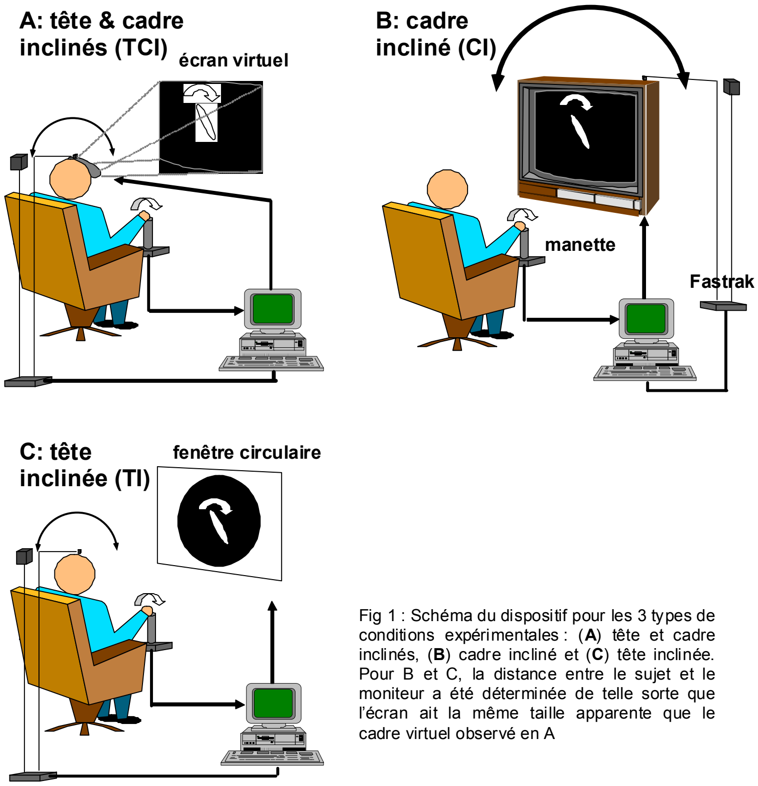

Fig 1 : Schéma du dispositif pour les 3 types de conditions expérimentales : (**A**) tête et cadre inclinés, (**B**) cadre incliné et (**C**) tête inclinée. Pour B et C, la distance entre le sujet et le moniteur a été déterminée de telle sorte que l'écran ait la même taille apparente que le cadre virtuel observé en A

Fig.1 : Schéma du dispositif pour les trois types de conditions expérimentales : (A) tête et cadre inclinés, (B) cadre incliné et (C) tête inclinée. Pour (B) et (C), la distance entre le sujet et le moniteur a été réglée de telle sorte que l'écran ait la même taille angulaire que l'écran virtuel présenté en (A). L'ensemble de l'expérience a été réalisé dans l'obscurité. Les seuls objets visibles étaient le contour de l'écran et la baguette.

Fig.1: Schema of the set-up for the three kinds of conditions: (A) the visual frame was integral to the head and subjects tilted their head at 40 different orientations, (B) an earth-based visual frame was tilted at various orientations while the head remained upright, (C) the head was tilted at various orientations with a circular (non-oriented) visual frame. In (B) and (C), the distance between the subject and the screen was adjusted so that the size of the screen was identical to the size of the virtual screen in (A). The experiment was carried out in darkness. The subject could only see the contour of the screen and the rod.

II.2.A. *Conditions «tête et cadre inclinés» (TCI)*

Dans les conditions TCI (Fig. 1A), le sujet portait un casque vidéo qui donne la sensation de voir un écran informatique, centré sur l'axe interoculaire, d'une taille angulaire de 30° X 22,5°. L'écran virtuel apparaît comme un rectangle gris foncé sur un arrière plan totalement noir. Ce contraste de luminosité forme donc un contour perçu par les sujets comme un cadre visuel. Un récepteur magnétique (Polhemus Fastrak) était fixé sur le haut du crâne, pour mesurer l'orientation de la tête et du casque.

Le sujet, équipé du casque vidéo, plaçait sa tête à diverses orientations dans le plan frontal. Le cadre virtuel et la tête étaient donc inclinés de façon identique par rapport à la gravité. Le premier essai était toujours réalisé avec la tête droite. Ensuite, une nouvelle orientation de la tête était choisie et maintenue, le temps d'estimer la verticale. Immédiatement après la validation de la mesure, une nouvelle posture de la tête était adoptée. De cette façon, les essais s'enchaînaient sans que les phases de maintien statique de la tête ne durent plus de temps que celui nécessaire à l'ajustement de la baguette lumineuse.

Quatre conditions TCI ont été réalisées. Dans deux d'entre elles, le sujet bougeait la tête volontairement et choisissait lui-même l'amplitude de l'inclinaison. Auparavant, il avait été entraîné à exécuter des mouvements d'inclinaison de la tête, en étant attentif à n'y associer ni rotation de la tête vers la droite ou vers la gauche, ni mouvement des épaules ou du tronc. Par conséquent, les inclinaisons de plus de 40° n'étaient pas demandées. Le sujet avait pour instruction d'explorer l'ensemble des inclinaisons possibles de la tête, dans un ordre pseudo-aléatoire au cours des 40 essais. Dans les deux conditions TCI restantes, la tête était inclinée d'une orientation à une autre par l'expérimentateur. Le sujet avait pour consigne de ne pas résister au mouvement imposé par l'expérimentateur et, à l'opposé, de ne pas accompagner le mouvement. L'expérimentateur a pris soin de reproduire aussi adéquatement que possible les caractéristiques (vitesse, accélération) d'un mouvement naturel. Ainsi, que les mouvements de la tête aient été effectués activement ou passivement, l'estimation de la verticale était obtenue pour 40 orientations différentes, entre 40° d'inclinaison entre 40° dans le sens anti-horaire et 40° d'inclinaison dans le sens horaire.

Pour chaque type de mouvement (actif et passif), deux conditions ont été réalisées. Dans l'une d'elle, le sujet fermait les yeux pendant le mouvement. Il n'avait donc la vision du cadre visuel que lorsque l'orientation de la tête était stabilisée, c'est-à-dire pendant le temps nécessaire à estimer la direction de la verticale. Dans l'autre condition, le sujet gardait les yeux ouverts tout au long de la passation. Il voyait donc le cadre bouger avec sa tête.

II.2.B. *Conditions «cadre incliné» (CI)*

La baguette était cette fois présentée sur un moniteur 17", fixé sur une plate-forme qui pouvait être inclinée manuellement dans le plan frontal (Fig. 1B). Un récepteur magnétique était monté sur le moniteur afin d'enregistrer son orientation. Les contours de l'écran formé par l'ensemble des pixels formaient un cadre rectangulaire lumineux. Afin d'ajuster au mieux la distance entre le sujet et l'écran, le casque vidéo décrit précédemment était superposé à l'écran du moniteur (le casque était utilisé dans ce cas en mode «see through», qui permet de superposer l'écran virtuel au monde extérieur visible). Seuls les contours du cadre et la barre lumineuse étaient visibles dans un environnement totalement obscur par ailleurs.

Deux conditions CI ont été réalisées. Cette fois, la tête était maintenue droite par une sorte de minerve. L'expérimentateur changeait l'orientation du cadre en agissant sur la plate-forme inclinable. Pour chaque essai, une orientation était choisie au hasard, de telle sorte à ce que les 40 essais se répartissent entre 40° dans le sens anti-horaire et 40° dans le sens horaire. Dans l'une des conditions, le sujet avait pour consigne de fermer les yeux entre les essais et ne voyait le cadre visuel que lors des estimations de la verticale. Dans l’autre condition, il gardait les yeux ouverts et observait le cadre pendant ses rotations.

II.2.C. *Conditions «tête inclinée» (TI)*

Dans les conditions TI (Fig. 1C), la baguette était affichée sur l’écran utilisé dans les conditions CI, placé à la même distance, mais cette fois les références visuelles orientées fournies par le contour de l’écran étaient supprimées. A cette fin, un panneau noir, percé en son centre d’un orifice circulaire de 15° d’angle, était disposé devant le moniteur. La baguette apparaissait au centre de la fenêtre circulaire.

Deux conditions TI ont été réalisées. Suivant la même procédure que pour les conditions TCI, la tête du sujet était positionnée dans 40 orientations différentes, soit par un mouvement volontaire du sujet (mouvements actifs), soit par un mouvement imposé par l’expérimentateur (mouvements passifs). L’objectif de ces conditions étant d’évaluer l’influence de l’inclinaison de la tête *per se*, le sujet fermait les yeux pendant les mouvements de tête.

A la fin de l’expérience, les sujets étaient invités au cours d’un entretien libre à commenter les tâches effectuées. En particulier, il était demandé au sujet de s’exprimer au sujet de la difficulté à réaliser la tâche dans les différentes conditions expérimentales. L’expérimentateur a également cherché à s’assurer que les sujets avaient bien réalisé la tâche en première intention, sans mettre en jeu de stratégie particulière.

II.3. ANALYSE DES DONNEES

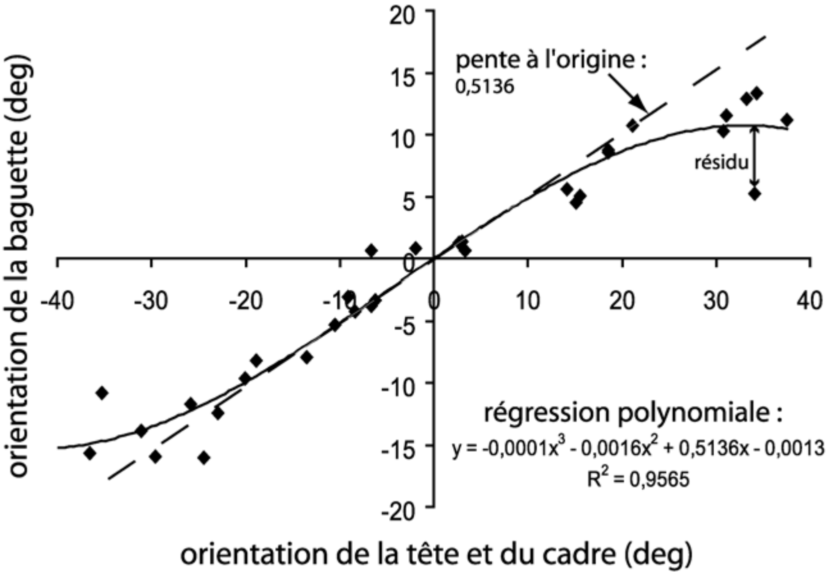

Fig. 2 : Courbe de réponse typique d’un sujet dans une des conditions TCI. Les réponses obtenues à chaque essai sont représentées, ainsi que la courbe de régression (polynôme de 3ème ordre). L’équation correspondant à la courbe de régression et le coefficient de détermination R^2 sont indiqués.

Fig. 2. Typical performance of one selected subject with the head-fixed visual frame (TCI condition). All trials are displayed together with the regression function. The equation of the regression curve (third order polynom) and the corresponding R2 coefficient are indicated.

Par convention, une inclinaison de la tête ou une erreur dans l'estimation de la verticale se voient assigner une valeur positive si elles sont dans le sens horaire et, négative, si elles sont dans le sens anti-horaire. La figure 2 montre les réponses données par un sujet dans

l'une des conditions TCI. Cet exemple est représentatif du caractère non-linéaire des comportements observés dans cette expérience, quelle que soit la condition expérimentale. En effet, les erreurs commises en estimant la verticale étaient, pour la plus grande partie des sujets, une fonction linéaire de l'inclinaison de la tête et/ou du cadre pour atteindre un maximum vers 25° d'inclinaison ou plus. Pour des inclinaisons supérieures, l'erreur cessait d'augmenter, voire diminuait. D'autres sujets, au contraire, présentaient des réponses purement linéaires. Cette variabilité interindividuelle est présente dans toutes les conditions expérimentales. Par conséquent, afin de résumer au mieux toutes les données individuelles avec la même méthode, nous avons réalisé des régressions polynomiales de 3ème ordre. De cette façon, chaque courbe de réponse peut être modélisée par l'équation suivante :

$$y = ax3 + bx2 + cx + d,$$

où y est l'estimation prédite de la verticale et x l'orientation de la tête et/ou du cadre. La composante de 3ème ordre de l'équation (a) reflète la tendance du sujet à commettre une erreur maximale avant d'atteindre l'inclinaison maximale de la tête et/ou du cadre. Le second paramètre (b) teste l'asymétrie de la courbe. Le troisième (c) est la pente de la courbe à l'origine. Enfin, la constante (d) représente l'erreur commise par le sujet lorsque sa tête était droite.

Puisque toutes les courbes de réponses pouvaient être résumées en grande partie par leur composante linéaire, la pente des courbes à l'origine est la valeur pertinente pour estimer la force de l'effet. De plus, la variabilité intra-individuelle a été évaluée en calculant la moyenne des résidus absolus (les valeurs absolues des différences entre les valeurs observées et les valeurs prédites par la courbe de régression pour le même angle d'inclinaison). Dans la section suivante, les moyennes de groupes des pentes et des résidus absolus moyens sont présentées avec les erreurs-types de la moyenne.

II.4. RESULTATS

La moyenne des pentes à l'origine obtenues lorsque les mouvements de tête étaient réalisés activement ne diffère pas de celle obtenue avec des mouvements passifs. Cette observation est valable dans les conditions TCI avec les yeux ouverts (actif : pente=0,31±0,07 ; passif : pente=0,28±0,08 **;** *t* (11)=0,64 ; *p*=.53), dans les conditions TCI avec les yeux fermés (actif : pente=0,26±0,09 ; passif : pente=0,30±0,10 ; *t* (11) =-0,90 ; *p*=.39) et dans les conditions TI (actif : pente=-0,01±0,04 ; passif : pente=-0,02±0,08 ; *t* (11) =0,10 ; *p*=.92). Par conséquent, les données obtenues avec mouvements actifs et mouvements passifs ont été moyennées et les analyses ultérieures ont été réalisées sur ces moyennes.

La figure 3 présente les courbes de réponses moyennes obtenues dans l'ensemble des conditions. On observe que, dans les conditions TCI, l'erreur d'estimation de la verticale correspond à 29% et 28% de l'inclinaison de la tête et du cadre, respectivement lorsque les yeux sont ouverts (pente=0,29±0,08) et fermés (pente=0,28±0,09). Dans les conditions CI, l'erreur de 17% commise avec les yeux fermés (pente=0,17±0,04) chute à 8% lorsque les sujets ont la possibilité d'observer les rotations du cadre visuel (pente=0,08±0,03). Enfin, incliner la tête en l'absence de référence visuelle ne produit pas d'effet significatif sur l'estimation de la verticale (pente=-0,01±0,06).

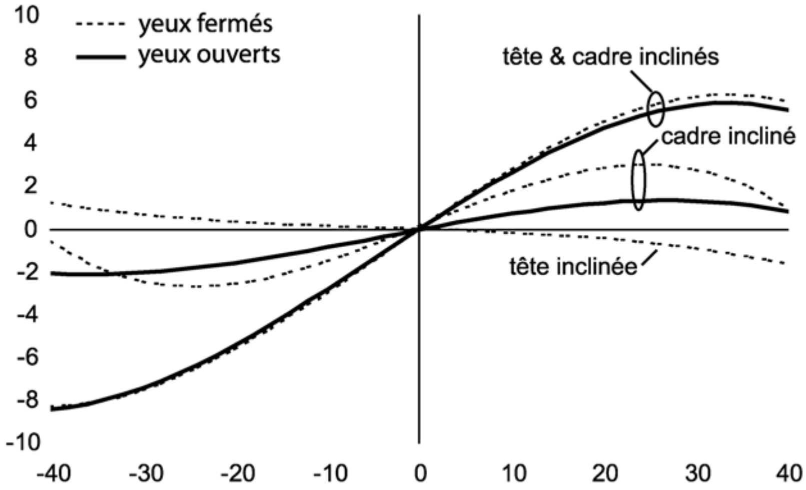

Fig. 3 : Estimation moyenne de la verticale (en degrés, 0° correspondant à la verticale gravitaire) en fonction de l'angle d'inclinaison de la tête et/ou du cadre dans toutes les conditions. Les courbes ont été obtenues en moyennant pour chaque angulation (pas de 2°), les réponses prédites par les régressions polynomiales (voir Fig.2).

Fig. 3: Average estimation of the vertical (in degrees, 0° corresponding to the gravitational vertical) as a function of the angle of tilt of the head and/or the frame in all conditions. The larger effects were observed with the head-fixed visual frame and were similar with or without vision of the frame during head rotations. The earth-based visual frame yielded a significant error in the same direction, but of a smaller magnitude. In contrast to the head-fixed visual frame, vision of the frame improved the performance. Tilting the head without a visual frame did not significantly affect vertical settings. The curves correspond to the predicted responses, based on polynomial regression analyses (see Fig. 2), averaged across subjects.

Une analyse de variance à mesures répétées 2 (cadre fixe par rapport à la tête / cadre dissocié de la tête) x 2 (yeux fermés / yeux ouverts) réalisée sur les pentes des courbes met en évidence un effet principal du type de cadre [$F(1;11)=5{,}96$; $p=.03$], une absence d'effet principal de la vision du cadre pendant la rotation [$F(1;11)=4{,}15$; $p=.07$] et une interaction significative entre les deux variables [$F(1;11)=12{,}76$; $p=.002$]. Les analyses post-hoc (tests de Newman-Keuls) révèlent que l'interaction est la conséquence d'un effet significatif de la vision continue du cadre dans les conditions CI (la pente est plus forte avec les yeux fermés, $p=.001$), mais pas dans les conditions TCI [$p=.50$].

Afin de tester l'hypothèse d'additivé des effets visuels et posturaux, nous avons ajouté les valeurs observées en TI aux valeurs observées en CI-yeux ouverts d'une part, et aux valeurs observées en CI-yeux fermés d'autre part, pour comparer chacun de ces calculs aux conditions TCI correspondantes. Dans les deux cas, la moyenne des pentes observées dans les conditions TCI est plus grande que l'addition des valeurs obtenues en CI et en TI. Cet effet est significatif avec les yeux fermés (t (11)=2 ;96 ; $p=.01$) et encore plus avec les yeux ouverts ($t(11)$=6;65 ; $p<.0001$).

Les résidus absolus moyens diffèrent selon les conditions expérimentales [$F(2 ;22)=9{,}99$; $p<.0001$]. Les analyses post-hoc révèlent que la variabilité intraindividuelle est plus faible dans les conditions CI que dans les conditions TCI ($p=.0008$) et que dans les conditions TI ($p=.009$). La différence entre les deux dernières conditions n'est pas significative ($p=.15$). Aucune autre manipulation expérimentale (yeux fermés/yeux ouverts, mouvements actifs/mouvements passifs) n'a d'effet significatif sur la variabilité de la réponse. La figure 4 décrit les résidus absolus moyens en fonction de l'inclinaison. Lorsque la tête est droite (conditions CI), les résidus restent presque constants, quelle que soit l'orientation du cadre. Au contraire, la variabilité augmente avec le degré d'inclinaison de la tête. Ce profil est frappant, particulièrement dans les conditions TCI.

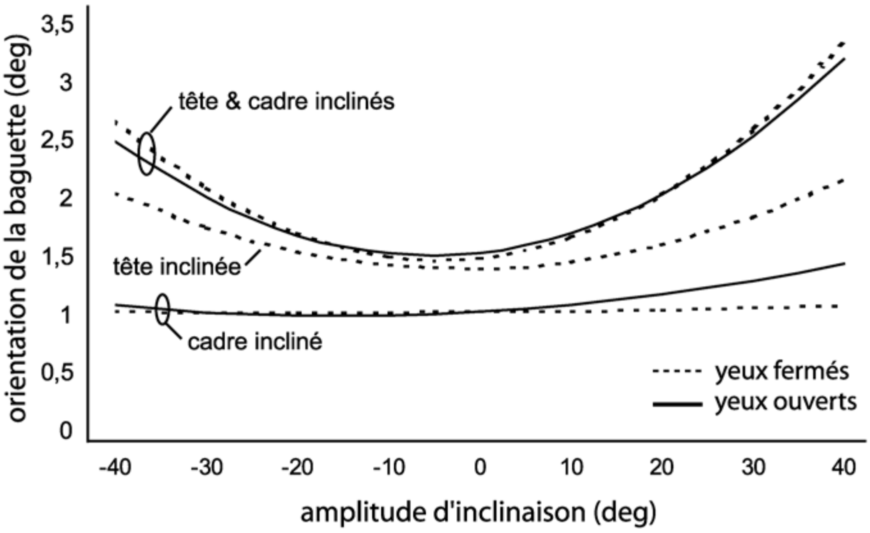

Fig. 4 : Distribution des résidus absolus moyens (variabilité de la réponse) en fonction de l'inclinaison dans toutes les conditions.

Fig. 4: Distribution of absolute residuals (response variability) as a function of the degree of tilt in all conditions. Variability increased with the degree of head tilt, especially with the head-fixed visual frame. In contrast, the degree of tilt of the earth-based visual frame did not significantly affect response variability.

II.5. DISCUSSION

L'expérience 1 s'intéresse aux effets d'un cadre visuel solidaire de la tête sur la verticale visuelle lorsque la tête est inclinée. Les effets d'une telle combinaison d'informations ont été comparés aux effets simples de l'inclinaison d'un cadre fixe dans l'espace et à ceux de l'inclinaison de la tête en l'absence de références visuelles orientées. Les inclinaisons du cadre et/ou de la tête ont été variées de façon systématique afin de pouvoir décrire précisément la forme des fonctions psychométriques résultantes. Deux résultats principaux peuvent être mis en avant. Premièrement, les erreurs dans l'estimation de la verticale sont nettement plus grandes lorsqu'un cadre visuel s'incline avec la tête que lors d'inclinaisons similaires d'un cadre fixe dans l'espace sans inclinaison de tête. L'augmentation de l'effet du cadre visuel ne peut pas être expliquée par l'addition d'un effet postural, puisque incliner la tête en l'absence de références visuelles n'influence pas, en moyenne, l'estimation de la verticale faite par les sujets. Deuxièmement, la vision continue du cadre lorsqu'il change d'orientation n'améliore la performance des sujets que lorsque la tête et le cadre sont dissociés, c'est-à-dire avec un cadre fixe dans l'espace.

II.5.A. *Réfutation de l'hypothèse d'additivité des effets visuels et posturaux*

Dans la grande majorité des expériences portant sur l'orientation spatiale, les effets induits par les stimulations visuelles sont nettement plus importants lorsque la tête est inclinée par rapport à la gravité que lorsqu'elle est maintenue droite (Dichgans, Diener, & Brandt, 1974 ; Witkin & Asch, 1948). Le débat est encore ouvert pour savoir si l'augmentation de la désorientation relève d'une addition des effets posturaux et des effets visuels ou si les deux effets sont interdépendants. Selon le modèle additif, l'erreur due à l'inclinaison de la tête ou du corps entier s'ajouterait intégralement aux erreurs provoquées par la perturbation visuelle. Autrement dit, la réponse fournie par le sujet lorsque les deux perturbations sont combinées serait le résultat de l'addition vectorielle des deux verticales perçues dans les situations où une seule manipulation expérimentale est réalisée. Pour le modèle interdépendant, l'influence de la vision sur la perception de l'orientation spatiale est limitée par le rôle inhibiteur des utricules et des informations somatosensorielles lorsque ceux-ci ne détectent aucun changement dans l'information gravitaire. Lorsque la tête est inclinée, la fiabilité des afférences otolithiques diminuerait et, par conséquent, la pondération des différentes sources d'informations serait modifiée en faveur des afférences visuelles. Récemment, Guerraz, Poquin et Ohlmann (1998) ont examiné la combinaison d'inclinaisons de la tête et de perturbations visuelles statiques (cadre incliné). Ils concluent que l'augmentation de l'effet cadre observée dans ces conditions ne serait que la conséquence d'un effet postural de type Aubert (erreur d'estimation dans la direction de l'inclinaison corporelle), ce qui contredit les conclusions de DiLorenzo et Rock (1982).

Les résultats de l'expérience 1 ne soutiennent pas l'hypothèse d'additivité, puisque nos sujets ont montré une influence du cadre visuel nettement accrue, sans effet Aubert. D'un point de vue plus général, il est difficile d'envisager la fusion des informations sensorielles provenant de différentes sources comme relevant d'une simple sommation. En effet, il existe la plupart du temps de grandes différences dans les caractéristiques spatiales et temporelles des systèmes sensoriels (Howard, 1997). Les modèles actuels essaient d'ailleurs d'expliquer l'intégration d'afférences sensorielles multiples en termes de combinaisons non-linéaires (Mergner, Huber, & Becker, 1997 ; Mergner, Nasios, & Anastasopoulos, 1998). En fonction des conditions, une modalité sensorielle peut prévaloir sur une autre ou, au contraire, voir son influence diminuer. Plus spécifiquement, les signaux de position de la tête semblent n'être fiables que lorsqu'ils sont intégrés au travers de processus dynamiques (Teasdale, Nougier, Barraud, Bourdin, Debu, Poquin, & Raphel, 1999). Par conséquent, lorsque la tête est inclinée et maintenue dans une orientation donnée, l'augmentation des erreurs dans la direction du cadre incliné reflète probablement un poids plus important affecté aux références visuelles.

II.5.B. *La désorientation spatiale : un phénomène à deux visages*

La variabilité de la réponse des sujets (quantifiée par la méthode des résidus) suggère également une fiabilité moindre des signaux de position de la tête lorsque celle-ci est inclinée. La variabilité intraindividuelle est faible lorsque la tête est droite, quelle que soit l'orientation du cadre visuel. En revanche, la variabilité est plus grande dès lors que la tête est inclinée et elle s'accroît avec l'amplitude d'inclinaison, que les références visuelles soient absentes ou fixes par rapport à la tête. Il est intéressant de remarquer que cette observation quantitative correspond aux commentaires des sujets. En effet, ils ont exprimé une plus grande difficulté à réaliser la tâche lorsque la tête était inclinée, en particulier en combinaison avec le cadre visuel. Dans ces dernières conditions, les sujets ont d'ailleurs souvent rapporté un fort sentiment d'incertitude quant à la précision de leurs ajustements. Ces résultats mettent l'accent sur le fait que la désorientation spatiale peut être définie de deux façons différentes. D'une part, l'erreur constante par rapport à la verticale gravitaire témoigne du résultat perceptif élaboré par le système nerveux central, en fonction des informations dont il dispose. En l'occurrence, lorsque le cerveau doit s'accommoder d'informations appauvries ou conflictuelles, la perception peut être biaisée en faveur d'une modalité sensorielle ou d'une autre. D'autre part, on peut considérer l'erreur variable qui atteste du niveau de reproductibilité de la réponse du sujet. En ce qui concerne les estimations subjectives, cette reproductibilité reflète souvent le niveau de confiance du sujet dans sa réponse. Dans ce cas, désorientation spatiale n'est pas nécessairement synonyme d'altération de performance moyenne. Nos résultats illustrent cette distinction. En effet, le biais perceptif atteint un plateau et décroît parfois (Fig. 3), alors que la variabilité (et sa contrepartie subjective) continue à augmenter avec l'amplitude de l'inclinaison de la tête (Fig. 4).

II.5.C. *Traitement de l'information visuelle en mouvement dans le référentiel céphalocentré*

Lorsqu'un cadre visuel solidaire des mouvements de la tête est porté par le sujet, la vision continue du cadre durant les inclinaisons n'améliore pas la performance finale. Dans ce cas, le système nerveux central doit composer avec des informations visuelles orientées, à la fois stables dans le référentiel céphalocentré et mobiles dans le référentiel gravitaire. En fait, l'orientation du cadre ne peut alors être appréciée que par le biais des signaux de position de la tête, c'est-à-dire grâce à l'information vestibulaire et à la proprioception du cou. La commande motrice ne semble avoir aucune influence puisque les résultats sont identiques, que les mouvements de tête soient effectués activement ou passivement. Les résultats obtenus avec le cadre solidaire de la tête contrastent nettement avec l'amélioration des jugements de verticalité apportée par la vision continue d'un cadre ancré dans l'espace extracorporel. Cette condition expérimentale se rapproche des conditions naturelles où la scène visuelle bouge dans le référentiel céphalocentré dès lors que la tête bouge ou que les éléments de l'environnement changent de position ou d'orientation. Le fait que le traitement continu de l'information visuelle ne réduise les erreurs que lorsque la tête et le cadre sont dissociés suggère que les indices visuels de mouvement doivent être intégrés dans le référentiel céphalocentré pour qu'ils puissent participer à la constance de l'orientation spatiale.

III. EXPERIENCE 2 : EFFETS D'UN CADRE VISUEL CEPHALOCENTRE SUR LA REORIENTATION DE LA TETE ET LA VERTICALE SUBJECTIVE LORS D'INCLINAISONS DU CORPS ENTIER

III.1. OBJECTIFS

L'expérience 2 s'intéresse cette fois à l'estimation de la verticale lorsque le corps entier du sujet est incliné dans le plan frontal, en présence soit d'un cadre solidaire de l'inclinaison du tronc, soit d'un cadre solidaire des mouvements de la tête. Dans les deux cas, le sujet est assis sur un siège monté sur une plate-forme inclinable en roulis. Le cadre solidaire du corps est fourni par les contours d'un écran, fixé sur la plate-forme à hauteur des yeux du sujet. Le cadre solidaire de la tête est fourni par le casque vidéo utilisé dans l'expérience 1. Lorsque l'orientation de la tête est maintenue dans l'alignement du tronc, les deux conditions sont strictement identiques, quelle que soit l'orientation du corps par rapport à la gravité. En revanche, lorsque la tête est mobile, les deux conditions diffèrent. En effet, si le cadre visuel est solidaire de la plate-forme, c'est-à-dire lorsqu'il s'incline avec le corps du sujet tout en restant dissocié de la tête, les mouvements de la tête produisent un déplacement du référentiel céphalocentré relativement au cadre. L'information visuelle dynamique qui est générée devrait contribuer à diminuer l'influence du cadre sur la verticale subjective. En revanche, lorsque le cadre visuel est solidaire des mouvements de la tête, bouger la tête provoque un mouvement du cadre dans le référentiel gravitaire, mais aucune variation de l'orientation du cadre dans le référentiel céphalocentré. Dans cette condition, loin d'améliorer la performance des sujets, les mouvements de la tête et du cadre visuel dans l'espace risquent de désorienter davantage le sujet.

L'expérience 2 étudie également l'influence des deux types de cadres visuels sur le positionnement de la tête et ses conséquences sur la perception de la verticale. A cette fin, il est demandé au sujet de repositionner sa tête dans l'alignement du tronc après avoir effectué une série de mouvements céphaliques, puis, une fois la posture adoptée, d'estimer la verticale. Là encore, on peut supposer un effet différencié des deux types de cadres visuels. En effet, certains travaux montrent que des références visuelles orientées peuvent influer sur la posture céphalique. Un cadre visuel incliné, par exemple, induit une réorientation de la tête dans la direction de l'inclinaison du cadre (Guerraz, Yardley, Bertholon, Pollak, Rudge, Gresty, & Bronstein, 2001 ; Isableu *et al*., 1997 ; Sarès, Prieur, Bourdin, Gauthier, Blouin., & Vercher, 2002). Le système nerveux central utiliserait donc l'information visuelle statique disponible dans l'environnement pour réorienter la partie supérieure du corps, avec très certainement pour finalité de faire de la tête un référentiel spatial stable et orienté adéquatement pour la perception du monde visuel (Amblard, Cremieux Marchand, & Carblanc, 1985 ; Gresty & Bronstein, 1992).

Dans l'expérience décrite ici, le cadre visuel solidaire de la plate-forme et l'axe céphalocaudal du sujet (axe Z) sont colinéaires. Par conséquent, il est fort probable que, dans cette condition, les sujets tirent avantage de la présence du cadre pour mener à bien la tâche de réorientation de la tête. En revanche, le cadre visuel solidaire de la tête n'a pas d'ancrage dans l'espace extra-corporel. Son orientation ne peut être évaluée qu'à partir des signaux de position de la tête. L'information visuelle est donc présente, mais non-utilisable pour réorienter la tête. On peut donc faire l'hypothèse que le repositionnement de la tête sera moins précis dans cette condition. En outre, toute erreur de repositionnement risque d'avoir des conséquences sur l'estimation de la verticale. En effet, le cadre étant solidaire de la tête, son inclinaison dans l'espace sera modifiée de la même amplitude que l'erreur de repositionnement de la tête. L'expérience 2 vise donc à (1) quantifier les éventuelles erreurs de repositionnement de la tête en présence ou en l'absence de références visuelles ancrées dans l'espace extra-personnel, et (2) déterminer dans quelle mesure ces erreurs interagissent avec les références visuelles pour influencer la perception de la verticale.

III.2. METHODES

Les résultats de 6 hommes et 3 femmes ont été retenus pour cette expérience. Aucun sujet n'a déclaré souffrir ou avoir souffert de troubles vestibulaires. Leur vision était normale ou normalement corrigée.

Les sujets étaient assis sur un siège baquet fixé sur une plate-forme verticale (Fig. 5). La plate-forme pouvait être inclinée dans le plan frontal autour d'un axe de rotation situé approximativement au niveau du centre de masse du sujet. Les sujets étaient fermement maintenus immobiles dans le siège par un ensemble de sangles au niveau des pieds, des jambes, du bassin, de la poitrine et des épaules. La tête pouvait également être maintenue dans l'alignement du tronc, lorsque les conditions expérimentales l'exigeaient, grâce à deux presses appuyant sur les tempes.

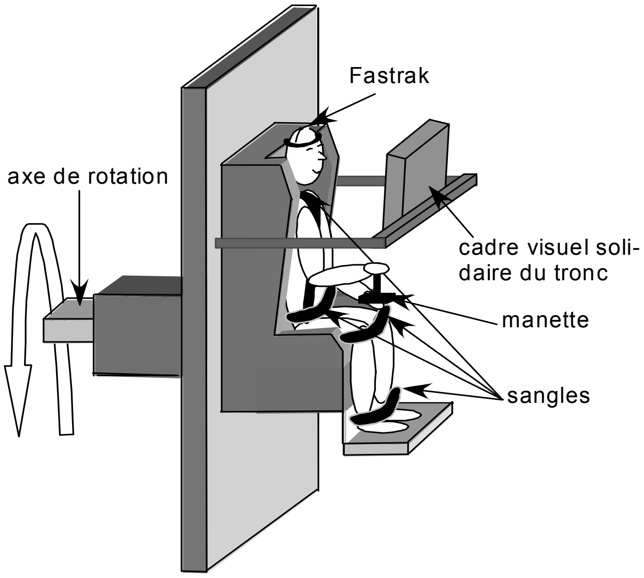

Fig. 5 : Schéma du dispositif expérimental dans la condition où le cadre visuel est solidaire du tronc (tête mobile). Dans les conditions «tête fixe», la tête est maintenue immobile dans l'axe du corps par deux presses latérales.

Fig. 5: Schema of the set-up where the visual frame was integral to the trunk and the head was not restrained. The platform was tilted in the frontal plane and subjects were instructed to keep the head in alignment with the trunk during the rotation and while estimating the vertical. In another condition, the head was kept in alignment with the trunk by means of two lateral pressing devices.

La baguette visuelle utilisée pour indiquer la verticale était la même que celle de l'expérience 1. La baguette était présentée soit dans le casque vidéo utilisé dans l'expérience précédente, lequel présentait un écran virtuel dont les contours fournissaient un cadre solidaire des mouvements de la tête, soit sur un écran placé fixé face au sujet sur la plate-forme (Fig. 5). Les cadres visuels formés par les bords de chaque écran avaient une taille angulaire de 30° x 22,5°. Seuls les contours de l'écran et la barre lumineuse étaient visibles dans un environnement totalement obscur par ailleurs.

Un dispositif magnétique Fastrak mesurait l'orientation de la tête par rapport au tronc. L'émetteur était fixé sur la plate-forme à la droite du sujet et un récepteur était attaché à un casque ajustable, porté par le sujet.

Les sujets ont passé 30 conditions expérimentales correspondant au plan d'expérience suivant : $I_5*C_3*M_2$, où I est le degré d'inclinaison de la plate-forme, C le type de cadre visuel présenté et M la condition de mobilité de la tête. Pour chacune des 30 conditions, 5 essais étaient réalisés. Les conditions étaient présentées dans un ordre pseudo-aléatoire.

III.2.A. *Inclinaisons du corps*

Le corps des sujets a été incliné avec la plate-forme à 15° et 30° dans le plan frontal, dans le sens horaire et dans le sens anti-horaire. Des mesures de référence ont également été effectuées lorsque la plate-forme était verticale. Les inclinaisons s'effectuaient avec une accélération initiale de $3°.s^{-2}$, jusqu'à une vitesse de $3°.s^{-1}$. Cette vitesse était maintenue constante jusqu'à la phase de décélération, elle aussi effectuée à $3°.s^{-2}$. Durant la rotation, les sujets avaient pour consigne de garder les yeux ouverts et de regarder le cadre visuel.

III.2.B. *Type de cadre visuel*

La baguette visuelle apparaissait au centre de trois types de cadre visuel, dont l'ordre de présentation a été contrebalancé. Le casque vidéo fournissait un cadre solidaire de la tête (conditions CST). L'axe vertical du cadre visuel restait donc constamment aligné sur l'axe vertical de la tête, quelle que soit l'orientation de celle-ci. Les contours de l'écran fixé à la plate-forme fournissaient un cadre visuel solidaire de la plate-forme (conditions CSP). L'axe vertical du cadre restait cette fois constamment aligné avec l'axe vertical du corps du sujet (axe Z). Une fenêtre circulaire entourant la baguette formait un cadre visuel non-orienté (conditions CNO).

III.2.C. *Mobilité de la tête*

Dans la moitié des conditions expérimentales, la tête du sujet était maintenue dans l'alignement du tronc par les presses latérales. Pendant la rotation et les estimations de la verticale, le sujet avait pour instruction de regarder le cadre visuel. Dans l'autre moitié des conditions expérimentales, la tête du sujet était libre. Pendant les rotations, le sujet avait pour instruction de maintenir la tête dans l'alignement du tronc. En revanche, avant d'estimer la verticale, il devait réaliser des mouvements de la tête pendant quelques secondes. Les mouvements devaient être effectués dans toutes les directions de l'espace, tout en gardant le regard dirigé vers le cadre visuel. Finalement, le sujet devait réorienter la tête de façon à la remettre dans l'alignement du tronc et estimer la verticale. Avant le début de l’expérience, l’expérimentateur entraînait le sujet à effectuer ces tâches et s’assurait en particulier que les mouvements de tête soient globalement similaires pour tous les sujets (quantité de mouvements, distribution homogène dans toutes les directions de l’espace).

III.3. RESULTATS

La figure 6 montre les estimations de la verticale dans toutes les conditions expérimentales. Pour la clarté de l'illustration et pour mieux mettre en évidence la linéarité des effets en fonction de l'inclinaison du sujet, une erreur dans l’estimation de la verticale se voit assigner une valeur positive, si elle est dans le sens horaire, et négative, si elle est dans le sens anti-horaire. Pour les analyses statistiques, en revanche, les valeurs de références obtenues sans inclinaison corporelle ont été retranchées aux données obtenues lorsque le corps était incliné. Les erreurs d'appréciation de la verticale étaient alors positives si elles étaient commises dans le sens de l'inclinaison du corps (et du cadre) et négatives dans le sens opposé. Par conséquent, le plan d’analyse est le suivant : $A_3*D_2*C_3*M_2$, où A est l’amplitude de l’inclinaison, D la direction de l’inclinaison, C le type de cadre visuel présenté et M la condition de mobilité de la tête.

En ce qui concerne les effets principaux, l'analyse révèle un effet significatif du type de cadre visuel [*F*(2 ;16)=15,96 ; *p*=.0002], pas d'effet de la mobilité de la tête [*F*(1 ;8)=0,43 ; *p*=.53], une tendance non-significative à commettre des erreurs plus importantes lorsque le corps était incliné à droite plutôt qu’à gauche [*F*(1 ;8)=5,15 ; *p*=.06] et un effet significatif de l'amplitude d'inclinaison [*F*(1 ;8)=37,73 ; *p*=.0003]. Parmi toutes les interactions possibles, une seule est significative. Il s'agit de l'interaction de premier ordre entre le type de cadre visuel et la mobilité de la tête [*F*(2 ;16)=4,72 ; *p*=.02]. Les tests post-hoc effectués sur cette interaction montrent que, dans la condition CST, les erreurs augmentent de façon significative lorsque la tête est en mouvement avant l'estimation de la verticale (*p*=.04). En revanche, la réduction des erreurs observées lorsque la tête est libre n'est significative ni dans la condition CSP (*p*=.81), ni dans la condition CNO (*p*=.79). Si l'on considère les erreurs d'estimation de la verticale en proportion de l'amplitude d'inclinaison de la plate-forme, on observe que les erreurs commises dans les conditions CSP «tête fixe» et «tête libre» correspondent respectivement à 26% et 20% de l'inclinaison de la plate-forme. L'erreur commise en CST «tête fixe» est équivalente puisqu'elle atteint 22%. Cette proportion augmente à 34% en CST «tête libre».

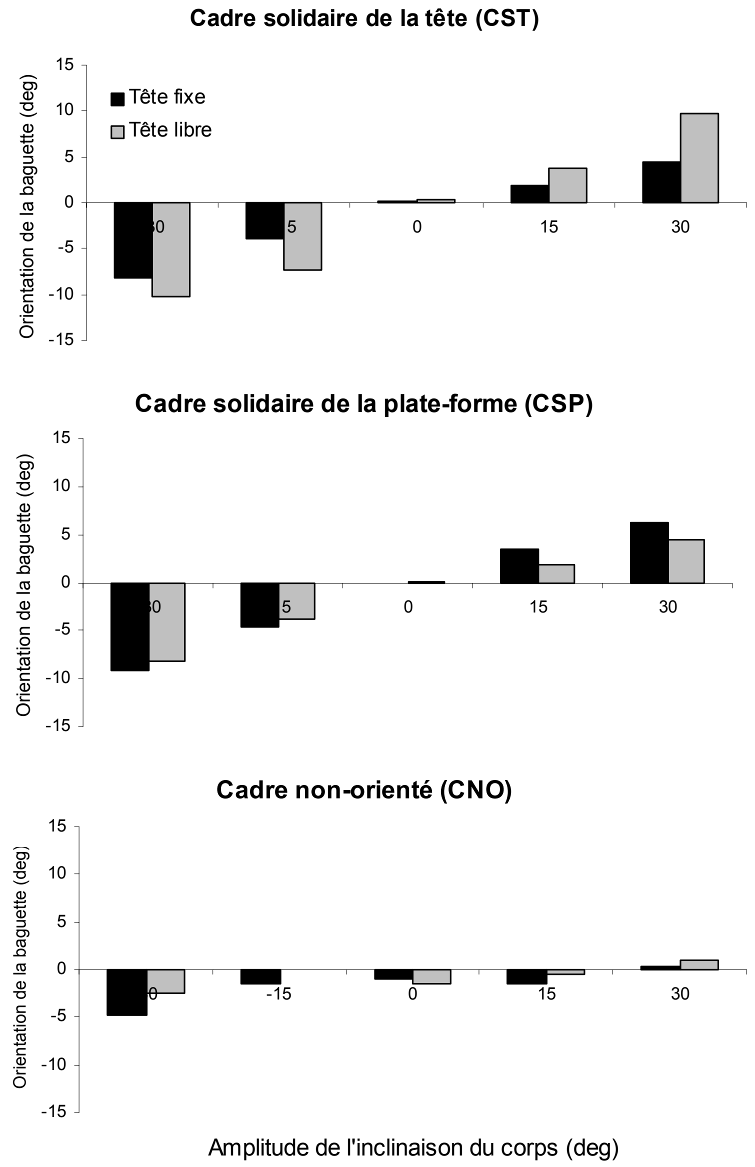

Fig. 6 : Estimation de la verticale en fonction de l'inclinaison du corps, du type de cadre visuel et de la mobilité de la tête. Dans la condition CST, bouger la tête avant l'estimation augmente l'erreur, commise en direction de l'inclinaison du corps et du cadre. Dans la condition CSP, on observe une légère amélioration, non significative, de la performance, lorsque le mouvement de la tête est permis. Les valeurs positives et négatives représentent des inclinaisons respectivement dans le sens horaire et dans le sens anti-horaire.

Fig. 6: Vertical settings as a function of the degree of body tilt (15° or 30°), of the kind of visual frame (from top to bottom: head-fixed rectangle frame, trunk-fixed rectangle frame, circular frame) and of head mobility (head restrained in black, head free in grey). With the head-fixed visual frame, moving the head before the vertical settings increased the error. With the trunk-fixed frame, moving the head slightly reduced the error, but the effect was not significant. Positive and negative values represent clockwise and counterclockwise tilts, respectively.

En ce qui concerne la tâche de réorientation de la tête, les erreurs de repositionnement de la tête commises dans le sens de l'inclinaison de la plate-forme se voient attribuer une valeur positive, alors que les erreurs commises dans la direction opposée sont négatives. Les valeurs de référence obtenues sans inclinaison corporelle ont là aussi été retranchées aux données obtenues pendant les inclinaisons. Les erreurs de repositionnement sont à la fois très faibles en moyenne et très variables selon les sujets. Un effet du type de cadre visuel sur les erreurs de repositionnement de la tête peut cependant être mis en évidence en calculant l'erreur moyenne indépendamment de la direction et de l'amplitude de l'inclinaison du corps (Fig. 7) et en comparant ces moyennes à zéro. On observe alors que la tête est significativement déviée dans le sens de l'inclinaison de la plate-forme dans la condition CST (*t* (1,8)=2,73 ; *p*=.03), mais pas dans la condition CSP (*t*(1,8)=0,72 ; *p*=.49), ni dans la condition CNO (*t* (1,8)=-0,06 ; *p*=.96).

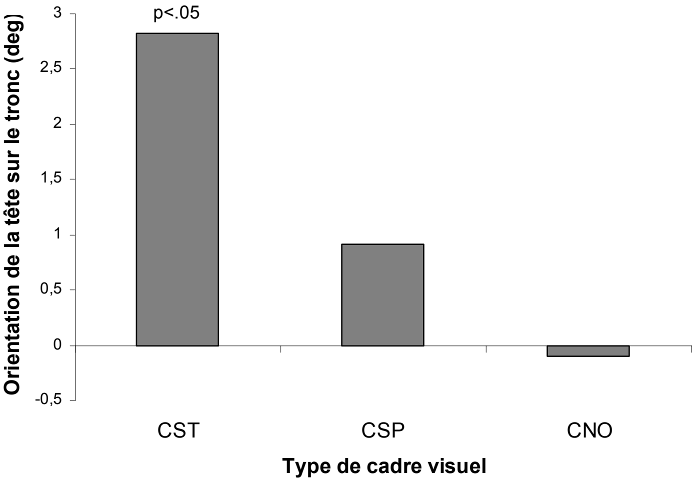

Fig. 7 : Erreur moyenne de repositionnement de la tête en fonction des trois types de cadres visuels étudiés. Une valeur positive représente une erreur dans le sens de l'inclinaison du corps. Seule l'erreur commise avec le cadre solidaire de la tête est significativement différente de zéro.

Fig. 7: Average error of head reorientation as a function of the kind of visual frame (from left to right: head-fixed, trunk-fixed, circular). Positive values represent an error in the direction of body tilt. With the head-fixed frame only, the error significantly differed from zero.

Les liens entre les erreurs de repositionnement de la tête et les erreurs d'estimation de la verticale peuvent être mis à jour en effectuant une série de corrélations linéaires. Ces corrélations ont consisté à mettre en rapport, d'une part, l'erreur de repositionnement de la tête dans les conditions «tête libre» et d'autre part, la différence entre les erreurs d'estimation de la verticale dans les conditions «tête libre» et celles observées dans les conditions «tête fixe» (Fig. 8). Elles montrent que les deux variables ne sont significativement corrélées que dans la condition CST (r=0,64 ; *p*<.001). La régression appliquée sur ces données révèle que l'erreur supplémentaire observée en CST-«tête libre» correspond à 71% de l'inclinaison de la tête.

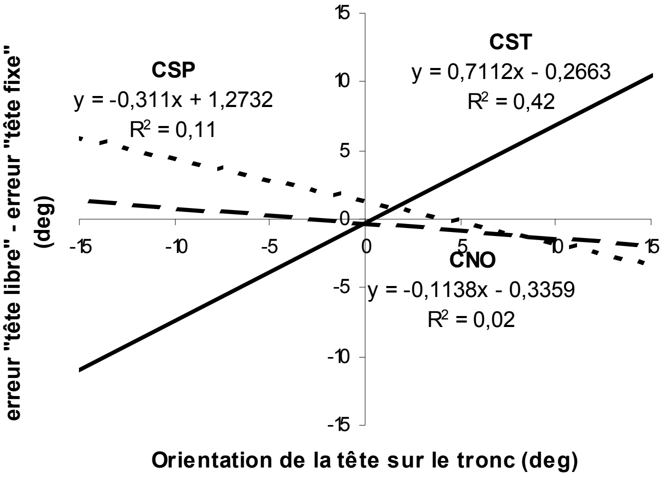

Fig. 8 : Différences d'estimation de la verticale entre les conditions «tête libre» et «tête fixe» en fonction des erreurs de repositionnement de la tête. La corrélation n'est significative que lorsque le cadre visuel est solidaire de la tête.

Fig. 8: Difference between vertical settings made in the "head free" conditions and the "head fixed" conditions as a function of errors in head reorientation. The correlation is significant only when using the head-fixed visual frame.

III.4. DISCUSSION

L'expérience 2 visait principalement à comparer les effets de deux types de cadres visuels lors d'inclinaison du corps dans le plan frontal, à la fois sur la perception de la verticale et sur le maintien de la tête dans l'alignement du tronc. L'un des cadres était solidaire de l'orientation de la tête, l'autre s'inclinait avec le corps du sujet, sans toutefois être asservi à la tête. Lorsque la tête est mobile, un cadre visuel céphalocentré génère des erreurs supérieures dans l'estimation de la verticale. Le comportement des sujets dans la tâche de réorientation de la tête diffère également. Les sujets tendent en moyenne à repositionner leur tête dans l'alignement du tronc en présence de références visuelles ancrées dans l'environnement extérieur. Par contraste, la tête est inclinée dans la direction de l'orientation du corps, lorsque le cadre visuel est solidaire de la tête.

III.4.A. *Ancrage des références visuelles et réorientation de la tête*

La stabilisation de la tête dans l'espace aurait deux fonctions primordiales (Massion, 1994 ; Pozzo, Berthoz, & Lefort, 1989). D'une part, elle intervient comme un élément déterminant dans le contrôle postural et le maintien de l'équilibre et d'autre part, elle permet de fournir aux systèmes perceptifs un référentiel stable. Pour maintenir la tête droite, plusieurs sources d'informations sont utilisées. Premièrement, les indices vestibulaires commandent le réflexe vestibulo-collique, dont l'effet est de redresser la tête dès lors qu'elle n'est plus alignée avec la direction de la gravité. Deuxièmement, les informations proprioceptives issues des muscles du cou participent au réflexe cervico-collique qui tend à maintenir la tête dans l'alignement du tronc. On accorde habituellement une importance moindre à la vision sur le maintien de l'orientation de la tête en condition normale, même s'il est reconnu qu'elle peut avoir une influence significative (Guitton, Kearney, Wereley, & Peterson, 1986).

Lorsque les références visuelles d'orientation ne sont pas alignées sur la verticale, l'influence de la vision peut être clairement mise en évidence par une réorientation de la tête dans la même direction (Guerraz *et al.*, 2001 ; Isableu *et al.*, 1997; Sarès *et al.*, 2002). Sarès *et al.* (2002) montrent en particulier que, dans un champ gravito-inertiel modifié, un cadre visuel incliné modifie considérablement le résultat de la compétition entre les réflexes vestibulo-colliques et cervico-colliques. Sur la base de l'ensemble de ces travaux, nous avions fait l'hypothèse qu'un cadre visuel incliné de la même amplitude que le corps améliorerait la performance des sujets dans une tâche consistant à réorienter la tête dans l'alignement du tronc, par rapport à une situation où les informations visuelles étaient solidaires de la tête. Les résultats confirment en partie seulement cette hypothèse. En effet, si la performance moyenne des sujets est meilleure en présence d'informations visuelles ancrées dans l'espace externe, la dispersion des données témoigne d'une assez grande variabilité interindividuelle dans toutes les conditions. Les idiosyncrasies habituellement observées dans les situations expérimentales telles que la nôtre semblent donc se manifester dans la contribution des informations visuelles au choix des «stratégies» de stabilisation de la tête, un phénomène cohérent avec les travaux d'Amblard, Assaiante, Vaugoyeau, Baroni, Ferrigno et Pedotti (2001). En l'absence d'ancrage des informations visuelles dans l'environnement externe au sujet, le comportement de la tête est nettement plus consistant. En effet, les sujets, dans leur majorité, ont tendance à laisser la tête inclinée dans la direction de l'inclinaison du corps. Dans cette condition, les informations visuelles solidaires de la tête sont sans aucune pertinence pour la réalisation de la tâche. En fait, la performance des sujets peut être considérée comme le strict résultat de la modulation volontaire de la compétition entre les réflexes cervico-colliques et vestibulo-colliques. Les premiers vont dans le sens d'une performance adéquate dans la tâche demandée. Les seconds doivent être inhibés pour éviter un redressement de la tête. Visiblement, dans les conditions expérimentales décrites ici, le réflexe vestibulo-collique est sur-compensé.

III.4. *Ancrage des références visuelles et verticale subjective*

Avec un cadre solidaire de la tête, l'estimation de la verticale faite par les sujets après la tâche de réorientation de la tête est significativement plus déviée dans le sens de l'inclinaison du cadre qu'avec un cadre dissocié de la tête. La question se pose alors de savoir quels facteurs peuvent expliquer cette augmentation des erreurs, puisque deux phénomènes coexistent dans cette condition. En effet, le cadre visuel étant solidaire de l'orientation de la tête, les mouvements précédant l'estimation de la verticale ne génèrent aucune variation de l'orientation du cadre dans le référentiel céphalocentré, contrairement à l'autre condition. De plus, si on considère les observations précédentes, il apparaît que les sujets tendent en moyenne à incliner la tête dans la même direction que le corps. Le cadre est donc lui-même incliné par rapport à la gravité d'une amplitude supplémentaire équivalente à celle de la tête.

Les corrélations représentées par la figure 7 ont été réalisées dans le but de déterminer dans quelle proportion cette inclinaison supplémentaire du cadre et de la tête peut expliquer l'augmentation de l'erreur dans l'estimation de la verticale. Alors que les erreurs de repositionnement de la tête ne présentent aucun lien avec les erreurs sur la verticale subjective lorsque le cadre est dissocié de la tête, la corrélation est clairement positive lorsque le cadre est solidaire de la tête. Elle montre que l'augmentation des erreurs observée entre les conditions «tête fixe» et «tête libre» correspond à 70% de l'inclinaison de la tête. Cette proportion est particulièrement élevée au regard des résultats obtenus dans l'expérience 1 où les effets de l'inclinaison de la tête par rapport au corps ont été étudiés. Rappelons que les erreurs observées sur la verticale subjective correspondaient alors à moins de 30% de l'inclinaison de la tête. L'inclinaison supplémentaire du cadre et de la tête dans l'espace peut donc expliquer, au mieux, la moitié de l'erreur supplémentaire observée dans l'expérience 2.

Une autre explication pourrait être avancée. Elle consisterait à dire que l'erreur de réorientation de la tête ne serait pas accessible au système perceptif et viendrait s'ajouter à l'erreur provoquée par l'inclinaison du cadre. Cependant, la logique de cette éventualité voudrait que l'erreur de repositionnement s'ajoute intégralement à l'erreur observée lorsque la tête est maintenue dans l'alignement du tronc par le dispositif de contention. Ce n'est pas le cas, ce qui nous amène à rejeter cette hypothèse.

Les résultats plaident donc en faveur de l'hypothèse, posée *a priori*, selon laquelle les mouvements de la tête provoquent un conflit informationnel, puisque le cadre visuel change d'orientation dans le référentiel gravitaire tout en restant fixe dans le référentiel céphalocentré. L'augmentation de l'erreur observée ici serait donc une autre démonstration de l'importance cruciale du traitement des informations spatiales relativement à la tête. Cette hypothèse prédisait également une diminution de l'effet cadre lorsque la tête était mobile en face d'un cadre indépendant de la tête. Cette diminution n'a été observée que chez trois sujets.

IV. CONCLUSION

Il a déjà été proposé que la tête serve d'origine à un référentiel important pour les jugements d'orientation (Friedman & Hall, 1996 ; Guerraz *et al.*, 1998 ; Spidalieri & Sgolastra, 1999). Les deux études que nous rapportons ici renforcent cette idée en démontrant les effets d'un cadre visuel céphalocentré sur la perception de la verticalité. Premièrement, lorsqu'un cadre visuel s'incline avec la tête, il donne lieu à des erreurs importantes qui ne peuvent être expliquées par l'addition d'effets visuels et posturaux. Deuxièmement, la vision du cadre lors de ses changements d'orientation dans l'espace ne diminue l'erreur perceptive que lorsque la tête et le cadre sont dissociés. De plus, lorsque le cadre visuel est solidaire de la tête, des erreurs de repositionnement de la tête peuvent survenir et entraîner indirectement des erreurs supplémentaires dans l'estimation de la verticale.

Ces résultats suggèrent que le traitement de l'information visuelle dans le référentiel de la tête est crucial pour le maintien d'une perception constante et adéquate de l'orientation spatiale. Par conséquent, inclure des références visuelles solidaires des mouvements de la tête dans les visiocasques n'est pas une démarche anodine au regard des mécanismes fondamentaux du traitement de l'information sensorielle. Bien entendu, la prudence s'impose en ce qui concerne l'extrapolation de nos résultats à une utilisation particulière des visiocasques. Nous nous sommes volontairement placés dans des conditions de laboratoire qui induisent de forts épisodes de désorientation spatiale, afin de pouvoir mettre en évidence les effets spécifiques de références visuelles céphalocentrées. De plus, une modification de la perception de la verticale, tout en étant un effet représentatif des processus d'intégration multisensorielle, ne peut pas être extrapolée sans une certaine prudence à d'autres tâches d'orientation dans l'espace. Cependant, les dispositifs de RA mobiles sont susceptibles de présenter un cadre visuel céphalocentré plus prégnant encore que celui utilisé dans notre expérience. C'est le cas du prototype MARS développé par Höllerer *et al.* qui inclut les contours d'un écran virtuel et une barre de menu horizontale (cf. introduction). On peut s'interroger sur le potentiel qu'auraient ces références visuelles de perturber l'orientation spatiale de l'utilisateur, avec pour conséquences des troubles ponctuels du maintien de l'équilibre.

En ce qui concerne les visiocasques utilisés en aéronautique, nos résultats laissent penser qu'il n'est peut-être pas judicieux d'aligner en périphérie du champ de vision des éléments de symbologie dont l'orientation est solidaire de celle de la tête. Ces éléments de symbologie formeraient alors un cadre visuel subjectif qui, même partiel, pourrait influer sur l'orientation spatiale du pilote. Ceci n'est valable que lors de vols sans visibilité, durant lesquels des épisodes de désorientation spatiale sont fréquemment rapportés, en raison de l'absence de repères visuels externes. Les informations visuelles céphalocentrées ne doivent pas nécessairement former un cadre complet pour être source de désorientation, puisqu'il a été montré qu'un cadre incomplet ou même des contours subjectifs peuvent induire des effets similaires, quoique moins importants (Antonucci, Fanzon, Spinelli, & Zoccolotti, 1995 ; Spinelli, Antonucci, Daini, Martelli, & Zoccolotti, 1999 ; Streibel, Barnes, Julness, & Ebenholtz, 1980). Là encore, il convient d'être prudent sur la généralisation de nos résultats à une application particulière comme la conception des visiocasques en aéronautique. Nos travaux expérimentaux ne permettent en aucun cas d'évaluer l'intensité ou les risques d'occurrence des épisodes de désorientation spatiale que des références visuelles céphalocentrées contribueraient à induire. Ils ne portent que sur la mise en évidence des mécanismes selon lesquels les visiocasques pourraient contribuer au phénomène de désorientation spatiale, si la symbologie choisie ne respecte pas les caractéristiques fondamentales du traitement de l'information sensorielle. Selon Previc (2000), cette démarche est essentielle dans le processus de conception des visiocasques, afin de lutter contre la désorientation spatiale, source importante d'accidents dans l'aviation de combat.

Enfin, les visiocasques sont de plus en plus utilisés comme des outils pour la recherche fondamentale en psychologie. Les environnements immersifs ou semi-immersifs permettent de manipuler à volonté les propriétés de l'environnement, ce qui offre de nombreuses perspectives de recherche, en particulier dans le domaine de la perception et de l'intégration sensori-motrices**.** Ce type de méthode a cependant un certain nombre d'inconvénients (Loomis, Blascovich, & Beall, 1999). La limitation du champ visuel induit par les visiocasques en est un, dans la mesure où elle restreint l'immersion du sujet. Nos travaux suggèrent que le cadre visuel formé par les contours de la fenêtre ouverte sur le monde virtuel peut également influencer les tâches nécessitant le maintien d'une perception correcte de l'orientation dans l'espace.

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RÉSUMÉ :

Les travaux présentés visent à déterminer comment la présence de références visuelles fixes dans le référentiel de la tête peut influencer la perception de l'orientation spatiale. Une première expérience étudie l'influence d'un cadre visuel céphalocentré sur la verticale subjective, lors d'inclinaison de la tête. Une seconde expérience s'intéresse aux effets d'un tel cadre visuel sur la verticale subjective et sur la performance dans une tâche de réorientation de la tête lors d'inclinaisons du corps entier. Les deux études mettent l'accent sur le rôle fondamental du référentiel céphalocentré dans le traitement des informations visuelles pour la perception de l'orientation spatiale. Elles suggèrent qu'un cadre visuel céphalocentré tel qu'on peut le trouver dans un visiocasque, peut contribuer à désorienter l'utilisateur, en particulier dans les environnements de réalité augmentée.

Mots-clés : Réferentiels spatiaux, Orientation spatiale, Verticale subjective, Visiocasque, Integration sensorielle, Vision, Réalité augmentée

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Influence du contenu de la scène visuelle

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Interaction between reference frames during subjective vertical estimates in a tilted immersive virtual environment

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Abstract. Numerous studies highlighted the influence of a tilted visual frame on the perception of the visual vertical ('rod-and-frame effect' or RFE). Here, we investigated whether this influence can be modified in a virtual immersive environment (CAVE-like) by the structure of the visual scene and by the adjustment mode allowing visual or visuo-kinaesthetic control (V and VK mode, respectively). The way this influence might dynamically evolve throughout the adjustment was also investigated in two groups of subjects with the head unrestrained or restrained upright. RFE observed in the immersive environment was qualitatively comparable to that obtained in a real display (portable rod-and-frame test; Oltman 1968, *Perceptual and Motor Skills* **26** 503 – 506). Moreover, RFE in the immersive environment appeared significantly influenced by the structure of the visual scene and by the adjustment mode: the more geometrical and meaningful 3-D features the visual scene contained, the greater the RFE. The RFE was also greater when the subjective vertical was assessed under visual control only, as compared to visuo-kinaesthetic control. Furthermore, the results showed a significant RFE increase throughout the adjustment, indicating that the influence of the visual scene upon subjective vertical might dynamically evolve over time. The latter effect was more pronounced for structured visual scenes and under visuo-kinaesthetic control. On the other hand, no difference was observed between the two groups of subjects having the head restrained or unrestrained. These results are discussed in terms of dynamic combination between coexisting reference frames for spatial orientation.

1 Introduction

Since the observations of Wertheimer (1912), who noticed that a room seen in a tilted mirror progressively appeared upright, the influence of a tilted visual frame on the ability to perceive the vertical has been extensively investigated (see Howard 1982 for a review). The pioneer work of Asch and Witkin (1948a, 1948b) demonstrated that a rod that was to be aligned with the gravitational vertical was actually displaced towards the tilted visual environment in front of which the observers stood. Not only tilted scenes containing familiar objects, but also simple tilted square frames, were found to affect the subjective vertical (SV) despite high interindividual differences (Witkin and Asch 1948). Further research on the differential aspects of verticality judgments (eg cognitive style—Witkin et al 1954) has led to the 'rod-and-frame test' (RFT), which requires SV judgments in front of a visual square frame tilted at different extents (Oltman 1968). Results are generally represented as a sinusoidal function of the tilt of the visual square. Hence, classical 'rod-and-frame effects' (RFEs) may be illustrated by this representation through which maximal deviations of the SV towards the tilted frame occur between 18° and 28° of visual tilt. Some 60 years later, virtual-reality displays became promising tools for investigating the influence of tilted 3-D visual scenes upon SV. Using this novel technology, the present study was designed to further investigate combined influences upon RFE, such as the structure of the visual scene and the mode of SV adjustment.

Head-mounted displays, although enabling to create 3-D visual information, suffer most of the time from a reduced field of vision and from the residual presence of a head-fixed visual frame which might concurrently influence the perception of verticality (Mars et al 2004). Projection-based immersive virtual environments with larger fields of vision have been recently developed and manipulated to study spatial orientation. The advantage of these large-scale displays is that they provide both experimental control and close-to-real situations (Loomis et al 1999). Most contributions involving such apparatus focused on the influence of stereoscopic moving scenes upon postural responses (Keshner et al 2006; Keshner and Kenyon 2000; Mergner et al 2005). To our knowledge, subjective orientation relative to the gravitational vertical in large-scale virtual-reality displays has been explored only by Jenkin and her colleagues (2003). In their study, the perceived direction of 'up' was investigated in a tilted virtual room by adjusting the orientation of a shaded disc until it appeared most convex, which has been shown to depend on the direction of illumination. The underlying assumption of this experiment was that light always comes from above. However, one might argue that other luminous sources, usually present in a room, could modify the lighting of objects, thus challenging the 'light from above' assumption. Despite these methodological differences with respect to classical SV estimates, it seems that the use of a large-scale virtual-reality display could generate an RFE when the virtual room was tilted. Nevertheless, no direct comparison between judgments of verticality performed in real-world and in immersive virtual environment was provided.

The first aim of the present study was to investigate whether the tilt of a large-scale immersive virtual environment could yield similar effects on the judgment of verticality as the tilt of real visual surroundings. In other words, we addressed the question of comparability of the RFE between real and virtual worlds. This first step would allow us to validate the immersive virtual environment as a powerful tool for studying the perceived orientation of objects in structured visual surroundings.

Numerous papers reported an influence of the characteristics of visual surroundings in front of which subjects had to set their SV. Regarding the size of the frame, some experimenters suggested that a larger frame is likely to induce a greater RFE (Brooks and Sherrick 1994; Spinelli et al 1991). However, retinal size was found more important than perceived size in the occurrence of the RFE (Ebenholtz 1977). Other studies emphasised the role of the gap between the ends of the rod and the inner edge of the frame in modulating the RFE, showing that rod orientation is affected by elements that immediately surround it in the visual field (Rock 1990; Nyborg 1977; Spinelli et al 1995, 1999; Zoccolotti et al 1993). In the same vein, Wenderoth and Beh (1977) emphasised the importance of axes of symmetry relative to different inducing figures in the RFE. Li and Matin (2005a, 2005b) also clearly demonstrated that the separate influences induced by the individual lines composing the frame are much more important than the effect produced by the whole frame itself. Overall, all these studies gave support to a 'geometrical' approach to the RFE, in which automatic visual-information processing determines its occurrence and magnitude (Ebenholtz 1985).

On the other hand, it has been shown that the RFE also depends on cognitive influences. By manipulating the polarity of different objects (eg a mouse, an elephant, a clock whose numbers were displaced but not tilted) used as surrounding frames, Cian et al (2001) showed that the orientation of the rod relative to vertical is also modulated by the tilt of meaningful visual features which contain neither geometrical shapes nor linear segments. This finding suggests that high-level cognitive processes might also be involved in the RFE when polarised objects (ie with a clearly defined up and down) constituting the visual surroundings are tilted. The importance of polarity of the visual frame has also been considered by Howard and Childerson (1994), who found a greater influence of a tilted furnished room upon vertical settings than that of a simple dotted room without floor or ceiling.

The second aim of the present study was to manipulate the 3-D structure of visual surroundings during SV estimates in order to characterise the implication of geometric and polarised features in the occurrence of the RFE.

Moreover, since Howard and colleagues (Howard and Childerson 1994; Howard and Hu 2001) reported occasional (and unprocessed) differences between settings performed with a visible rod and settings performed with an unseen 'felt' rod, we also examined the adjustment mode of SV, that is the manner in which subjects set the rod to the perceived vertical. The adjustment mode, which implies that one or several sensory channels are used in the control of settings, has been surprisingly often neglected in the literature. SV estimates of body tilt have been investigated in several studies through haptic or kinaesthetic settings: subjects were instructed to adjust a hand-held object (eg a rod, a joystick, or a glass of water) to the perceived vertical without visual feedback (Bauermeister 1964; Bortolami et al 2006; Lejeune et al 2004; Wright and Glasauer 2003, 2006). Specific effects of body tilt and context dependence upon SV were reported, but no direct comparison with adjustments performed under visual control was made. Although influences of kinaesthetic/haptic and visual orientational estimates were investigated in studies dealing with the oblique effect (Appelle and Gravetter 1985; Gentaz et al 2001; Lechelt and Verenka 1980; Luyat et al 2001; McIntyre and Lipshits 2008), the contrast between kinaesthetic and visual outputs in SV judgments was addressed only in the work of Mars et al (2001). Investigating the influence of galvanic vestibular stimulation on SV, these authors reported a weaker but significant effect when adjusting a hand-held light rod in darkness than when controlling the orientation of a visible rod. To our knowledge, there is no comparative study focusing on the influence of different adjustment modes of SV in the presence of a tilted visual frame.

The third purpose of the present study was therefore to question the role of the adjustment mode on the occurrence of RFE. Classical visual SV settings were compared to 'visuo-kinaesthetic' settings where the rod was seen and hand-held by observers. The originality of the following experiment was to investigate the interaction between the RFE-inducing power of the visual field and the sensory systems controlling the SV output. Specifically, we examined how this interaction evolved over time during single SV adjustments. In addition, we managed to determine whether the rod-and-frame influence upon posture, notably reported by Isableu et al (1997, 1998), may also have a repercussion upon SV estimates. To that aim, two group-independent conditions of head restriction (head restrained upright versus head unrestrained) were also tested.

2 Methods

2.1 *Subjects*

Thirty right-handed subjects with normal or corrected-to-normal vision participated in the experiment. Fifteen subjects (eight males, seven females; mean age 21.8 ± 3.0 years) were tested with their head unrestrained, and fifteen other subjects (six males, nine females; mean age 28.5 ± 3.6 years) were tested with their head restrained upright. None of them presented a previous history of vestibular and neurological symptoms. All gave informed consent in compliance with the ethical committee which governs and regulates human experimentation in France.

2.2 *Apparatus*

Two distinct setups were used to elicit the RFE. The first one is a replication of the RFT portable apparatus developed by Oltman (1968). It is composed of a box (57 cm deep × 31 cm wide × 31 cm high) made of wooden white surfaces whose inside edges and corners were marked by black painted lines. The interior of the box was illuminated and the entire device could be tilted by the experimenter at different roll orientations.

A black rod (30 cm long; apparent size: 29.5 deg), fixed to the centre of a black square frame (apparent side size: 30.5 deg), could be independently rotated by the subjects and the experimenter via distinct hand-levers. A protractor, displayed on a disc mounted at the rear of the box and visible only to the experimenter, indicated the deviation of both the frame and the rod from vertical (measurement accuracy: 0.2 deg). Each subject was seated so that his/her face was aligned with the front edge of the box (not seeing the outer environment), and the eye level coincided with the axis of rotation. Subjects were required to keep their unrestrained heads upright during the adjustment (head unrestrained group) or to fit their heads upright into a restriction device composed of a chin-rest and a head-rest (head restrained group).

The second setup manipulated in the present experiment is the immersive virtual-reality display (CAVE-like) housed in the Mediterranean Virtual-Reality Centre at Marseilles. It is constituted of a 3 m deep × 3 m wide × 4 m high cubic space, with three vertical screens for walls and a horizontal screen for the floor. The three vertical surfaces were back-projected and the ground received direct projection with a 1400 × 1050 pixels resolution and a 60 Hz frame rate. Stereoscopic projection of virtual environments was achieved by two DLP® (digital light processing) projectors attached to each projection surface. Stereoscopic separation between left-eye and right-eye images was ensured by colorimetric separation (Infitec® technological solution). Infitec® filters were installed in the projectors, and subjects were wearing glasses with the same filters for high-quality passive stereopsis. An anti-aliasing mode of projection was used in order to avoid any directional cue mediated by pixel alignment. The projection system was controlled by a cluster of 5 PCs (1 master + 4 slaves, each attached to a two-DLP® projection surface). Virtools® solution was used to build and control virtual scenarios. Finally, a head-tracking system (ArtTrack®), featuring infrared recognition of passive markers placed on the glasses, was used to record the subject's head position and orientation (accuracy: 0.05°), and to update in real-time the stereoscopic images in relation to the subject's point of view. Subjects were seated in the immersive environment, with their heads restrained or unrestrained, 2 m away from the front wall. Their field of vision was thus entirely stimulated by the visual display (the apparent size of the virtually projected rear frame reached 73 deg). A head-rest with straps and back support fixed behind the chair was used to keep the head orientation upright for the head-restrained group of subjects.

Subjects were randomly presented with three different virtual scenes (figure 1a). Scene 1 typically reproduced the RFT environment (with a much larger scale, however). Observers faced a 3 m × 3 m traditional square frame, being immersed in a tiltable cubic space bounded by contrasted orthogonal lines. Scene 2 consisted of an empty coloured wall-papered room with structured floor and ceiling. Features of the scene essentially reinforced the geometrical cues with increased parallel and orthogonal visual lines. Scene 3 corresponded to a fully furnished room. Virtual furniture included a red bookshelf, a desk with books and green plants, a halogen lamp, a well-known painting by Cézanne attached to the front wall, and a coffee table with a can of soft drink and an ashtray. These elements, lying at different distances from the subjects, added depth cues to the display and were also assumed to enhance high-level (ie cognitive) polarity cues for up and down (Howard and Childerson 1994).

SV judgments were assessed in two ways (figure 1b). In the first SV adjustment mode, subjects were asked to set a virtual rod to vertical by means of a computer mouse controlling its orientation in roll. The very small amplitude of mouse displacements (< 1.5 cm) could not yield accurate information about the angular motion of the rod. The projected rod was centred relative to subjects' eye level, at a distance where it could be held with the extended arm. Virtual rod features (colour, apparent size, distance to the observer, projected height) were computed on the basis of the

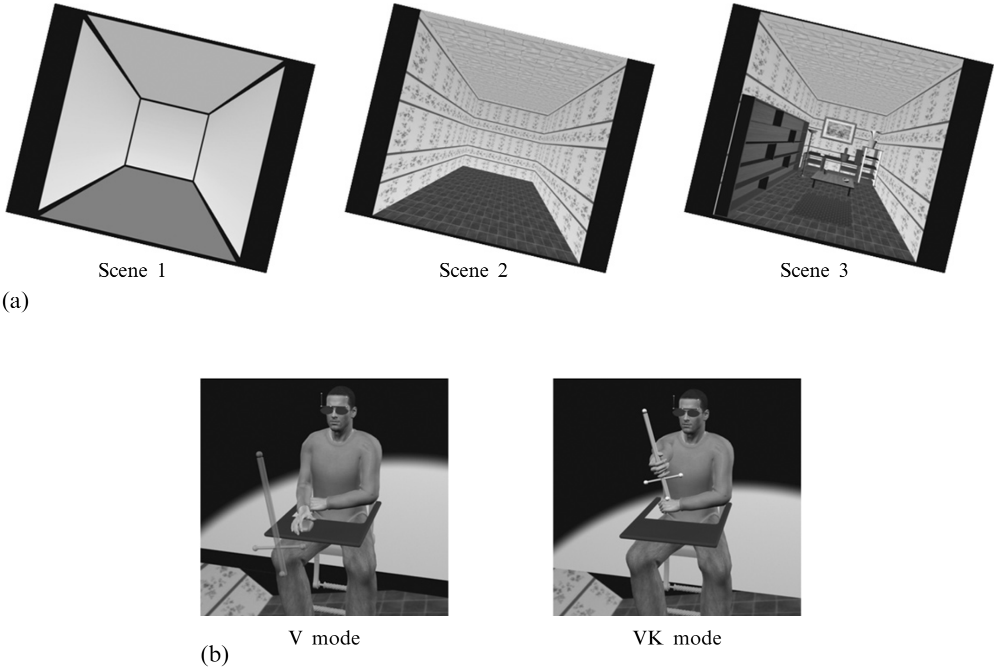

Figure 1. The experimental setup in the virtual immersive environment. (a) Subjects randomly faced three different stereoscopic virtual scenes. Scene 1 typically reproduced a classical 3-D rod-and-frame test (RFT) environment (with a much larger scale). Scene 2 consisted of an empty wall-papered room with structured floor and ceiling, increasing visual directional cues. Scene 3 corresponded to a full furnished room enhancing visual-polarity cues for up and down directions. (b) Subjects adjusted their subjective vertical in two ways: (i) through visual guidance only (V mode); (ii) through visuo-kinaesthetic control (VK mode, see text for further information).

characteristics of a real hand-held rod (used for the second adjustment mode) measured for each subject before starting the experiment. In this first condition, the rod orientation was controlled only by visual inputs (V mode). The second SV adjustment mode required the subject to hold a light plastic rod (40 cm long; 1 cm in diameter; weighing 60 g with uniform mass distribution) in the right dominant hand, and to adjust it along the vertical axis with an extended arm. Subjects were instructed to keep the centre of the rod at eye level and to look at it during adjustment. Markers positioned on the rod enabled us to continuously record its orientation via the ArtTrack® system (measurement accuracy: 0.05°), and ensured that the final location of the centre of the rod was kept around the same position across the trials. In that second adjustment mode, both visual and kinaesthetic inputs allowed the subjects to control the rod orientation (VK mode).

2.3 *Procedure*

The experiment was divided into two counterbalanced sessions, corresponding to the two adjustment modes manipulated in the immersive environment. Before the first session, both groups of subjects (head-unrestrained group and head-restrained group) were required to perform SV judgments through the portable RFT. Specifically, they were asked to “align the rod along the gravity axis” by rotating the hand lever. Nine frame tilts (+38°; +28°; +18°; +8°; 0°; −8°; −18°; −28°; −38°) and four initial rod orientations (+45°; +25°; −25°; −45°) were manipulated to define basic individual RFE profiles. Pseudo-random presentations of initial rod positions and frame tilts were counterbalanced in order to cancel any order effect.

For each experimental session in the immersive environment, subjects were first seated and equipped with stereoscopic glasses after their interocular distance had been measured and taken into account for binocular-vision calibration of the rendering software. They were initially familiarised with the task and environment by experiencing 10 blank trials. A typical trial went as follows: an auditory signal launched an 'exploration phase', lasting 5 s, during which subjects had to inspect their visual surroundings (ie one of the three visual scenes previously described). At that stage, the rod was either not projected in the scene (V mode), or handled out of sight by the subjects whose supporting arms rested in a gutter aside (VK mode). Before the end of this first phase, subjects with their heads unrestrained had to reorient them in a stereotyped neutral position, closest to the trunk alignment. A second auditory signal marked the beginning of the 'adjustment phase', lasting 5 s. In V mode, the virtual rod appeared in the visual field at pseudo-randomised roll orientations and subjects were instructed to use the mouse to set their SV. They were allowed to make corrective adjustments throughout this phase if they judged them necessary. In VK mode, subjects were asked to extend an arm straight ahead (relative to the mid-sagittal body axis) and to orient the hand-held rod to the vertical, again with possible online corrections during the adjustment. Finally, a third auditory signal marked the end of the adjustment phase, coinciding with the removal of the virtual scene (V and VK modes) and allowing the subjects to move the arm back in the gutter, alternating different prone and supine initial rod positions (VK mode). The subjects were deliberately free to set the angle of these initial orientations (ie randomly). In this way, they could not control the motor execution of a multi-joint coordinated arm movement so that it was similar across trials but, rather, they had to focus on the control of the rod orientation relative to vertical. A 1.5 s transition period was set before a new trial was initiated. A 5 min resting period was inserted in the middle of each session so that the subjects could keep a stable level of concentration throughout a session. Overall, each session in the immersive environment (V mode or VK mode), separated by an interval of two days, crossed 9 scene tilts (+38°; +28°; +18°; +8°; 0°; −8°; −18°; −28°; −38°) and three visual scenes (scene 1, scene 2, scene 3) with randomised initial rod orientations, for a total number of 162 trials (a similar set of combined conditions was repeated six times and averaged for subsequent statistical analyses).

2.4 *Data processing*

Final SV adjustments were collected during the RFT and averaged for obtaining mean individual signed deviations relative to the gravitational vertical (constant errors) for each scene tilt. Analyses of correlations (Bravais-Pearson tests) were performed to investigate the links between individual and mean subjective visual vertical settings recorded in real and virtual environment.

Rod and head location as well as orientation in 3-D were monitored by the tracking system throughout each trial in the immersive environment. For each trial, we selected two singular kinematic events during the adjustment phase, at which rod and head roll orientations were recorded, in order to characterise any evolution throughout the adjustment (figure 2). The first kinematic event corresponded to the moment at which the rod angular velocity reached zero for the first time during the adjustment (first movement endpoint). The second kinematic event corresponded to the end of the trial (SV final position).

Mean signed and unsigned deviations of the rod relative to the gravitational vertical (constant and variable errors, respectively) were processed for characterising SV judgments in the immersive environment.

Differences between 'raw' SV adjustments were tested by a multifactorial analysis of variance (ANOVA) conducted on the mean signed deviations of the rod relative to vertical.

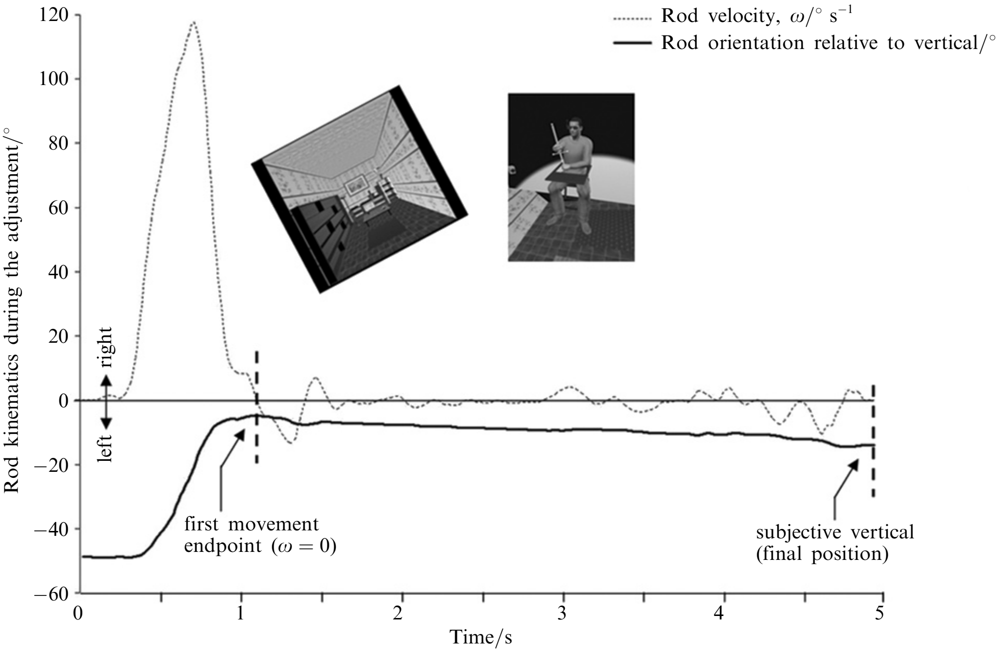

Figure 2. Typical recording of rod angular position in roll-over time during a subjective-vertical setting. The depicted trial corresponds to a setting performed by a subject under visuo-kinaesthetic control (VK mode) when facing scene 3 presented at −28° of tilt. Two events are distinguished in the trial: the 'first movement endpoint' corresponds to the rod orientation when angular velocity reaches zero for the first time. The subjective vertical (SV) corresponds to the rod orientation at the end of the trial. Noteworthily in this representative example the rod orientation is close to the physical vertical at the first movement endpoint, but is progressively drawn towards the scene orientation at the end of the trial (SV final position). Some other settings revealed a more sudden shift of SV after the first movement endpoint which was almost stabilised until the end of the trial. Although illustrated here for the VK mode only, the sample descriptors (first movement endpoint, final SV) were analysed in both V and VK modes.

The factors were: head restriction group (head restrained versus unrestrained), scene tilt (−38°; −28°; −18°; −8°; 0°; +8°; +18°; +28°; +38°), visual scene (scene 1, scene 2, scene 3), adjustment mode (V versus VK), and kinematic event (first movement endpoint versus SV final position). Repeated measures were applied for the last four factors.

Differences in RFE were tested by a four-way ANOVA conducted on the mean unsigned deviations of the rod relative to vertical, averaged across the different scene tilts. Factors were head restriction group (head restrained versus unrestrained), visual scene (scene 1, scene 2, scene 3), adjustment mode (V versus VK), and kinematic event (first movement endpoint versus SV final position). Repeated measures were applied on the last three factors.

The influence of experimental conditions on head orientation was also evaluated for the head unrestrained group with a four-way repeated-measures ANOVA applied to the mean signed deviations of the head relative to vertical. Factors were scene tilt (−38°; −28°; −18°; −8°; 0°; +8°; +18°; +28°; +38°), visual scene (scene 1, scene 2, scene 3), adjustment mode (V versus VK), and kinematic event (first movement endpoint versus SV final position).

The effect magnitude (η_p^2) and the power ($1-\beta$) of each test were provided. A posteriori analyses (Newman – Keuls tests) were conducted when necessary to further study significant interactions between factors.

3 Results

3.1 *SV in real and virtual environments*

As illustrated in figure 3, the SV appeared as a sinusoidal function of the scene tilt from −38° to +38° in both the RFT and the immersive environment. This shape is typical of classical RFE reported in the literature. The correlation between the mean data recorded in the RFT and the immersive environment was high and significant.

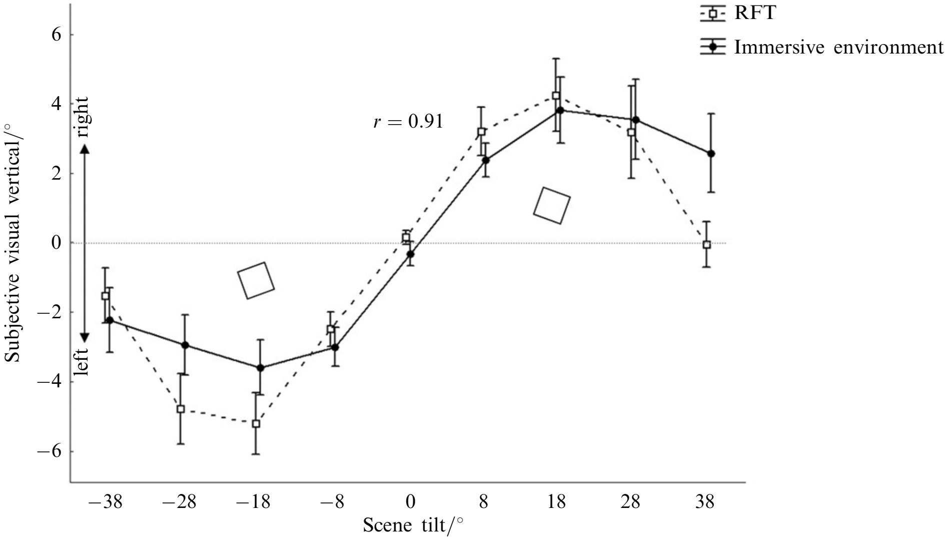

Figure 3. Mean SV settings as a function of tilt of the visual scene in real (portable rod-and-frame test, RFT) and the virtual immersive environment. Sinusoidal curve is typical of a classical rod-and-frame effect (RFE). Error bars represent 95% confidence intervals.

Correlation analyses conducted on each subject's set of data confirmed the previous observation. Except for subject 3, individual correlations were all high and significant (figure 4). Despite the difference between visual environments (eg apparent size, luminosity), the SV deviations elicited in both displays were qualitatively comparable within subjects and constituted specific 'signatures' of individual RFEs.

3.2 *Rod-and-frame effects in the immersive environment*

In line with the previous results, the ANOVA conducted on the mean signed deviations of the rod relative to vertical revealed a main effect of scene tilt ($F_{8,224} = 59.40$, $p < 0.001$, $\eta_p^2 = 0.68$, $[1 - \beta] = 1$). This confirmed the presence of RFE in SV estimates in the immersive environment, whatever the experimental condition.

3.2.1 *Influence of the visual scene on RFE.* A significant interaction was found between scene tilt and visual scene when comparing the mean signed deviation of the rod relative to vertical ($F_{16,448} = 28.93$, $p < 0.001$, $\eta_p^2 = 0.51$, $[1 - \beta] = 1$). It shows that the RFE increased as a function of the structure of the visual scene (figure 5a). Indeed, as revealed by the ANOVA performed on the mean unsigned deviations of the rod relative to vertical ($F_{2,56} = 57.82$, $p < 0.001$, $\eta_p^2 = 0.67$, $[1 - \beta] = 1$) and illustrated in figure 5b, the RFE magnitude was larger for scene 3 than for scene 2 ($p < 0.001$), and was larger for scene 2 than for scene 1 ($p < 0.001$).

3.2.2 *Influence of the adjustment mode on RFE.* A significant interaction was also found between scene tilt and adjustment mode when comparing the mean signed deviations of the rod relative to vertical ($F_{8,224} = 12.75$, $p < 0.001$, $\eta_p^2 = 0.31$, $[1 - \beta] = 1$).

It shows that the RFE was greater for SV adjustments performed in V mode than in VK mode (figure 6a). This was further supported by a main significant effect of adjustment mode on the mean unsigned deviations of the rod relative to vertical ($F_{1,28} = 20.48$, $p < 0.001$, $\eta_p^2 = 0.42$, $[1 - \beta] = 0.99$; figure 6b).

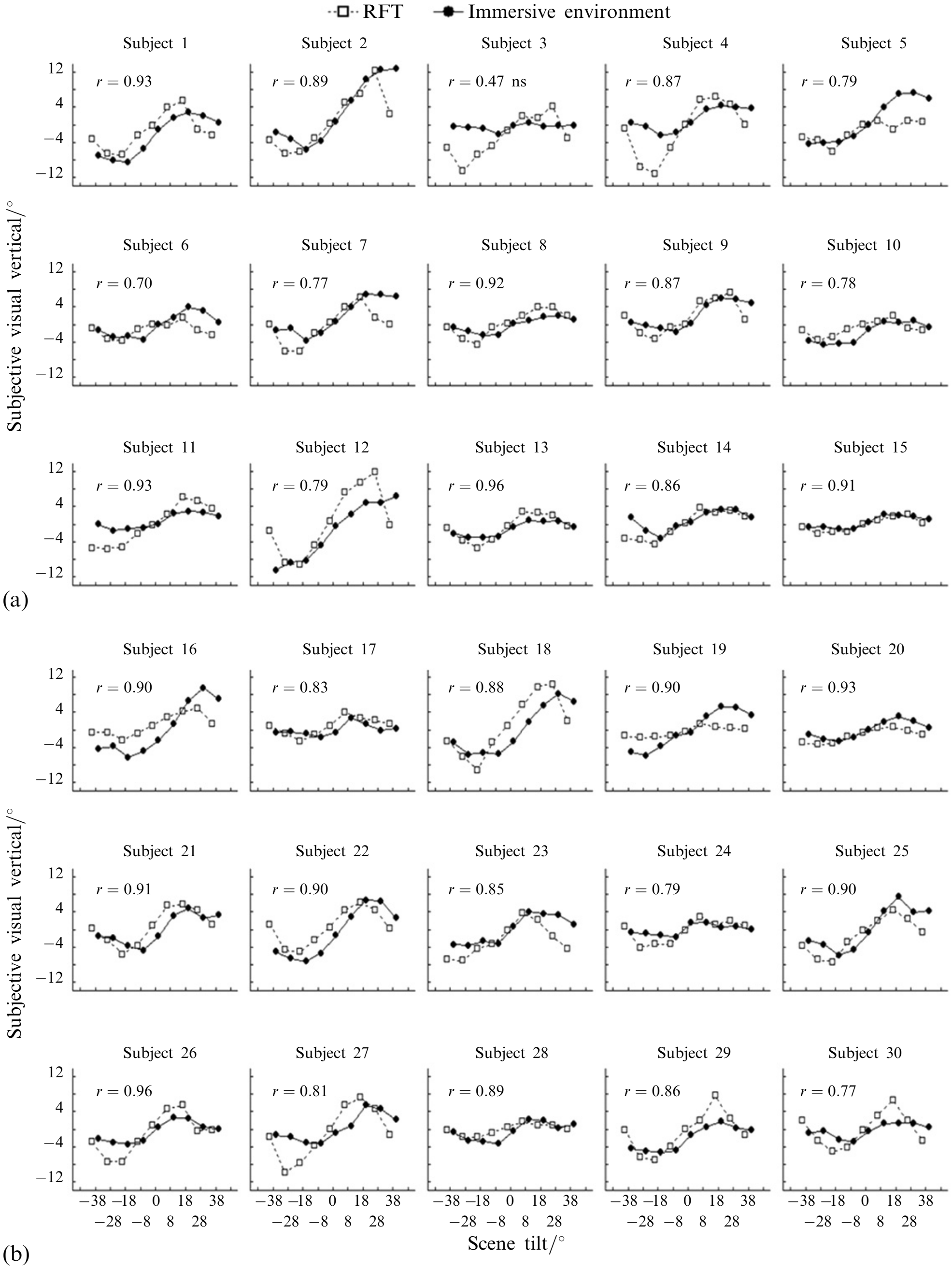

Figure 4. Individual correlations between SV settings recorded in the rod-and-frame test (RFT) and the immersive environment. Except for one subject, individual measures are highly and significantly correlated. (a) Head unrestrained (fifteen subjects); (b) head restrained (fifteen subjects).

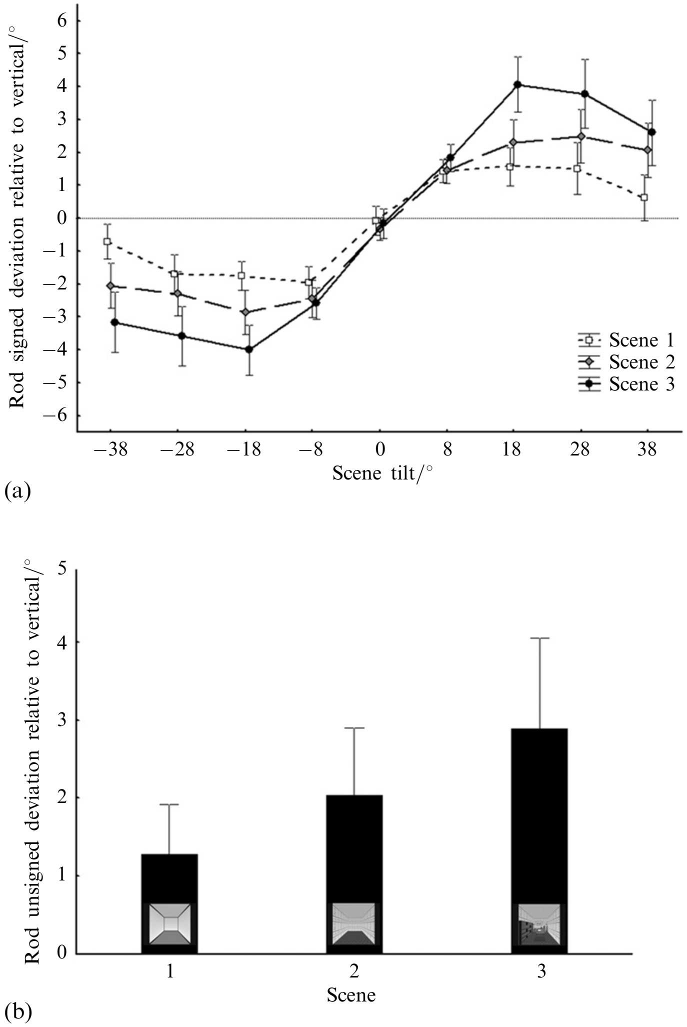

Figure 5. (a) Mean signed deviation of the rod relative to vertical during SV settings as a function of tilt and structure of the visual scene. (b) Mean unsigned deviation of the rod relative to vertical across the different scene tilts as a function of structure of the visual scene. Error bars represent 95% confidence intervals. The more structured the scene, the greater the rod-and-frame effect (RFE).

3.2.3 *Evolution of the RFE as a function of kinematic event.* Finally, a significant interaction was also found between scene tilt and kinematic event when comparing the mean signed deviations of the rod relative to vertical ($F_{8,224} = 19.26$, $p < 0.001$, $\eta_p^2 = 0.41$, $[1 - \beta] = 1$). It shows that the RFE was greater at the end of the trial (SV final position) than at the moment corresponding to the first movement endpoint of the rod. This was further supported by a main significant effect of kinematic event on the mean unsigned deviations of the rod relative to vertical ($F_{1,28} = 34.06$, $p < 0.001$, $\eta_p^2 = 0.55$, $[1 - \beta] = 1$), with larger deviations observed at the end of the trial.

Further analyses of interactions showed that the effect of kinematic event upon RFE was modulated by the visual scene and the adjustment mode.

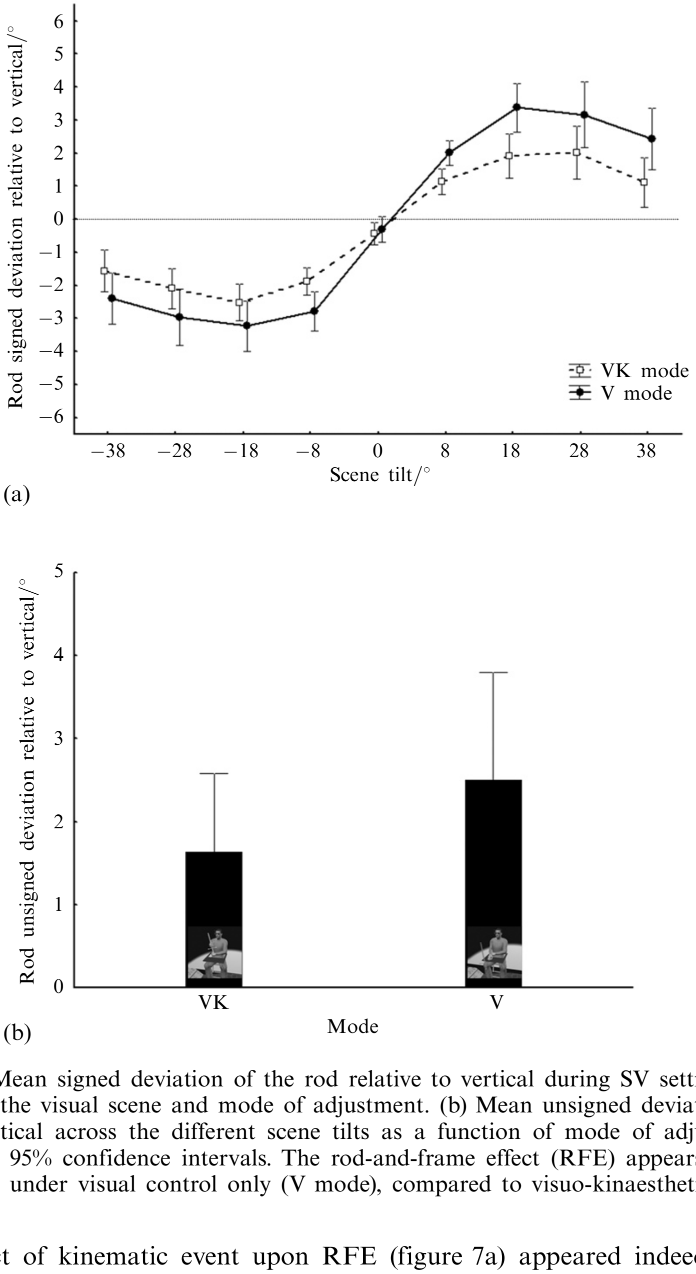

Figure 6. (a) Mean signed deviation of the rod relative to vertical during SV settings as a function of tilt of the visual scene and mode of adjustment. (b) Mean unsigned deviation of the rod relative to vertical across the different scene tilts as a function of mode of adjustment. Error bars represent 95% confidence intervals. The rod-and-frame effect (RFE) appears greater when SV is assessed under visual control only (V mode), compared to visuo-kinaesthetic control (VK mode).

The effect of kinematic event upon RFE (figure 7a) appeared indeed smaller for scene 1 than for scene 2 and scene 3, as revealed by the kinematic event × visual scene × scene tilt interaction found on the mean signed deviations of the rod relative to vertical ($F_{16,448} = 2.87$, $p < 0.001$, $\eta_p^2 = 0.09$, $[1 - \beta] = 0.99$). This was confirmed by the significant interaction between kinematic event and visual scene observed on the mean unsigned deviations of the rod relative to vertical ($F_{2,56} = 13.84$, $p < 0.001$, $\eta_p^2 = 0.33$, $[1 - \beta] = 0.1$). As illustrated in figure 7b, if larger deviations were observed at the end of the trial (SV final position) relative to the first movement endpoint when facing scene 1 ($p < 0.01$), this effect tended to increase when facing scene 2 and scene 3 ($p < 0.001$).

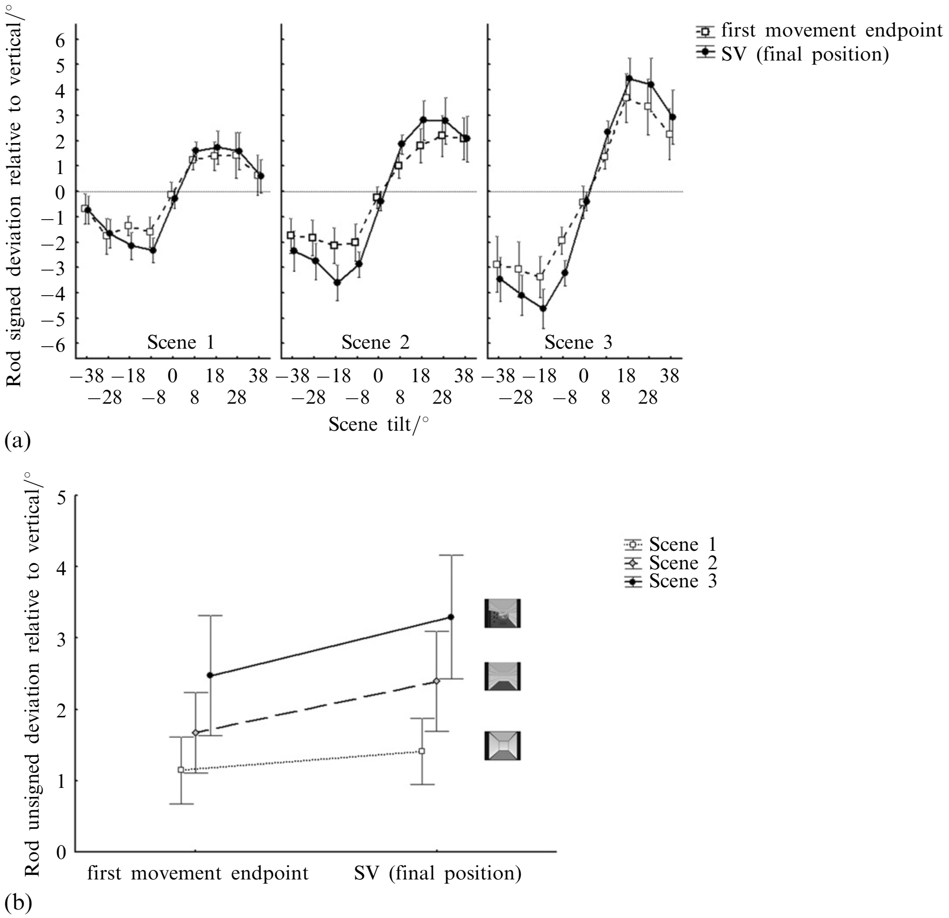

Figure 7. (a) Mean signed deviation of the rod relative to vertical during SV settings as a function of tilt and structure of the visual scene and kinematic event. (b) Mean unsigned deviation of the rod relative to vertical across the different scene tilts as a function of structure of the visual scene and kinematic event. Error bars represent 95% confidence intervals. The rod-and-frame effect (RFE) appears greater at the end of the adjustment (SV final position) than at first movement endpoint, this RFE increase being more pronounced for structured visual scenes.

The effect of kinematic event upon RFE (figure 8a) appeared also larger in VK mode than in V mode, as revealed by the kinematic event × adjustment mode × scene tilt interaction found on the mean signed deviations of the rod relative to vertical ($F_{8,224} = 4.79$, $p < 0.001$, $\eta_p^2 = 0.15$, $[1 - \beta] = 1$). This was confirmed by the significant interaction between kinematic event and adjustment mode shown on the mean unsigned deviations of the rod relative to vertical ($F_{1,28} = 14.64$, $p < 0.001$, $\eta_p^2 = 0.34$, $[1 - \beta] = 0.96$). As illustrated in figure 8b, if larger deviations were found at the end of the trial (SV final position) relative to the first movement endpoint in V mode ($p < 0.01$), this effect appeared to increase in VK mode ($p < 0.001$).

3.3 *Head orientation influences in the immersive environment*

Statistical analysis of the influence of experimental conditions on head orientation for the head-unrestrained group revealed a main effect of scene tilt ($F_{8,112} = 14.59$, $p < 0.001$, $\eta_p^2 = 0.51$, $[1 - \beta] = 1$). As illustrated in figure 9, the tilt of the visual scene exerted a comparable, although weaker, sinusoidal influence on head orientation as on rod orientation during SV adjustments.

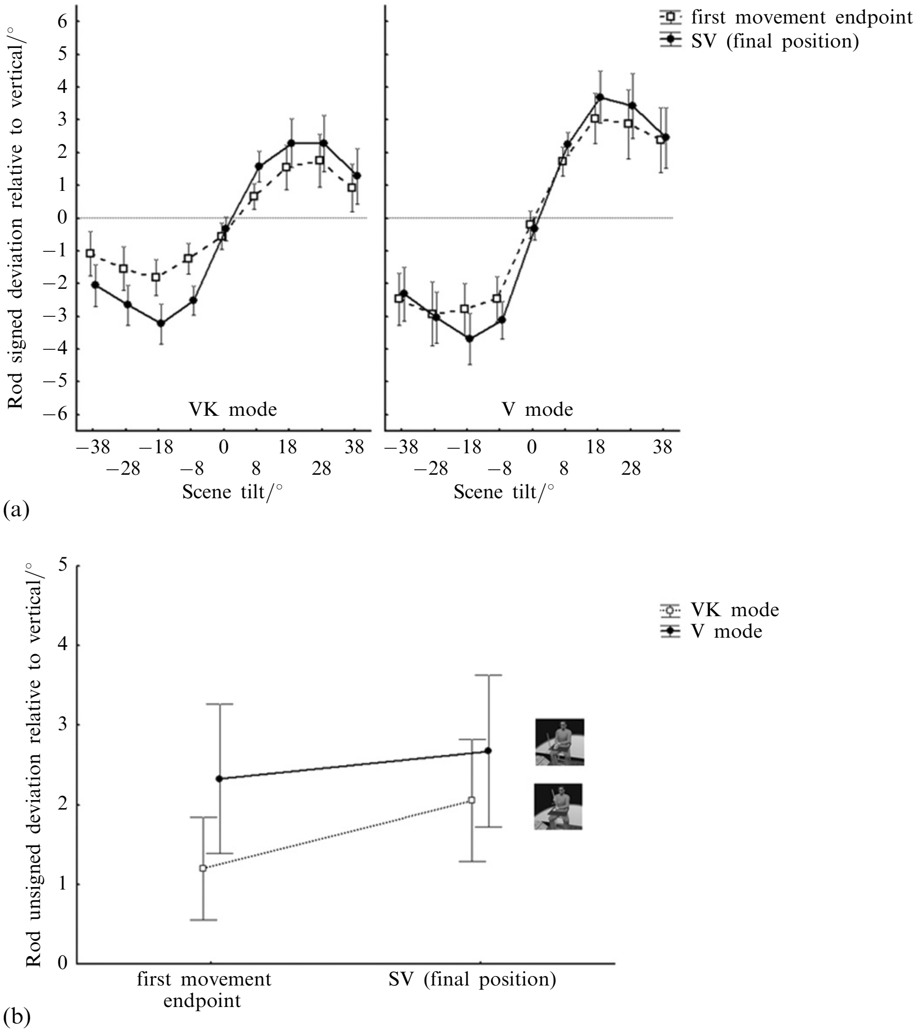

Figure 8. (a) Mean signed deviation of the rod relative to vertical during SV settings as a function of tilt and mode of adjustment and kinematic event. (b) Mean unsigned deviation of the rod relative to vertical across the different scene tilts as a function of mode of adjustment and kinematic event. Error bars represent 95% confidence intervals. The rod-and-frame effect (RFE) appears greater at the end of the adjustment (SV final position) than at first movement endpoint, this RFE increase being more pronounced under visuo-kinaesthetic control.

Despite the slight influence of scene tilt on head orientation, no difference was found between the two head-restriction groups when comparing the mean unsigned deviations of the rod relative to vertical ($F_{1,28} = 0.02$, $p = 0.90$, $\eta_p^2 = 0.001$, $[1 - \beta] = 0.05$). Furthermore, no significant interaction was found between the head-restriction group and scene tilt ($F_{8,224} = 0.14$, $p = 0.99$, $\eta_p^2 = 0.005$, $[1 - \beta] = 0.09$) as well as for the other factors when comparing the mean signed deviations of the rod relative to vertical. In other words, subjects having their head unrestrained, although exhibiting a slight influence of scene tilt upon their head orientation, did not differ from subjects having their head restrained when assessing SV.

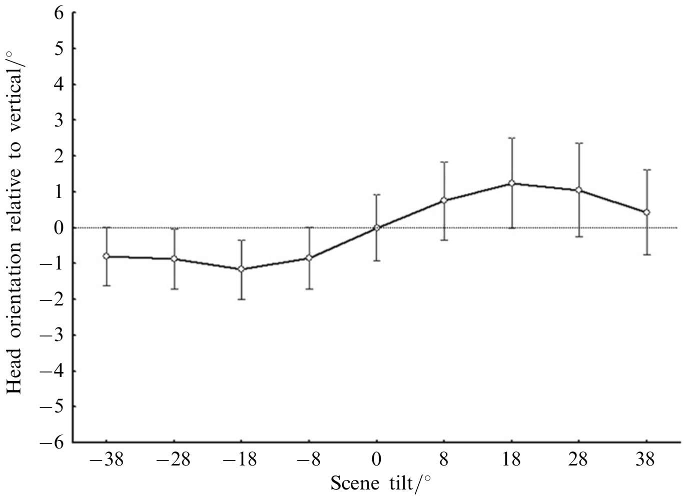

Figure 9. Mean head orientation relative to vertical during SV settings as a function of tilt of the visual scene in the head unrestrained group. This illustrates the existence of a significant although small 'postural frame effect'.

4 Discussion

The main purpose of the present study was to further investigate how the structure of the visual scene and the mode of adjustment may exert combined and dynamic influences upon SV judgments in a virtual-reality setup. The first part of this work was to determine whether a large-scale immersive virtual environment was able to induce comparable influences on SV as a classical rod-and-frame display (eg a portable RFT apparatus; Oltman 1968). This first step would allow us to focus on the dynamic influences regarding the visual characteristics of the scene and the sensorimotor control of adjustment.

4.1 *Virtual reality as a valid tool for investigating the rod-and-frame effect*

Our results clearly demonstrated the strong inductive properties of the immersive environment for eliciting RFE. Furthermore, the sinusoidal shape of the subjective visual vertical as a function of scene tilt is typical of that reported in the literature, in the range of the test orientations (Oltman 1968). These observations were also supported by the significant individual correlations between visual vertical estimates performed in real versus virtual environments, despite the structural differences between the two displays (eg frame apparent size or luminosity).

Our results confirmed the claim of Jenkin and collaborators (2003), who suggested that virtual-reality displays may be of relevance for manipulating the role of visual cues when observers had to determine the physical direction of gravity (and, more precisely, the perceived direction of 'up'). Mergner et al (2005) also reported comparable effects between real and virtual large-scale displays upon postural responses to visual motion, and stressed the advantage of virtual technology in its capacity to generate and modify a realistic visual stimulus with little effort in highly controlled conditions.

Physiological, behavioural, and perceptual responses recorded in virtual-reality displays may account for the level of subjective presence of an observer immersed in these virtual environments (Burkhardt 2003; Sanchez-Vives and Slater 2005). Presence may be defined as a state of consciousness of being inside a virtual environment (Slater 2002), and may be related to the responsiveness of the virtual environment to human actions (Heeter 1992). The underlying assumption is that the more a subject feels present in a virtual environment, the closer his/her responses will be to those he/she would show in a similar real environment (Slater 2002). We therefore assume that the occurrence of RFE in virtually tilted visual scenes may indicate a level of presence of the immersed observer.

4.2 *Multimodal and dynamic influences in the induction of the rod-and-frame effect*

Having qualitatively validated the immersive setup as a powerful tool for inducing RFE, we aimed to investigate the structural influence of the projected visual scene and the effect of adjustment mode upon SV estimates. In addition, we analysed the evolution of these potential influences by comparing the rod orientations relative to vertical at two moments (ie specific kinematic events) of the adjustment phase.

First, our results clearly showed that RFE was modulated by the features of the visual scene (figure 5). The more 3-D geometrical cues the scene contained (ie the amount of parallel and orthogonal features in scene 2 versus scene 1) and the more additional cognitive cues determining visual up and down direction the scene comprised (ie the amount of meaningful polarised objects in scene 3 versus scene 2), the larger the RFE. Hence, as reflected by the significant difference in RFE between scene 1 and scene 2 on one hand, and between scene 2 and scene 3 on the other hand, the present study gives support to both the low-level 'geometrical' hypothesis, in which RFE is mainly explained by automatic visual processes (Ebenholtz 1985; Li and Matin 2005a, 2005b; Wenderoth and Beh 1977), and the 'cognitive' hypothesis in which high-level representations of up and down direction are involved (Cian et al 2001; Howard and Childerson 1994; Howard and Hu 2001).

As regards the adjustment mode, a significant reduction of the RFE was found when subjects controlled their settings via both visual and kinaesthetic cues, as compared to classic adjustments involving visual control only (figure 6). The mass of the rod maintained in VK mode (weak and uniformly distributed) cannot account for this effect. This clearly suggests that kinaesthetic cues (cues including proprioceptive inputs and information about the motor command) may contribute to counteract the visual attraction induced by the visual frame. This new finding with regard to sensory influences upon the RFE magnitude is in line with previous studies assuming that the kinaesthetic system is highly specialised for perceiving earth-fixed axes (Darling and Hondzinski 1999). Specifically, it was shown that errors in aligning the forearm parallel to the earth-fixed vertical were lower than to body-fixed axes or external visual axes (Darling and Bartelt 2003). More generally, this result demonstrates that the perceived vertical is critically dependent on the sensory inputs available during measurement (Carriot et al 2008).

Another concern was related to the online evolution of the RFE during a single adjustment, in order to better understand how the previously described multimodal influences may occur and dynamically interact over time. Strikingly, RFE occurred as early as the first movement endpoint of the adjustment. In addition, a significant increase of the RFE was found over time, from the first movement endpoint to the SV final position. This RFE increase during the adjustment phase was also found to be modulated by the type of visual scene and by the adjustment mode. Instead, SV judgments deviated towards scene tilt between both kinematic events to a greater extent when the visual scene contained geometric and meaningful 3-D features, and when the adjustment enabled visuo-kinaesthetic control. This might illustrate the progressive increase of visual influence depending on its relevance for orientation judgments and on the presence of other additional sensory inputs. The presence of online modifications regarding the RFE magnitude is in accordance with some findings related to vection phenomena. Vection intensity, defined as the strength of a visually induced perceived self-motion, was shown to evolve over time, with different perceptual stages (Howard and Howard 1994). Online transitions between these stages (such as vection entrance latency or vection saturation) have been found sensorily related (Lepecq et al 1999), depending on the weight accorded by the central nervous system (CNS) to visual or vestibular inputs during the integration process.

A last issue concerned the involvement of head orientation in the reported RFE. As shown for subjects having their heads unrestrained, the scene tilt exerted a significant, although smaller, effect upon head posture. This result is in accordance with a 'postural frame effect' which has been shown to exist at the head level as well as for the whole-body in both field-dependent or field-independent subjects (Isableu et al 1997, 1998). Nevertheless, no significant difference was found between the two groups of subjects (head restrained versus head unrestrained) when comparing their SV estimates. This may suggest that the head deviation from vertical observed in the head-unrestrained group was too small to yield an additional postural influence (eg E-like effect—Bischof 1974; Müller 1916; or A-like effect—Aubert 1861; Mittelstaedt 1986) upon the perceived orientation of objects relative to gravity.

Overall, our results suggest that the RFE exerted by the tilted scene is not only influenced by the visual structure of the scene but also by the mode of adjustment, and may also rapidly evolve over time. In parallel to the previous sensory interpretations, these results may be explained in terms of interaction between different reference frames for orientation judgments.

4.3 *The subjective vertical as the result of a combination between reference frames*

As proposed by Howard (1982, 1986), different reference frames may contribute to the cognitive determination of the SV. A reference frame may be defined as a system of coordinates including sets of axes or references used to code and update the location and the orientation of objects in space (Batista 2002). For instance, the rod tilt may be referred to the direction of gravity (geocentric reference frame), to the main head-and-trunk axis (egocentric reference frame), or to the spatial features of the surrounding scene (allocentric reference frame). However, as shown in the present study, SV estimates are not fully aligned with any one of the above references. Therefore, the existence of subjective 'composite' reference frames (Luyat et al 2001; Bringoux et al 2008) may be advanced to explain our results.

It is well-known that SV is not only influenced by the visual frame, but also by body tilt (Schöne 1964) and by modifications of the gravitational field (Clark and Graybiel 1968). This clearly suggests that all the reference frames mentioned above are potentially involved in the perceptual elaboration of the SV. The question remains how they may interact and combine at the CNS level to yield a unique—currently used—subjective reference frame. In line with our hypothesis, we can reasonably assume that a specific weight is attributed to each reference frame in the combination process, and that this weight may be dynamically modified, depending on task constraints. To illustrate this in our experiment, one may consider that the allocentric reference frame could be differentially weighted as a function of some initial task constraints (eg tilt and structure of the visual scene, adjustment mode), and might also be re-weighted over time during the adjustment, depending on the same task constraints. Consequently, the CNS might have integrated this information with a specific weight when combining the multiple reference frames.

The analogy with the sensory re-weighting processes which have been found to occur during multisensory integration (Carver et al 2006) is, of course, intentional. However, we claim that different sensory inputs may be processed in the same reference frame, although some are naturally specialised to convey information relative to a specific coding. For instance, if visual inputs are essentially related to the allocentric reference frame, and vestibular signals are referred to the geocentric reference frame, somatosensory cues could convey information related to either egocentric (eg limb position relative to others—Sherrington 1900), geocentric (eg gravitational torque referred to the limb orientation in space—Darling and Hondzinski 1999), or even allocentric (eg haptic spatial representation for blind subjects) coding. Recent studies confirmed the existence of neurophysiological substrates related to allocentric, egocentric, or geocentric coding (Committeri et al 2004; Galati et al 2000; Lopez et al 2005). However, further research is needed to better understand the role of sensory inputs in the construction as well as in the combination between reference frames.

5 Conclusion

To our knowledge, the present study is the first to show dynamic influences related to the visual structure of a virtual environment and to the mode of adjustment upon the perception of verticality. These effects may result from the dynamic combination between reference frames, which may occur and evolve throughout the SV adjustment. The use of a virtual immersive environment has been found to be effective in easily manipulating the structure of the visual scene, and promising for further investigations concerning the richness of the visual scene as a function of the sensory modalities involved in the perception of verticality.

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Approche différentielle et spécificité du jugement de l'orientation verticale d'un objet versus du corps

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Slow changing postural cues cancel visual field dependence on self-tilt detection

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ABSTRACT

Interindividual differences influence the multisensory integration process involved in spatial perception. Here, we assessed the effect of visual field dependence on self-tilt detection relative to upright, as a function of static vs. slow changing visual or postural cues. To that aim, we manipulated slow rotations (i.e., 0.05° s^{-1}) of the body and/or the visual scene in pitch. Participants had to indicate whether they felt being tilted forward at successive angles. Results show that thresholds for self-tilt detection substantially differed between visual field dependent/independent subjects, when only the visual scene was rotated. This difference was no longer present when the body was actually rotated, whatever the visual scene condition (i.e., absent, static or rotated relative to the observer). These results suggest that the cancellation of visual field dependence by dynamic postural cues may rely on a multisensory reweighting process, where slow changing vestibular/somatosensory inputs may prevail over visual inputs.

1. Introduction

Since observations by Aubert [1], it is well known that the perception of spatial orientation is biased by static roll body tilt yielding, for instance, a deviation of the perceived longitudinal body axis in the direction of tilt (e.g., [2]). Similar deviations induced by static body tilt appear in pitch when visually estimating the body longitudinal axis [2,3] or the egocentric eye level [4].

In parallel, static tilt of a visual scene has also been found to influence subjective visual vertical (SVV; e.g., [5]) as well as self-orientation estimates, such as adjusting the body to vertical (body adjustment test; [6,7]). In their pioneer work, Asch and Witkin conducted a set of experiments in which they showed that SVV deviates in the same direction as the static roll tilt of the visual scene [8,9]. Strikingly, they observed large interindividual differences, which were interpreted as reflecting that some individuals may rely more on vision than others, namely visual field dependent ('FD') or independent ('FI') subjects.

Available data regarding the influence of combined changes in body and visual scene orientation were rarely issued from dynamic rotations (e.g., [10]), and rather concerned static tilts with a variable time delay between the end of body tilt and the task onset [4,11–13]. In this context, while some studies showed that errors during combined head and visual scene static tilts appeared as an additive combination of the errors observed for each single tilt [4,11], other studies revealed that these errors were mainly induced by the visual tilt [12,13]. Although the influence of visual field dependence on spatial perception has been investigated during static tilt of the body/head and a visual scene [14], it has never been studied during very slow rotations, where cues were continuously – although slowly – refreshed.

Here, we assessed visual field dependence on self-tilt detection relative to upright, during slow continuous rotations of the body and/or the visual scene (i.e., 0.05° s^{-1}) performed below semicircular canals stimulation [15]. Slow rotation profiles were previously shown to impair self-tilt detection in subjects who were not a priori selected on the basis of their degree of field dependence [16]. We expected that FD would be more sensitive to slow visual rotation alone compared to FI. However, we hypothesized that these interindividual differences would disappear during actual slow body rotation, whatever the presence and the orientation of the visual background. This second hypothesis

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was supported by recent data suggesting a 'vestibular/somatosensory capture' relative to visual cues as soon as the body is not upright anymore [17].

2. Methods

2.1. Participants

In order to drastically select subjects relative to their visual field dependence, 100 participants (55 males; 45 females; mean age ± SD: 20.6 ± 2.3 years) were recruited among the students of Aix-Marseille University, and were submitted to a portable rod-and-frame test (RFT). Subjects reported having normal or corrected-to-normal vision and no neurological or sensorimotor disorders. All participants gave written informed consent prior to the experiment, in accordance with the 1964 Declaration of Helsinki.

The RFT consisted in setting a tilted visual rod along the gravitational vertical when facing a tilted visual frame (i.e., SVV task). Three roll frame tilts (0 and ±18°) and random initial rod orientations of ±18° were manipulated. According to Nyborg and Isaksen's method [18], we computed the 'frame effect' (tendency to align the visual rod towards the frame) at 18°. The magnitude of the 'frame effect' determined the degree of visual field dependence, with high scores for visually-dependent subjects and low scores for visually-independent subjects [8]. Extreme scores (i.e., highest and lowest scores) were identified and enabled us to define two groups of eight subjects being either highly visually-dependent (8 females; 19.6 ± 1.3 years; mean 'frame effect': 8.6 ± 1.3°) or visually-independent (3 females and 5 males; 20.1 ± 1.1 years; mean 'frame effect': 1.0 ± 0.3°). Strikingly, the sample size of both groups was in the range of those manipulated in [18,19]. Furthermore, we considered that the strict selection process, leading to a marked differentiation between groups, increased the chance of finding a significant difference, if it actually existed.

Finally, prior to the experiment, stereoscopic vision acuity was checked for each selected subject using the Randot Stereotest® with all individual scores greater than 70 s of arc.

2.2. Apparatus

Subjects were seated in a tilting chair, firmly maintained by a six-point seatbelt. The chair could be rotated in the pitch dimension, around an axis positioned under the seat (see Fig. 1a). The rotation was produced by lengthening/shortening an electric jack (Phoenix Mecano®, thrust: 3 kN, clearance: 0.6 m, precision 0.12 mm) attached to the back of the seat. The angular profile of the tilt was servo-assisted using an inclinometer fixed to the chair (AccuStar®; resolution: 0.1°; range: ±60°). The rotation velocity was set at $0.05^\circ\,s^{-1}$ following an acceleration phase at $0.005^\circ\,s^{-2}$, below the threshold for semicircular canals stimulation [15]. During the experimental trials, earphones provided white noise to mask any auditory cues. Two push buttons held by subjects in both hands were used to sample the digital response for judgement settings.

A 3D head-mounted display (HMD, 3D Cybermind hi-Res900®, Cybermind Interactive Nederland, The Netherlands; resolution: 800 × 600 pixels; field of view: 31.2° diagonal for each eye) was fixed horizontally onto a headrest attached to the seat. This headrest was adjustable in elevation to the subject size. As illustrated in Fig. 1, the HMD was used to display a stereoscopic 3D visual background, composed of a full furnished and polarized room. The room was 3 m width × 2.25 m height, which corresponded to a relative standard room size, and was 6 m length. The distance of the virtual scene front was set at 1.7 m from subjects' eye in the transverse plane, in order that the front wall could be fully visible according to the HMD field of view. The virtual room displayed in the HMD could rotate in the pitch dimension around the same axis as the rotating chair. Overall, the HMD device prevented subjects from having visual feedback from the experimental setup and about their current body location.

A real-time acquisition system (ADwin-Pro®, Jäger, Lorsch, Germany) running at 10 kHz was driven by a customized software (Docometre) to synchronously control visual background and/or chair rotations. The lag measured between visual and chair stimulus was negligible (<55 ms, that is, less than 0.003°).

2.3. Procedure

During the experiment, subjects, seating in the rotating chair, were asked to indicate whether they felt being tilted forward, i.e., away from vertical [16,21,22]. To that aim, subjects were required to respond to a binary choice via the push buttons, thus indicating 'Yes, I feel being tilted forward' by pressing the right hand-held button or 'No, I do not feel being tilted forward' by pressing the left hand-held button.

For each condition, the chair and the visual background were initially set at 0° (i.e., at vertical). Subjects gave their subjective response when prompted by an auditory tone every 1°, from 0° to 18° of body and/or visual scene rotations. Once the body and/or the visual scene was rotated by 18°, the visual scene disappeared. If the body was actually rotated, the chair was rotated back to 0° with a profile in which we varied the magnitude and duration of the acceleration and deceleration phases. This pseudo-random profile was chosen such that the subjects did not infer the angle of tilt they previously reached. Between trials, the HMD was removed and a period of rest in full ambient light, during at least 1 min, was consistently provided before the next condition started. This resting period was used to suppress post-rotational effects due to semicircular canal stimulation [15] and to limit possible fatigue. The subsequent body and/or visual scene rotations condition began only when subjects did not feel tilted anymore.

During the experiment, we manipulated tilts of the body and/or the visual scene in the pitch dimension with forward body rotation and backward visual scene rotation up to 18°. The same velocity profile was used to reach 18° as subjects were asked to perform the task during the continuous rotation(s), so that these rotations were comparable. Overall, 4 experimental conditions were presented: S_{bwd}: backward visual scene rotation (top towards the observer) without body rotation; B_{fwd}: forward body rotation without scene (no visual background); $B_{fwd}S$: forward body rotation with a visual **s**cene remaining static relative to the subject; $B_{fwd}S_{bwd}$: forward body rotation with backward visual scene rotation relative to the observer.

All 16 subjects performed 3 repetitions in each of the 4 aforementioned conditions, which were presented in a pseudo-random, counterbalanced order, to avoid any potential learning effect. A training session without body and/or visual scene rotations was provided before data collection actually started, to familiarize subjects with the task. The whole experimental session lasted about 2 h.

2.4. Data processing

We first determined the threshold for body tilt detection in each condition. Responses were converted into binary values, with '1' corresponding to the response 'Yes, I feel being tilted forward' and '0' to the response 'No, I do not feel being tilted forward'. A Probit model, using a non-linear regression analysis for binomial values

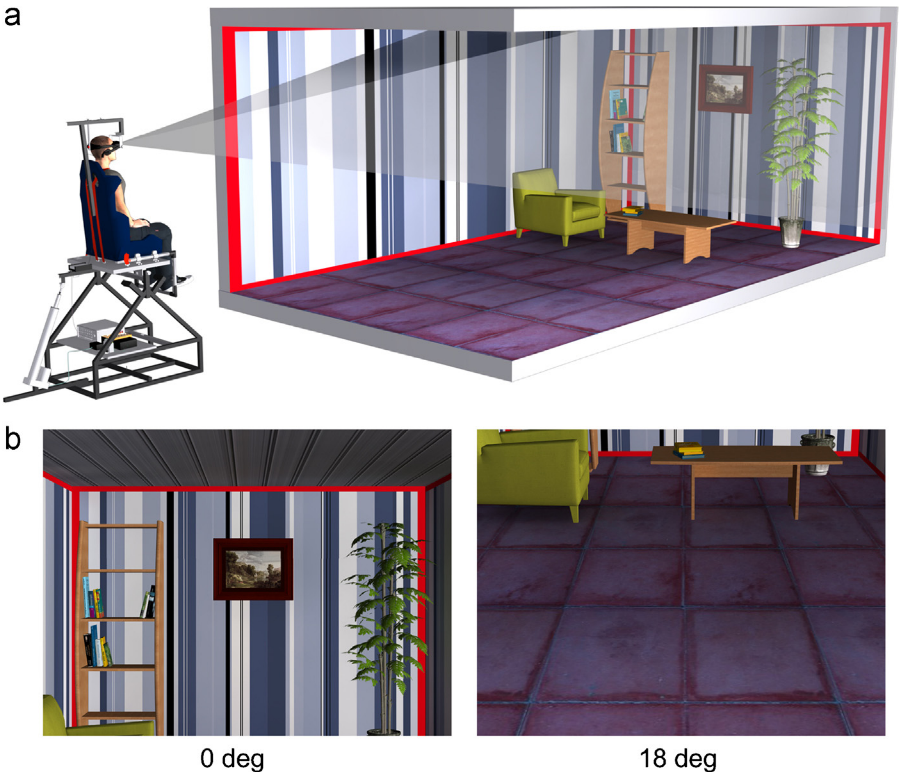

Fig. 1. Experimental setup. (a) Global view of the apparatus including the tilting chair, the HMD and the 3D visual scene at virtual scale. (b) Visual scene actually viewed by a subject at the beginning of the trial (0°) and the end of the visual scene rotation (18°) when provided (i.e., S_{bwd} and $B_{\mathrm{fwd}}S_{\mathrm{bwd}}$).

was adjusted to the data, to determine the tilt detection threshold corresponding to 50% of probability of the feeling of being tilted (0.5 value). Probit function was defined as follows:

$$Pi = \frac{1}{1+(At/T)^b}$$

'*P*' is the confidence probability in the feeling of being tilted for a given condition '*i*'. '*At*' corresponds to the *Angle of Tilt* during this condition and '*T*' to the tilt *Threshold* for this condition (i.e., angle of tilt for $P = 0.5$). '*b*' is the slope of the tangent at the inflection point of the curve and constitutes an estimation of the discrimination sensitivity relative to the chosen increments. A prior analysis of the consistency of the threshold detection sensitivity over conditions was performed, using a 4 condition repeated-measures ANOVA applied on '*b*' values. This analysis did not reveal any significant difference between discrimination sensitivity across conditions.

Noticeably for some subjects, we could not determine any tilt detection threshold for visual scene rotation (S_{bwd}) as they never reported a feeling of being tilted in this condition. In such cases (5/8 FI subjects and 1/8 FD subjects), a threshold was arbitrary set to 20°, that is, just over the largest magnitude of tilt presented in the experiment. We then compared the mean thresholds of body tilt using a 2 group (FD, FI) × 4 condition (S_{bwd}, B_{fwd}, $B_{\mathrm{fwd}}S$, $B_{\mathrm{fwd}}S_{\mathrm{bwd}}$) repeated-measures ANOVA. As we wanted to avoid any potential effect of the arbitrary threshold set when subjects never felt tilted in the S_{bwd} condition, we repeated the same analysis on the mean percentage of positive responses (i.e., 'Yes, I feel being tilted') for a given condition.

Overall, post hoc tests (Newman–Keuls) were performed when necessary and the level of significance was set at .05 for all statistical analyses. The effect size ($\eta^2 p$) and the power ($1-\beta$) of each test were computed.

3. Results

Statistical differences between groups and conditions were first investigated by comparing body tilt thresholds obtained from the fitted Probit function (Fig. 2). The ANOVA failed to reach significance for group ($F_{(1,14)} = 2.9$; $p = .11$; $\eta^2 p = .17$;

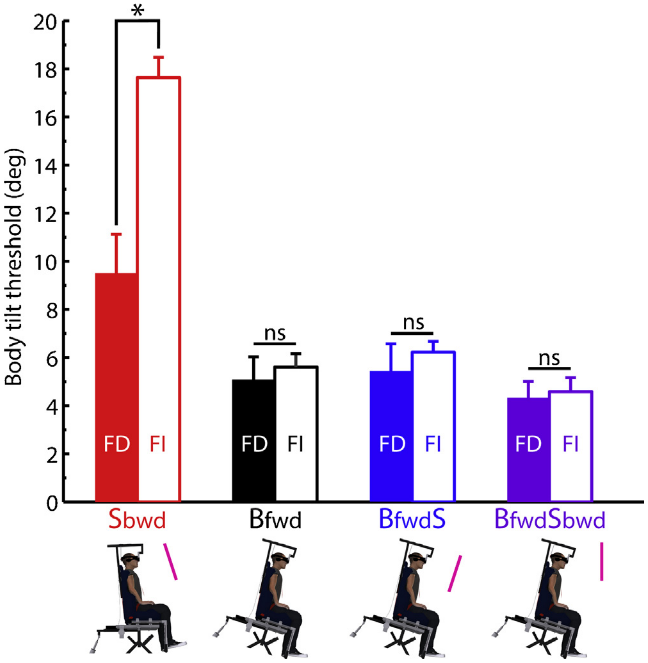

Fig. 2. Self-tilt detection threshold as a function of group (FD: coloured bars, FI: white bars) and condition (S_{bwd}, B_{fwd}, $B_{\mathrm{fwd}}S$, $B_{\mathrm{fwd}}S_{\mathrm{bwd}}$). Vertical bars denote positive standard errors. *: $p < .05$; ns: non significant comparison. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

$(1-\beta) = .36$) but showed a significant main effect of condition ($F_{(3,42)} = 38.3$; $p < .001$; $\eta^2 p = .73$; $(1-\beta) = 1.00$) as well as an interaction group × condition ($F_{(3,42)} = 7.8$; $p < .001$; $\eta^2 p = .36$; $(1-\beta) = .98$). Both groups (FD, FI) exhibited higher body tilt thresholds when only the visual scene was rotated (mean ± SE: 13.6 ± 1.6°), as compared to other conditions involving body rotation (B_{fwd}: 5.3 ± 0.8°, $B_{fwd}S$: 5.8 ± 0.8°, $B_{fwd}S_{bwd}$: 4.5 ± 0.6°). Indeed, S_{bwd} statistically differed from all body rotation conditions ($p < .001$ for all comparisons) while body rotation conditions were not different from each other (B_{fwd} vs. $B_{fwd}S$: $p = .61$; B_{fwd} vs. $B_{fwd}S_{bwd}$: $p = .37$ and $B_{fwd}S$ vs. $B_{fwd}S_{bwd}$: $p = .34$). As a core finding, although tilt detection thresholds were markedly different between FD and FI subjects in the condition involving a rotation of the visual scene alone (FD: 9.5 ± 1.6° vs. FI: 17.6 ± 0.8°; $p < .05$), there was no difference between both groups for all body rotation conditions, whatever the presence and the orientation of the visual scene (B_{fwd}, $p = .98$; $B_{fwd}S$, $p = .96$; $B_{fwd}S_{bwd}$, $p = .93$). This absence of difference between FD and FI was observed despite our subjects' selection criteria, which were expected to magnify statistical differences (see Section 2.1).

Similar results appeared when comparing the mean percentage of positive responses. Indeed, the ANOVA revealed no effect of group ($F_{(1,14)} = 1.9$; $p = .19$; $\eta^2 p = .12$; $(1-\beta) = .25$) but showed a main effect of condition ($F_{(3,42)} = 36.0$; $p < .001$; $\eta^2 p = .72$; $(1-\beta) = 1.00$) as well as an interaction group x condition ($F_{(3,42)} = 8.76$; $p < .001$; $\eta^2 p = .39$; $(1-\beta) = .99$). Post hoc analyses showed that the percentage of positive responses was lower for S_{bwd} (32 ± 7%) compared to the other body tilt conditions B_{fwd} (67 ± 4%, $p < .001$), $B_{fwd}S$ (64 ± 4%, $p < .001$), $B_{fwd}S_{bwd}$ (72 ± 3%, $p < .001$) which remained statistically not different from each other (B_{fwd} vs. $B_{fwd}S$, $p = .43$; B_{fwd} vs. $B_{fwd}S_{bwd}$, $p = 0.23$; $B_{fwd}S$ vs. $B_{fwd}S_{bwd}$, $p = 0.12$). Here again, the interaction between group and condition showed that the percentage of positive responses in the S_{bwd} condition was significantly higher for FD (50 ± 8%) compared to FI (14 ± 5%; $p < .05$), whereas it was not different between groups when actual body rotation was involved (B_{fwd}: 68 ± 7% vs. 66 ± 4%, $p = .92$; $B_{fwd}S$: 71 ± 5% vs. 73 ± 4%, $p = .88$; $B_{fwd}S_{bwd}$: 64 ± 8% vs. 63 ± 4%, $p = .96$, for FD and FI, respectively).

4. Discussion

This experiment was designed to investigate whether visual field dependence could influence self-tilt detection relative to upright under different contexts of body/visual slow rotation. The core findings of the present study rely on the different influence of visual field dependence/independence on self-tilt detection regarding the combination of static vs. dynamic visual and postural stimulations. While thresholds for self-tilt detection substantially differed between both groups when the rotation of the visual scene alone was involved, this difference was no longer present when the body was actually rotated, whatever the visual scene condition (i.e., absent, static or in rotation).

Body tilt threshold was consistently lower for FD, as compared to FI subjects during slow rotation of the visual scene alone. More precisely, most of FD subjects felt being tilted from vertical in this condition, while most of FI subjects never felt being tilted, even when the potential effect of the visual scene tilt was maximal (i.e., 18° of tilt; [23]). This result shows that, as for SVV estimates [8,9], visual scene tilt impacts self-tilt perception as a function of visual field dependence. A similar influence of visual field dependence on SVV has also been revealed when facing a dynamic rotation of a visual scene (e.g., [24]). Here we showed that a very slow rotation (i.e., $0.05^\circ\,s^{-1}$) of a structured visual scene differently influenced self-tilt detection relative to upright according to visual field dependence, the latter being classically determined by SVV estimates (i.e., RFT; see Section 2.1). During this particular visuo-postural conflict, FD may largely depend on continuously updated visual cues relative to static postural cues. Specifically, the backward rotation of the visual scene may induce an illusory perception of body rotation in the reverse direction that may lead FD subjects to respond that they feel being tilted forward, in accordance with [25].

By contrast, our data did not reveal any difference between FD and FI in self-tilt detection during actual body rotation, whatever the visual stimulation. In other words, the link we found between visual influence on SVV and self-tilt detection when only the visual background was rotated is abolished as soon as postural orientation changed. Overall, we confirmed that slow pitch body tilts at $0.05^\circ\,s^{-1}$ delayed the detection of body tilt [16], independently from visual field dependence, suggesting that very slow changes in otolith inputs are non-sufficient to convey relevant information for updating actual self-orientation. This assumption is supported by the absence of difference between bilateral labyrinthine-defective subjects and normal subjects in slow self-tilt detection [22]. Somatosensory inputs, and more precisely cutaneous pressure cues might play a major role compared to vestibular cues for body tilt detection [16,26] as well as for postural control [27]. Here, the weight of postural inputs, mediated by touch and pressure cues, might increase as compared to visual cues when the former are regularly refreshed by afferent slow changes. This large influence of postural cues relative to visual cues is in accordance with recent data on spatial perception (e.g., [17,28]).

Here we suggested that sensory reweighting of postural cues, and more likely somatosensory inputs, may be at work for subjects exhibiting a strong dependence on visual cues in otherwise static postural conditions. Visual field dependence may be modulated by the nature of postural cues: static (i.e., unchanged body orientation) vs. dynamic (i.e., actual – even slow – body rotation). Previous studies already claimed for a multisensory reweighting process subjected to interactions between proper singularities and context [14,20,21,29]. For instance, gender influence on SVV estimates was found to depend on postural constraints, since it was recently shown that gender-related differences also disappeared when the body was tilted (i.e., lying on a side; [29]). Gender could also play a role in our study since it constitutes a distinguishing attribute of field dependency (i.e., FD: 8 females vs. FI: 5 males and 3 females), as previously reported [30].

Overall, the results of this study support the hypothesis that the expression of visual field dependence during self-tilt detection relies on postural context. The cancellation of visual field dependence during actual body tilt needs to be extended to other orientation tasks (e.g., subjective body tilt or SVV estimates) to investigate the potential generalization of this attribute [31]. Presumably however, such dominance of dynamic postural cues overruling visual field dependence might be rather task-specific, as it was shown that the weighting of visuospatial inputs during static scene tilt depends on task requirements [32].

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Conflict of interest statement

The authors have declared that no competing interests exist.

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Conséquences de l’absence d’indices somesthésiques. Cas d’une patiente désafférentée

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Do Visual and Vestibular Inputs Compensate for Somatosensory Loss in the Perception of Spatial Orientation? Insights from a Deafferented Patient

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The present study aimed at investigating the consequences of a massive loss of somatosensory inputs on the perception of spatial orientation. The occurrence of possible compensatory processes for external (i.e., object) orientation perception and self-orientation perception was examined by manipulating visual and/or vestibular cues. To that aim, we compared perceptual responses of a deafferented patient (GL) with respect to age-matched Controls in two tasks involving gravity-related judgments. In the first task, subjects had to align a visual rod with the gravitational vertical (i.e., Subjective Visual Vertical: SVV) when facing a tilted visual frame in a classic Rod-and-Frame Test. In the second task, subjects had to report whether they felt tilted when facing different visuo-postural conditions which consisted in very slow pitch tilts of the body and/or visual surroundings away from vertical. Results showed that, much more than Controls, the deafferented patient was fully dependent on spatial cues issued from the visual frame when judging the SVV. On the other hand, the deafferented patient did not rely at all on visual cues for self-tilt detection. Moreover, the patient never reported any sensation of tilt up to 18° contrary to Controls, hence showing that she did not rely on vestibular (i.e., otoliths) signals for the detection of very slow body tilts either. Overall, this study demonstrates that a massive somatosensory deficit substantially impairs the perception of spatial orientation, and that the use of the remaining sensory inputs available to a deafferented patient differs regarding whether the judgment concerns external vs. self-orientation.

Keywords: spatial orientation, body tilt, multisensory integration, deafferented patient

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INTRODUCTION

The perception of spatial orientation relies on the central processing of multisensory information such as vestibular, visual and somatosensory inputs (MacNeilage et al., 2008 for a review) and prior knowledge about gravity (Lacquaniti et al., 2014). The contribution of sensory signals to spatial perception has been notably addressed by studying the effect of sensory deficits. On the one hand, impairments in spatial abilities have been observed even years after the deficit occurrence (e.g., Foster, 1994). On the other hand, remarkable compensatory mechanisms have been shown in sensory-impaired patients, allowing them to preserve or even enhance spatial perception (Lessard et al., 1998; Van Boven et al., 2000; Bavelier et al., 2006). Such sensory compensation, based on the unimpaired sensory inputs, seems to depend on the type of sensory deficit, environmental properties and task requirements (Lacour et al., 2009; Cousins et al., 2014). Here, we investigated how a massive loss of somatosensory inputs may impact spatial perception by studying the ability of a deafferented patient to use some remaining visual and vestibular cues in two distinct spatial orientation tasks involving external vs. self-orientation judgments.

A large amount of studies which investigated how sensory impairments could influence spatial perception dealt with the impact of visual deficits (Pasqualotto and Proulx, 2012 for a review). Considering the critical implication of vision for spatial orientation (Howard, 1982), one may expect that visual impairment could bias the perceived orientation of objects and/or the body. While some studies indeed reported degraded spatial abilities in congenitally-blind subjects (e.g., Seemungal et al., 2007), some others have shown similar or even improved spatial performance in blind subjects as compared to subjects without visual deficit. For instance, the haptic perception of objects orientation did not differ between blind and blindfolded sighted subjects (Gentaz and Hatwell, 1998). Furthermore, the perception of self-motion direction was found more accurate in congenitally blind with respect to blindfolded sighted subjects (Moser et al., 2015). Presumably in these conditions, vestibular and somatosensory signals may have compensated for the absence of vision.

When considering the influence of vestibular deficits on the perception of spatial orientation, it has been shown that unilateral vestibular loss yields detrimental effects on the adjustment of a visual rod to gravitational vertical (i.e., Subjective Visual Vertical or SVV, Tabak et al., 1997; Lopez et al., 2007) and on the perception of body orientation (Aoki et al., 1999). However, bilateral vestibular loss does not result in such significant impairments (Bisdorff et al., 1996; Ito and Gresty, 1996; Anastasopoulos et al., 1999; Bringoux et al., 2002) In this case, compensatory processes, mainly based on vision (Bronstein et al., 1996; Guerraz et al., 2001; Lopez et al., 2007) and possibly on somatosensory signals, may also account for the preserved perception of spatial orientation.

Less is known regarding the consequences of somatosensory loss on the perception of spatial orientation, although its influence has been extensively studied in the context of motor control (Rothwell et al., 1982; Sanes et al., 1984; Sainburg et al., 1993; Sarlegna et al., 2010). Stroke patients suffering single-hemisphere somatosensory lesions exhibit a substantial bias during SVV adjustments toward the hypoesthetic side (Anastasopoulos et al., 1999) and adjustments are also more variable (Barra et al., 2010; Saeys et al., 2012). On the other hand, only severe hemihypoesthesia biases the subjective postural vertical (SPV), that is the alignment of whole-body orientation with the gravitational vertical (Anastasopoulos et al., 1999). In the same vein, a peripheral and symmetric somatosensory loss did not prevent the control of sitting posture without back-support (Blouin et al., 2007) suggesting that vestibulo-spinal pathways remain sufficient to control body posture without touch and proprioception.

The purpose of the present study was to assess the perception of spatial orientation in a rare case of massive yet selective somatosensory deafferentation. Such a sensory deficit raises the issue of compensatory mechanisms when only visual or vestibular inputs remain available for spatial perception. In line with recent models of multisensory integration, the remaining cues following sensory deficit should be reweighted according to their noise properties and processed with priors that the patients may have built with experience and perceptual expectancies (Vingerhoets et al., 2009; Clemens et al., 2011). In the present study, a well-characterized deafferented patient (GL; Forget and Lamarre, 1987; Blouin et al., 1995; Sarlegna et al., 2010) was compared to age-matched subjects in two spatial orientation tasks involving gravity-related judgments. First, the perception of object/external orientation was addressed through a SVV task in which participants had to align a rod with the gravitational vertical while visual surroundings could be tilted (i.e., portable Rod-and-frame Test [RFT], Oltman, 1968). Second, the perception of body/self orientation was investigated through a self-tilt detection task in which participants had to judge whether they felt tilted forward from vertical while facing different visuo-postural conditions, as in our previous work on healthy young participants (Scotto Di Cesare et al., 2014). Comparing the results in these two experimental tasks enabled us to investigate whether compensatory processes following somatosensory loss, if any, could generalize to different spatial perception tasks. Overall, we expected that the patient with a massive somatosensory loss would exhibit a greater reliance on visual and/or vestibular cues compared to Controls.

MATERIALS AND METHODS

Participants

One 65-year-old somatosensory-deafferented patient and 8 healthy, age-matched "Controls" (5 females and 3 males; mean age ± SD: 65.2 ± 4.6 years) participated in this study. All the subjects were naive to the specific purpose of the experiment, which was approved by the institutional review board of the Institute of Movement Sciences. They gave their informed consent prior to the study, in accordance with the ethical standards set out in the 1964 Declaration of Helsinki. Participants were self-declared right-handed and had normal or corrected-to-normal vision. Stereoscopic vision was checked using the Randot Stereotest®, with all individual scores greater than 70 s of arc. None of the Controls had any relevant medical history as no neurological or sensorimotor disorder was reported. The deafferented patient, known as GL, had two severe episodes of extensive polyneuropathy (at the ages of 27 and 31 years) affecting her whole body below the nose (for detailed descriptions, see Forget and Lamarre, 1987; Cole and Paillard, 1995; Sarlegna et al., 2010). Clinical tests revealed a specific loss of large-diameter, myelinated Aβ afferents which resulted in a complete loss of touch, vibration, pressure, tendon reflexes, and sense of movement and position in the four limbs, the trunk being moderately affected. Tests carried out in the ENT Department (Clairval, Marseille) showed that her vestibular function is preserved, in accordance with previous reports (Cole and Paillard, 1995; Guillaud et al., 2011). Similarly, according to tests performed in the Ophthalmology Department (La Timone, Marseille), no deficit in visual acuity and perimetry was found.

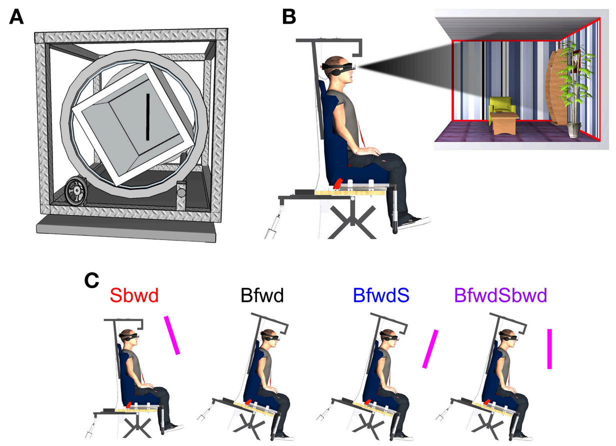

FIGURE 1 | (A) Illustration of the portable rod-and-frame apparatus (RFT) replicated from Oltman (1968). **(B)** The tilting chair and the visual scene projected in the Head-Mounted Display. **(C)** Experimental conditions manipulated in the self-tilt detection session. ***Sbwd***: backward rotation of the visual scene (top toward the subject) without body rotation; ***Bfwd***: forward rotation of the body without any visual scene; ***BfwdS***: forward body rotation with a visual scene remaining static relative to the subject; ***BfwdSbwd***: forward body rotation with backward visual scene rotation relative to the subject.

Experimental Setup

Apparatus for the Rod-and-Frame Test (RFT)

In the first part of the experiment (RFT session), we used a replication of the portable RFT apparatus developed by Oltman (1968) to measure SVV estimates while visual surroundings were tilted. The device was composed of a box (57 cm deep × 31 cm wide × 31 cm high) made of translucent white surfaces whose inside edges and corners were marked by black lines (**Figure 1A**). Subjects were seated upright so that their face was aligned with the front, open edge of the box (the center of the box corresponding to their straight ahead). From this open edge, subjects could not see the outer environment and could only see inside the box, in particular the black square frame and a black rod at the opposite end (apparent size of the square: ~30.5°). The bright interior of the box was shadowless and no orientation cues from external lighting were available. The whole box, and thus the frame, could be tilted by the experimenter at different roll orientations. A black rod (1 cm large and 30 cm long; apparent length: ~29.5°) could be rotated around the center of the frame by the subject or by the experimenter via independent hand-levers. A protractor, fixed on a disc mounted at the rear of the box and visible only to the experimenter, indicated the deviation of the frame and the rod from gravitational vertical. Subjects' eye level coincided with the axis of rotation of the rod and the frame. Their head was stabilized with a chin-rest and a head-rest.

Tilting Chair and Virtual Reality Head-Mounted Display

In the second part of the experiment (Self-tilt detection session), subjects were seated and firmly attached to a tilting chair with a 6-point seatbelt. The tilting chair could be rotated in pitch, around an axis positioned under the seat (**Figure 1B**). The rotation was produced by lengthening/shortening an electric jack (Phoenix Mecano®, thrust: 3 kN, clearance: 0.6 m, precision 0.12 mm) attached to the back of the seat. The angular profile of the tilt was servo-assisted using an inclinometer fixed to the chair (AccuStar®; resolution: 0.1°; range: ±60°). Throughout the trials, earphones provided white noise to mask any auditory cues. Two push buttons (one per hand) were used to record subjects' response about self-tilt perception.

A 3D head-mounted display (HMD, 3D Cybermind hi-Res9001®; resolution: 800 × 600 pixels; field of view: 31.2° diagonal for each eye) was fixed onto a headrest attached to the seat. This headrest was adjustable in height to the subjects' size. The HMD was used to display a stereoscopic 3D visual scene composed of a fully furnished and polarized room (3 m wide × 6 m long × 2.25 m high, **Figure 1B**). The distance of the virtual scene front from subjects' eye in the transverse plane was set at 1.7 m, such that it remained fully visible according to the HMD field of view. The virtual scene could rotate in pitch around the same axis as the rotating chair. The HMD device prevented subjects from viewing the experimental setup and their actual body configuration with respect to the external space. A real-time acquisition system (ADwin-Pro®) running at 10 kHz and a customized software (Docometre®) were used to synchronously record subjects' responses and control the HMD visual background and/or chair rotations.

Procedure

RFT Session

Participants were first asked to perform SVV judgments in a classic RFT procedure. Specifically, they had to align a tilted rod along the gravitational vertical when facing a visual frame. The frame orientation was modified according to a standardized order (Isableu et al., 1997; Bringoux et al., 2009; Scotto Di Cesare et al., 2015): 0°, −18°, +18°, −8°, +8°, −28°, +28°, −38°, +38°, 0° positive values indicate rightward tilts while negative values indicate leftward tilts relative to the gravitational vertical). For each of the 9 frame orientations, 2 trials were performed with initial rod orientations alternatively set right or left at a magnitude ranging from ±10° to ±50° relative to vertical.

Prior to the session, instructions were given to the subjects: special attention was given to the definition of "gravitational vertical" using verbal explanations and sketches. Subjects were required to keep their eyes closed throughout the session except when they were explicitly asked to align the rod with the gravitational vertical. To that end, Controls rotated a hand-lever allowing them to adjust rod orientation with their unseen left hand, while GL, who was unable to manipulate the hand-lever without vision, gave verbal instructions to the experimenter for setting the rod at the desired orientation (e.g., further left, or further right). Pre-tests confirmed that both response modes yielded similar results on SVV settings. When participants were satisfied about their judgment, they verbally informed the experimenter and closed their eyes until the next trial. Overall, this RFT session comprised 36 trials and lasted 20 min on average. It was repeated twice for GL, before and after the self-tilt detection session, to verify responses' consistency, which is well established in healthy subjects (Bergman, 1979).

Self-Tilt Detection Session

In this second experimental session, participants, seating on the tilting chair, were asked to indicate whether they felt being tilted forward (that is, away from the gravitational vertical). Specifically, they were forced to either answer: "Yes (I feel tilted forward)" or "No (I do not feel tilted forward)." Controls had to respond either with the left or right hand-held push button, which corresponded to Yes and No respectively, while GL, who could not use push-buttons with her unseen hands, was instructed to verbally give her response "Yes" or "No."

Each trial began with the chair and the visual scene aligned with the gravitational vertical (i.e., upright). The chair and/or the visual scene rotated up to 18° at $0.05°s^{-1}$ following a 10 s acceleration phase at $0.005°s^{-2}$, below the threshold for semicircular canals stimulation (Benson, 1990). Subjective responses were prompted by an auditory tone at each degree of tilt, i.e., every 20 s. At the end of the trial, participants were asked to close their eyes, and the chair was brought back to vertical if it actually had moved. The chair rotation back to vertical varied in terms of kinematics, so that the subjects could not infer the angle of tilt previously reached. Between trials, the HMD was removed and a period of rest in full ambient light, during at least 1 min, was consistently provided before the next trial started. This resting period was used to suppress post-rotational effects and to limit possible fatigue.

In this self-tilt detection session, four experimental conditions were presented (**Figure 1C**; see also Scotto Di Cesare et al., 2015): ***Sbwd***: backward rotation of the visual scene (top toward the subject) without body rotation; ***Bfwd***: forward rotation of the body without any visual scene; ***BfwdS***: forward body rotation with a visual scene remaining static relative to the subject; ***BfwdSbwd***: forward body rotation with backward visual scene rotation relative to the subject. All subjects performed 3 trials in each of the 4 aforementioned conditions, which were presented in a pseudo-random, counterbalanced order, to avoid any potential learning effect. A training phase without body and/or visual scene rotation was provided before the data collection actually started, to familiarize subjects with the task. Two catch trials without effective body and scene tilt were randomly inserted in the session, to further assess the reliability of subjects' estimates. The whole experimental session lasted about 2 h.

Data Analysis

From the RFT session, we analyzed the SVV measures for each frame orientation and computed the mean RFT score for each subject according to the classic Nyborg and Isaksen's method (Nyborg and Isaksen, 1974), following the equation:

$$RFTscore = \sum \mathrm{Err}(R)/R - \sum \mathrm{Err}(T)/T$$

"$\mathrm{Err}(R)$" is the signed error recorded when the frame was tilted 18° rightward; "R" is the number of rightward frame tilts; "$\mathrm{Err}(T)$" is the mean signed error recorded at 18° of both rightward and leftward frame tilts; "T" is the total number of rightward and leftward frame tilts.

From the Self-tilt detection session, individual thresholds were determined for each experimental condition. Responses were converted into binary values, with "1" corresponding to the response "Yes, I feel being tilted forward" and "0" to the response "No, I do not feel being tilted forward." A Probit model, using a non-linear regression analysis for binomial values (least square fitting) was applied to the data in order to determine the threshold corresponding to 50% of probability of expressing the feeling of being tilted (**Figure 2**).

The Probit function was defined as follows:

$$Pi = \frac{1}{1 + \left(\frac{At}{T}\right)^{b}}$$

"P" is the probability in expressing the feeling of being tilted for a given condition "I." "At" corresponds to the angle of tilt during this condition and "T" to the self-tilt detection threshold for this condition (i.e., angle of tilt for $P = 0.5$). "b" is the slope of the tangent of the curve at its inflection point and constitutes an estimate of the discrimination sensitivity relative to the chosen increments.

To compare GL's data to those of Controls in the RFT session, *t*-test comparisons of a single value to a population sample were used (Sarlegna et al., 2010). In the self-tilt detection session, mean data of Controls across conditions were compared using a one-way repeated measures analysis of variance (ANOVA) and appropriate *post-hoc* comparisons (i.e., Newman-Keuls tests) since data respected normality assumption (i.e., Lilliefors tests).

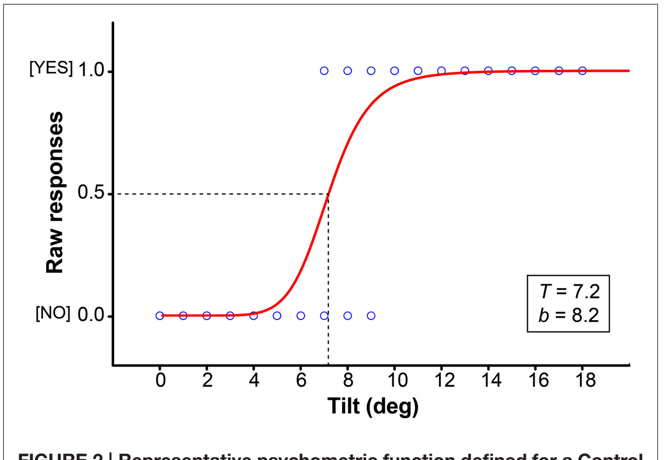

FIGURE 2 | Representative psychometric function defined for a Control subject in a typical trial (e.g., *Bfwd* condition). A non-linear regression (Probit) was applied to the raw judgments to define a threshold for self-tilt detection.

In this session, GL performance was evaluated with respect to the mean ±95% confidence intervals characterizing Controls' performance in each condition. For all tests, the significance threshold was set at 0.05.

RESULTS

Rod-and-Frame Test (RFT)

Figure 3A illustrates the mean SVV settings (i.e., mean signed errors in rod adjustment relative to gravitational vertical) for the deafferented patient GL and age-matched Controls as a function of frame tilt. Beyond the usual between-subjects variability, Controls exhibited typical sinusoidal SVV profiles characterizing a classic "frame effect" (e.g., Bringoux et al., 2009). Their maximal SVV deviations away from the vertical, and thus toward the tilted frame, were recorded for ±18° or ±28° of tilt, while their adjustments tended to become closer to vertical for smaller (i.e., ± 8°) or larger frame tilts (i.e., ±38°, close to a diagonal frame). Both Controls and GL were particularly accurate for SVV settings when facing a non-tilted frame (i.e., less than 1° of error on average for a 0° frame orientation). One of the main findings of the present study is that GL estimates drastically differed from those of Controls when the frame was tilted (See **Table 1** for statistical comparisons between GL and Controls at each frame tilt magnitude). Her SVV adjustments were almost systematically equal to the angle of frame tilt (see video in Supplementary Materials), even at the largest tilts (i.e., ±38°). This was observed in both RFTs performed by GL before and after the self-tilt detection session (**Figure 3A**).

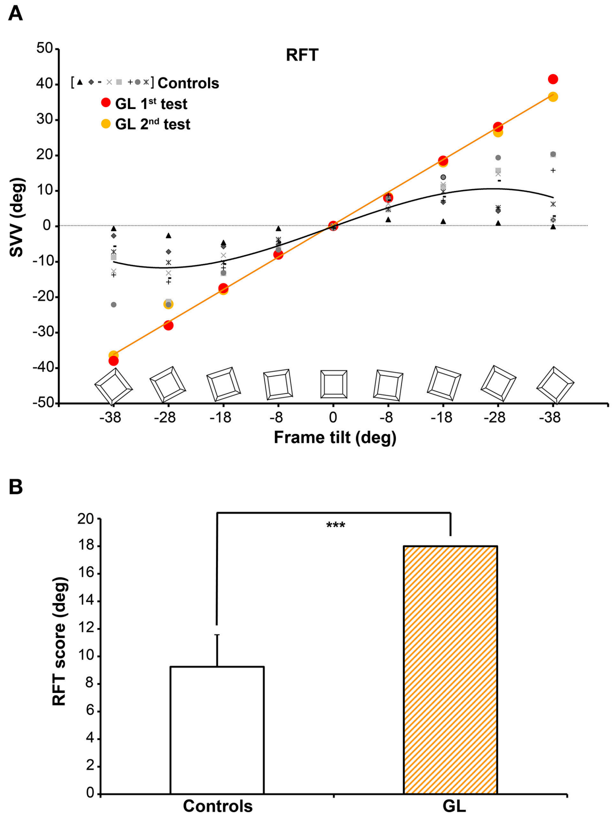

FIGURE 3 | (A) SVV settings as a function of frame tilt in the RFT session for Controls. Each symbol represents a given subject. While SVV classic sinusoidal modulations as a function of frame tilt magnitude were observed for Controls ($y = -0.0003x^3 - 0.0006x^2 + 0.62x - 0.08$; $R^2 = 0.99$), SVV estimates corresponded ~100% to the frame orientation for the deafferented patient ($y = 0.98x + 0.52$; $R^2 = 1.00$). **(B)** Mean RFT scores obtained for Controls and the deafferented patient GL. Since 0° score corresponds to extreme visual field independence and 18° score corresponds to extreme visual field dependence, this figure shows that the deafferented patient is entirely field dependent according to RFT classification. Error bars for Controls data represent 95% confidence interval. ***$p < 0.001$.

A further quantitative analysis of the frame effect revealed that despite the high RFT score obtained for Controls (see Scotto Di Cesare et al., 2015 for a comparison with younger adults), GL score, averaged across the two repetitions, was even higher than that of Controls [$t_{(8)} = -7.49$; $p < 0.001$]. GL score was indeed largely beyond the 95% confidence interval of the Controls score, as illustrated in **Figure 3B**. GL score (18°) actually corresponded to the orientation of the visual frame, meaning that she exhibited full visual field dependence for the perception of object orientation.

Self-Tilt Detection Threshold

Overall, although the task was considered difficult by the subjects, the perceptual transitions in the feeling of being tilted -when existing- appeared relatively suddenly in almost all trials. Furthermore, subjects never reported any self-tilt sensation during the catch trials, suggesting that they were compliant with the task requirements.

Among all the trials carried out by Controls, few of them led to no self-tilt sensation (***Sbwd***: 8/24: ***Bfwd***: 0/24; ***BfwdS***: 2/24; ***BfwdSbwd***: 1/24). The consistency of the self-tilt detection sensitivity across conditions was analyzed for Controls using a 4-condition repeated-measures ANOVA on the "b" values of the Probit functions. This analysis did not reveal any significant difference between the discrimination sensitivity across conditions ("b" *[Mean ± SD]* = 6.3 ± 3.5; $F_{(3,\ 12)} = 1.03$; $p = 0.42$).

The ANOVA on the mean self-tilt detection thresholds for Controls revealed a significant effect of experimental conditions [$F_{(3,\ 21)} = 3.43$; $p < 0.05$; **Figure 4**]. *Post-hoc* analysis revealed that the threshold was significantly higher when the visual scene alone was rotated (***Sbwd*** = 12.6°), as compared to when the body alone was rotated (***Bfwd*** = 7.3°; $p < 0.05$) or when both the body and the visual scene were rotated (***BfwdSbwd*** = 5.9°; $p < 0.05$).

Most importantly and as a core result, GL' self-tilt detection threshold differed from that of Controls in all conditions, since that the patient never reported any self-tilt sensation, in any trial of any condition (see video in Supplementary Materials). The maximal angle of tilt we manipulated (18°), up to which GL never felt tilted, was out of the 95% Confidence Intervals calculated on the threshold values for Controls in the 4 experimental conditions (**Figure 4**). In contrast to Controls, visual scene manipulation had no influence on GL self-tilt detection and none of the -extremely slow- physical tilt up to 18° (i.e., ***Bfwd***, ***BfwdS***,

TABLE 1 | Rod and Frame Test.

	Controls		GL					
Frame tilt	$\overline{X}$	+/−95% CI	$\overline{X}$ 1st Test	Statistical comparison		$\overline{X}$ 2nd Test	Statistical comparison	
				t	p		t	p
−38°	−9.2	[−15.0/−3.4]	−38.0	11.82	<0.001	−36.5	11.20	<0.001
−28°	−13.4	[−18.9/−7.8]	−28.0	6.21	<0.001	−22	3.66	<0.01
−18°	−9.7	[−12.4/−7.0]	−17.5	6.79	<0.001	−18	7.22	<0.001
−8°	−4.4	[−6.0/−2.9]	−8	5.42	<0.001	−8	5.42	<0.001
0°	−0.1	[−0.4/0.2]	−0.25	1.18	ns	0.0	−1.00	ns
8°	5.8	[4.0/7.7]	8.0	-2.80	<0.05	8.25	−3.12	<0.05
18°	8.8	[5.6/12.0]	18.5	-7.15	<0.001	18	−6.78	<0.001
28°	9.8	[4.2/15.4]	28.0	-7.71	<0.001	26.5	−7.07	<0.001
38°	8.6	[1.3/15.9]	41.5	-10.67	<0.001	36.5	−9.05	<0.001

Statistical report for mean Subjective Vertical comparisons between Controls and GL estimates at each frame tilt.

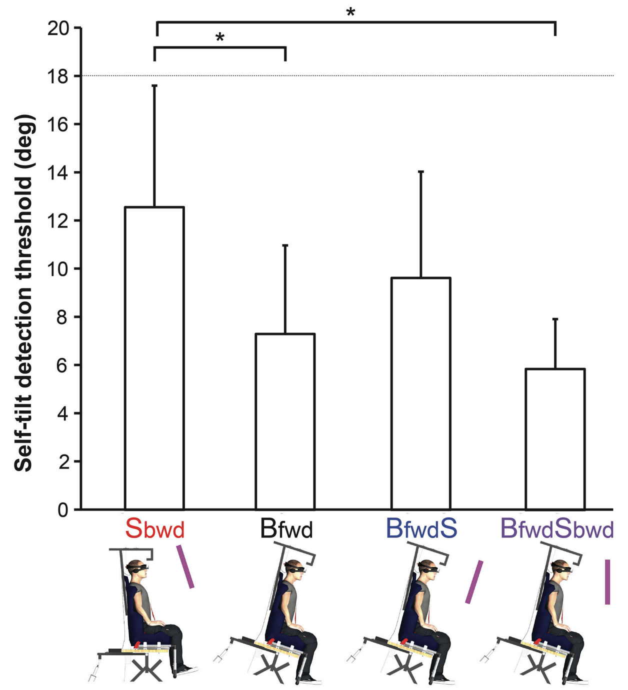

FIGURE 4 | Mean self-tilt detection thresholds as a function of experimental conditions for controls. The deafferented patient never felt any tilt up to the largest tilt angle (dashed line) across the different trials in all the conditions she was exposed to. Error bars represent 95% confidence intervals. *$p < 0.05$.

BfwdSbwd) evoked a self-tilt sensation for the deafferented patient.

DISCUSSION

The present study aimed at investigating whether a massive loss of somatosensory inputs may drastically change the perception of spatial orientation. By testing external (object) orientation and self-orientation perception of a deafferented patient (GL), we expected to highlight compensatory processes based on visual or vestibular inputs. GL's perception of external orientation, investigated by SVV judgments in a RFT, was found to strikingly depend on visual inputs. However, for self-orientation perception, GL never felt being tilted during slow tilts of the visual scene, her body or a combination of both up to 18°, contrary to healthy Controls who were able to detect changes in self-orientation relative to vertical. Overall this study demonstrates that critical somatosensory deficit yields substantial impairments in spatial orientation perception, and that the use of the remaining sensory inputs available to a deafferented patient differs regarding whether the estimate concerns external vs. self-orientation. The implication of these findings will be discussed in the following sections.

Self- vs. External Orientation Perception: Different Contributions of Vision

For external orientation perception, the deafferented patient GL seemed to exclusively refer to vision, as her SVV estimates were fully biased by the frame tilts. Between +38° and −38° of tilt, mean responses from the patient almost differed by 80° (contrary to Controls who tended to better align their SV with gravity at these large angles). It is possible that the systematic succession of left and right presentations of frame tilt led to strong expectations relative to the main direction of the -anchoring- visual reference for GL. In addition, the slight but existing asymmetry between the orientation of the frame sides (bottom/up vs. left/right) relative to the longitudinal body axis at ±38°, may have also helped GL determine the main visual axis of reference for orientation (i.e., the closest lines of the frame relative to her idiotropic axis constituting the directional reference for her judgments). Overall, the key finding in the RFT session is that GL completely relies on the main orientation of the visual frame to perform her SVV estimates, contrary to Controls.

This is in line with previous work highlighting the reliance of deafferented patients on vision for motor control (Rothwell et al., 1982; Blouin et al., 1993; Sarlegna et al., 2010). It is also coherent with other findings which reported greater visual field dependence in people suffering from Parkinson's disease, also known to alter somatosensory processing (Azulay et al., 2002). The prominent role of vision in the perception of spatial orientation is well established. Pioneer studies (Asch and Witkin, 1948; Witkin and Asch, 1948) first attempted to quantify this visual influence upon the perception of object orientation by asking observers to adjust a rod surrounded by a tilted frame at the gravitational vertical (i.e., RFT). While the orientation of the visual frame consistently influences some subjects (i.e., field-dependent subjects, FD), others remain relatively immune to visual cues (i.e., field-independent subjects, FI). According to a general assumption, FD subjects are supposed to rely less on gravity-related vestibular and/or somatosensory inputs, as compared to FI subjects (Isableu et al., 2010). In line with this idea, the fact that the deafferented patient fully relied on visual cues for setting a rod to the vertical suggests that she may not use gravity-related vestibular cues for the perception of external orientation.

Surprisingly, in the self-tilt detection task, GL did not use visual orientation cues from the surroundings. This shows that visual dependence, defined on the basis of SVV judgments in a RFT session, does not necessarily extend to a self-orientation perception task. This is consistent with previous studies which investigated the generalization of field dependence across spatial perceptual abilities and demonstrated that the classification of FD/FI subjects based on RFT may be invalid in other spatial judgments (Barnett-Cowan et al., 2010; Scotto Di Cesare et al., 2015). Indeed, perceptual upright estimates when tilted (Barnett-Cowan et al., 2010) or self-tilt detection involving slow changes in postural cues (Scotto Di Cesare et al., 2015) were not significantly related to FD/FI categorization issued from RFT. Overall, these data highlight a clear dissociation between self-orientation perception and external orientation perception. This gives additional support to the view that judging postural orientation and judging object orientation rely on distinct sensory integration processes (Bronstein, 1999).

Are Gravity-Related Vestibular Cues of Any Help for Orientation Perception?

The present findings showed that visual orientation cues were not used by the deafferented patient for self-orientation perception. Based on current theories on cross-modal plasticity (Auvray and Harris, 2014), one could expect that vestibular cues could take over the lack of visual contribution in the self-tilt detection task. Surprisingly, the results of the deafferented patient did not confirm a greater use of vestibular inputs for self-orientation perception compared to healthy controls. Although the very slow body tilts prevented any motion sensation issued from the semi-circular canals (Benson, 1990), the otoliths, usually presented as gravity-sensitive organs (Goldberg and Fernandez, 1984), remained susceptible to convey informative cues about whole-body orientation. That GL is able to use vestibular system has been shown in previous studies investigating sensorimotor processes (vestibulo-ocular: Blouin et al., 1995; vestibulospinal: Blouin et al., 2007). Therefore, the fact that GL was never able to detect self-tilt up to 18° may mainly result from her inefficiency to calibrate changes in vestibular inputs at a perceptual level. Similar conclusions have been drawn by Blouin et al. (1995) who investigated magnitude estimates of passive whole-body rotations in yaw with the same deafferented patient. The inefficiency of using vestibular inputs for slow self-tilt detection may not be specific to a deafferented patient however, since healthy subjects embedded in a full body cast were also greatly impaired in perceiving very slow body tilts on the sole basis of their remaining otolith inputs (Bringoux et al., 2003). Overall, our findings strongly suggest that isolated otolith signals cannot be considered as an accurate source of graviception at a perceptual level.

Previous findings have stressed that otolith sensitivity to dynamic stimuli is greater than to static ones, outlining the importance of the rate of change of the vestibular afferent information (Gianna et al., 1996). Also, the phase response of the vestibular neurons in the brain stem (Angelaki et al., 2004) or in the parieto-insular vestibular cortex (Chen et al., 2010) has been reported to span from jerk to velocity (i.e., no signal of position). Furthermore, the vestibular system rarely works alone (Barnett-Cowan, 2013) and may require other sensory signals to be interpreted at a perceptual level. In line with this idea, primary as well as secondary afferent vestibular projections are known to merge with other sensory inputs in several brain areas (e.g., vestibular nuclei, Jamali et al., 2014; Parieto-Insular Vestibular Cortex, Lopez and Blanke, 2011) to solve stimulus ambiguity and help signal interpretation. Additional studies are thus necessary to test the hypothesis that the deafferented patient may use vestibular inputs mostly as a trigger for motion perception, when the change in the stimulus is highly noticeable and possibly requires fast decisional reactions.

Sensory Compensation vs. Reference Frame Selection

The extreme visual dependence observed for the deafferented patient GL in the RFT session may illustrate the prominent role of vision for compensating somatosensory loss when judging the orientation of external objects. Alternatively, this may also reflect the exclusive use of an allocentric frame of reference (i.e., here relative to visual surroundings) for coding the orientation of objects (Howard, 1982; Bringoux et al., 2009; see also Blouin et al., 1993). In the self-tilt detection session however, both visual and vestibular cues were not used by the patient, demonstrating that there was no sensory compensation at work for GL when considering self-orientation perception. It may also suggest that the task was performed neither in an allocentric nor in a geocentric (i.e., gravity-related) frame of reference.

Previous studies have already highlighted the involvement of an egocentric frame of reference for spatial orientation perception, even when the task requires the judgments to be performed relative to external references (Coleman and Durgin, 2014). For instance, estimates of the subjective horizon (i.e., the plane orthogonal to gravity passing through the eyes) were found to be linearly biased as a function of the magnitude of head or body pitch tilt (Bringoux et al., 2007; Bourrelly et al., 2014). According to the pioneer work of Mittelstaedt (1983), the longitudinal body axis could also define an "idiotropic vector" toward which vertical estimates are attracted, particularly when the body is tilted. In line with this interpretation, some more recent data support the existence of prior estimates for upright perception, based on the idiotropic vector (MacNeilage et al., 2007, 2008; De Vrijer et al., 2008; Vingerhoets et al., 2009; Clemens et al., 2011), that could become critical under unusual sensory contexts (i.e., microgravity). Here we postulate that somatosensory loss may considerably enhance the "prior for upright" as a reference for self-orientation perception. This may have led the deafferented patient to ignore slow-changing information for judging her body orientation. In other words, the absence of somatosensory inputs could increase perceptual state expectations of being upright during self-tilt detection at slow velocities.

Our data also fit with models using Bayesian rules that may operate on sensory reweighting processes and particularly with predictions based on the noise properties of the sensory modalities involved in spatial orientation (Vingerhoets et al., 2009; Clemens et al., 2011). Specifically, due to the noise level of body sensors, Clemens et al. (2011) predicted large errors in subjective body tilt and subjective visual vertical for patients with somatosensory loss, even though the otolith signal is accurate. This is exactly what we found in this study.

CONCLUSION

The present findings showed that sensory compensation following somatosensory loss is present for external orientation perception, but is lacking for self-orientation perception. Clearly, the massive loss of somatosensory inputs resulted in a complete reliance on vision for the perception of object's verticality. However, visual and vestibular inputs are inefficient to provide relevant information for self-tilt detection at slow velocities. The role of sensory expectations and priors (Summerfield and de Lange, 2014) could be here critical in the reference frame selection, in particular for self-orientation perception. Yet, the way sensory integration may interact with central predictions of the actual perceptual state needs to be further investigated, notably in patients with sensory impairments.

AUTHOR CONTRIBUTIONS

LB designed and performed experiments, analyzed data and wrote the paper; CS designed and performed experiments, and wrote the paper; LB wrote the paper; TM performed experiments; FS designed experiments and wrote the paper.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: http://journal.frontiersin.org/article/10.3389/fnhum.2016.00181

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RESEARCH ARTICLES

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Influence of whole-body pitch tilt and kinesthetic cues on the perceived gravity-referenced eye level

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Abstract We investigated the effects of whole body tilt and lifting the arm against gravity on perceptual estimates of the Gravity-Referenced Eye Level (GREL), which corresponds to the subjective earth-referenced horizon. The results showed that the perceived GREL was influenced by body tilt, that is, lowered with forward tilt and elevated with backward tilt of the body. GREL estimates obtained by arm movements without vision were more biased by whole-body tilt than purely visual estimates. Strikingly, visual GREL estimates became more dependent on whole-body tilt when the indication of level was obtained by arm lifting. These findings indicate that active motor involvement and/or the addition of kinesthetic information increases the body tilt-induced bias when making GREL judgements. The introduction of motor/kinaesthetic cues may induce a switch from a semi-geocentric to a more egocentric frame of reference. This result challenges the assumption that combining non-conflicting multiple sensory inputs and/or using inter-modal information provided during action should improve perceptual performance.

Keywords Perception · Horizon · Body orientation · Kinesthetic system · Frame of reference

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Introduction

The perceived eye level is commonly considered as a cardinal reference for distance judgement (Ooi et al. 2001) and for up and down egocentric location (Li et al. 2001; Matin and Li 1995). For instance, when observers in complete darkness state that a luminous visual object appears to be higher or lower than themselves, location is specified to their perception of their own eye level (Raphel and Barraud 1994; Stoper and Cohen 1989). However, in the simplest circumstances, "eye level" can be referred to a plane parallel to the transverse plane of the head (i.e. head-referenced eye level, HREL), or normal to the direction of gravity (i.e. gravity-referenced eye level, GREL; Stoper and Cohen 1989). It should be noted that these planes are coincident when the observer is stationary and erect, but differ when the observer is tilted forward or backward.

Whereas HREL judgements can be assessed in a purely egocentric frame of reference, GREL estimates require to adjust the perceived horizontal direction to eye level, that is to link an external system of coordinates with an egocentric component (Howard 1986). Consequently, the nature of the task, for instance, asking a subject to look "straight ahead" (i.e. HREL judgement) or to look at the "earth horizon" (i.e. GREL judgement) would certainly lead to different results when the body is tilted. Similarly, purely geocentric tasks such as subjective visual vertical or horizontal estimates in the pitch plane (Correia et al. 1968; Ebenholtz 1970) cannot directly be compared to GREL judgements, since they did not specifically rely on eye level (i.e. egocentric component). Nevertheless, any environmental influence on GREL estimates will have important repercussions in the perception of the external space.

This paper aims then at investigating the perception of GREL for different whole-body pitch orientations and under different sensorimotor conditions.

It has been shown that the visually perceived GREL in darkness when the head is upright is lower than the true eye level (i.e. the physical plane passing through the eyes and normal to gravity; Raphel and Barraud 1994), but remains nevertheless highly consistent and accurate (Mc Dougall 1903; Stoper and Cohen 1986). Pitching of the visual environment largely influences GREL estimates with respect to true eye level, from 12 deg downward for 20° forward tilts of the visual field to 11 deg backward for 20° backward tilts of the visual field (Matin and Li 1992). However, this effect is independent of the pitch head orientation over a ±20° range.

Schöne (1964) investigated the influence of different head and body pitch orientations on the GREL perception in darkness under different gravity field strengths. To that purpose, subjects sat in a swing-out centrifuge, able to generate gravitational force levels from 1 to 1.9 g. Head and body pitch position ranged from 30° backward to 20° forward. Judgements were found to be highly modified by body tilt under increased field strength. For instance, GREL estimates varied from about 15 deg upward for −20° backward body tilts to 10 deg downward for 20° forward body tilts under 1.6 g. However, as mentioned by the author himself, the GREL in normogravity was perceived "approximately correctly" within the tested range of body tilt. It should be pointed out, however, that the axis scale of the reported figures in this paper were chosen for representing the large effects of hypergravity on GREL estimates, but could have hidden any weaker potential effects under 1 g. Moreover, GREL values at different tilts under 1 g were not statistically analysed in that study.

On the other hand, a recent experiment suggests that GREL perception is influenced by pitch head orientation in complete darkness when the subject's whole-body is slowly rotated (Bourdin et al. 2001). In that situation, the absolute errors in visually adjusting the GREL are directly proportional to the up-to-8° pitch tilt. The shifts in GREL estimates induced by body tilt might have been the consequence of head tilt underestimation due to the extremely slow pattern of rotation ($\omega = 0.05°.s^{-1}$), well below the semicircular canals' threshold (Benson 1990). The first purpose of the present study is thus to investigate whether a comparable GREL perceptual shift can be induced by suprathreshold whole-body rotations to greater angles of pitch tilt.

The second aspect of this work relates to the fact that most experiments involving visual GREL settings were carried out through passive assessments with immobilised subjects, in spite of the fact that numerous studies have shown that action can improve perception (cf. Viviani 1990, for a review). In this respect, Ballinger (1988) investigated the effect of pointing movements on the visually perceived GREL in upright subjects facing a tilted visual field. The magnitude of the mean pointing error due to the tilted visual field was approximately half of the magnitude of the mean error assessed verbally. However, the subjects were not successful at pointing to eye level when they could not see their hand in relation to their surroundings. Fouque et al. (1999) investigated the influence of motor-kinesthetic involvement on the visually perceived HREL (i.e. egocentric judgement) for different whole-body pitch tilts. Comparing passive estimates with pointing errors towards remembered targets located at HREL, the authors concluded that the action of pointing improves the accuracy of judging eye level. However, the presence of a conflicting visual field for HREL passive estimates (e.g. upright visual field with body tilted or vice versa) as well as the difference of task between passive and active conditions (i.e. adjusting a target at a certain height vs. pointing towards a flashed memorized target) might have led to such results.

Nevertheless, recent data suggested that arm lifting movements do provide information about orientation in space by generating additional cues about the direction of gravity (Gooey et al. 2000; Luyat et al. 2001). For instance, the dynamic gravitational torque generated by arm lifting movements may be involved in limb position sense in space (Bock 1994; Gooey et al. 2000; Worringham and Stelmach 1985) and may improve a more general geocentric perception about the direction of gravity (Fitger 1976; Gentaz and Hatwell 1996; Luyat et al. 2001), the latter being involved in GREL judgements (Stoper and Cohen 1989). The second purpose of the present study is then to investigate whether judgements made with active arm lifting movements (i.e. "motor-kinesthetic involvement") can lead to increased accuracy of GREL estimates performed during whole-body tilts.

Herewith we report two experiments, for which we hypothesized that the perceptual GREL estimates would be influenced by whole-body tilt as well as by the method of assessment (i.e. the use of arm movement). More precisely, we expected that large body pitch tilts would lead to a consistent perceptual shift of the GREL in the direction of tilt, which could be attenuated when the moving arm is involved in the judgement.

Material and methods

Subjects

A total of 17 healthy subjects gave informed consent to participate in the present study according to local ethic committee guidance and the Helsinki convention. Ten subjects (five males and five females ranging from 22 to 48 years, mean age = 28±5.7 years) took part in Experiment 1. Three of them also took part in Experiment 2, together with seven new subjects (six males and four females ranging from 22 to 51 years, mean age = 32 years).

Apparatus

The subjects were seated and tightly restrained in a padded chair with a four-points pilot seat belt (Fig. 1A). The chair was supported between bearings within an earth fixed supporting frame and its position could be adjusted so that the subjects' trans-ocular axis coincided with its axis of rotation. The chair was motorized and rotated slowly in pitch. The subjects' head, oriented in the natural upright position when the plane of the seat back was parallel to the gravitational vertical, was firmly restrained by a headrest and a bite bar fixed to the chair frame. Backward and forward tilts were delivered at a constant velocity of 1.5 $deg.s^{-1}$, with initial accelerations and final decelerations (1.5 $deg.s^{-2}$) above the semicircular canals' threshold (Benson 1990).

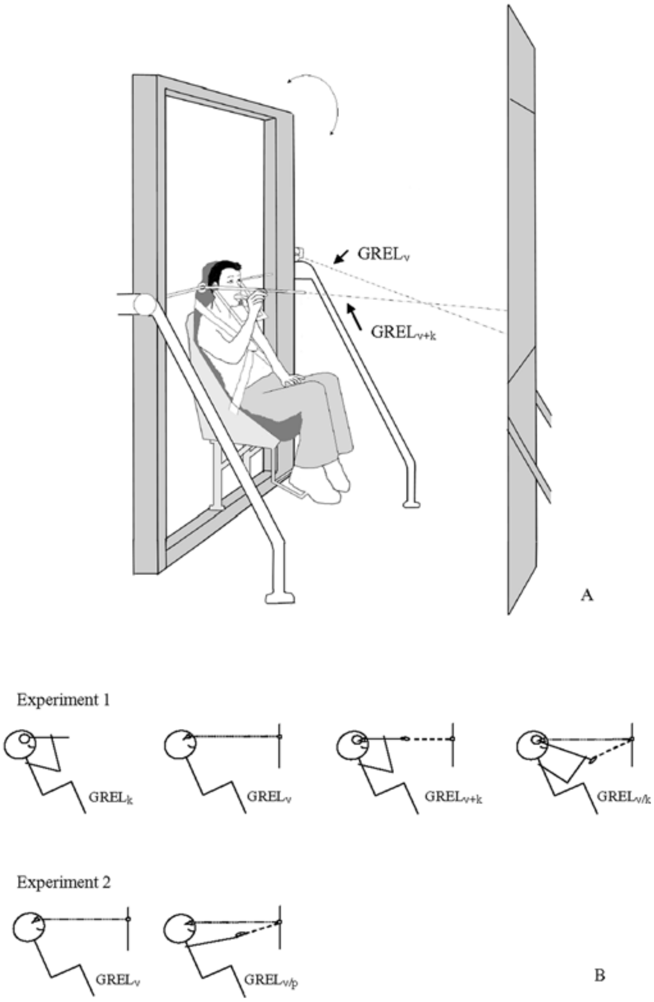


Fig. 1. A Illustration of the experimental setup. The motorized chair rotated around the inter-ocular axis. **B** Schematic representation of the experimental conditions tested in the two experiments

In Experiment 1, GREL estimates were performed by manually adjusting the orientation of a tilting rod, pivoted at eye level, or by setting the height of a small adjustable laser dot projected on a board placed at 1.5 m from the subjects remotely with a dial. The tilting rod (length: 65 cm; diameter: 1 cm) was free to rotate in pitch about one end which was mounted in a bearing fixed to the body tilting device and aligned at the level of the subjects' trans-ocular axis. Subjects were thus able to move the rod up or down with their right hand to adjust its sagittal orientation. The laser pointer was free to rotate about its long axis and was mounted on a small, motorized support, external to the tilting device and coincident with the chair rotation axis. Alternatively the laser pointer could be fixed to the end of the tilting rod at different relative orientations in pitch. The external laser pointer was either controlled by the experimenter or by the subjects themselves, by means of a remote control dial, so that the beam could be positioned vertically in the sagittal plane. The rod and the external laser pointer were connected to a potentiometer, which recorded angular position with an accuracy of 0.05 deg.

In Experiment 2, GREL judgements were either performed by setting the height of the projected laser beam via the dial controlled laser pointer as in Experiment 1, or via arm pointing with the laser fixed with adhesive tape onto the subjects' index finger. For this experiment, measures were directly taken from the dot location on the board, which was recovered with a grid (Fick coordinates; i.e. angular projections on a plane surface). A dim blue light diffused in the experimental room allowed recordings of the dot position with respect to the grid. Subjects wore blue filter goggles, so they could not see the grid.

Procedure

The subjects' task was to judge in darkness their perceived GREL, defined as the plane through the eyes, which is always parallel to the floor. Subjects were also indicated that its projection corresponds to their perceived horizon, defined as "where the sky meets the sea". Drawings illustrating the experimental conditions and the objective GREL plane with tilted subjects (Fig. 1B) were finally presented to avoid any confusion about the nature of the judgement required.

In Experiment 1, the four experimental conditions required the subjects to perform the task 1) under purely kinesthetic control without vision, by setting the orientation of the rod through arm lifting (GREL$_k$); 2) under purely visual control without arm movement, by setting the height of the visual target provided by the external laser pointer via the remote control (GREL$_v$.); 3) under visual and kinesthetic control, by setting the height of the visual target provided by the rod-fixed laser through arm lifting. In this condition, both the rod and the laser were co-planar (i.e. coplanar visual and kinesthetic information: GREL$_{v+k}$); and 4) under visual control with no "goal-directed" kinesthetic information, by replicating the same condition as in 3, except that the sagittal orientations of the rod and the laser were divergent about 20° (i.e. non-coplanar visual and kinesthetic information: GREL$_{v/k}$). In Experiment 2, two conditions were presented. The first one replicated the GREL$_v$ protocol. For the second condition, subjects used natural arm pointing movements to project the visual dot towards their perceived GREL (GREL$_{v/p}$). Subjects were asked to concentrate on the visual dot location rather than on arm position.

The experimental conditions were randomly presented in separate sessions lasting 30–45 min. Six whole-body pitch orientations were deployed (upright; backward tilts: 10°, 20°, 30°; forward tilts: −10°, −20°). Larger angles of tilt would have interfered with the visual perception of the target onto the board. A session began and ended in "upright" position, between which subjects were tilted randomly into successive pitch orientations. Ten GREL estimates were executed for each orientation within a time interval of 2 min. Once tilted, the subjects waited still during approximately 20 s (allowing the semi-circular canals' response to be close to zero) before being asked to perform their first setting. They were told to keep their eyes closed during the entire experiment (GREL$_k$) or before and after each visual setting (GREL$_v$; GREL$_{v+k}$; GREL$_{v/k}$; GREL$_{v/p}$). This allowed the experimenter to position the visual target at a random location, above or below the physical projection of GREL (GREL$_v$), or the subjects to bring back the rod or their arm in the same initial resting position (GREL$_k$; GREL$_{v+k}$; GREL$_{v/k}$; GREL$_{v/p}$). Once the ten settings were performed, the chair was brought back to the upright for 20 s before a new re-orientation was presented.

Results

Experiment 1

When seated upright, subjects tended to estimate their perceived GREL lower than the physical reference (i.e. true eye level) for all the conditions (mean position: −2.4 deg). No significant difference was found between conditions in this upright orientation.

In order to test whether there is a linear relationship between perceived GREL and whole-body tilt, a linear regression analysis was applied to the mean individual data recorded in the six body orientations for each of the four experimental conditions. The results, summarized in

Table 1, showed a significant linear influence of the angle of tilt on GREL$_{k}$ ($F_{(1,58)}=27.82$; $p<.001$), GREL$_{v}$ ($F_{(1,58)}=5.93$; $p<.01$), GREL$_{v+k}$ ($F_{(1,58)}=13.57$; $p<.001$), and GREL$_{v/k}$($F_{(1,58)}=26.35$; $p<.001$). All GREL estimates seemed to be lowered with forward tilts and elevated with backward tilts (Fig. 2).

In order to study the magnitude of this “body tilt effect” (that is, the displacement of GREL in the direction of the tilted body) in each of the experimental conditions, an analysis of variance (ANOVA) was applied to the slope coefficients calculated for each individual regression line in the four experimental conditions. Results showed a main effect of condition, i.e. a difference in the magnitude of the body tilt influence upon GREL settings according to condition ($F_{(3,27)}=12.15$; $p<.001$). Post hoc analyses (Newman-Keuls test) showed that the tilt effect was not significantly different between GREL$_{v}$ and GREL$_{v+k}$. However, it became significantly higher for GREL$_{v/k}$vs. GREL$_{v}$($p<.05$) and for GREL$_{k}$vs. GREL$_{v/k}$ ($p<.01$; Fig. 3).

In order to determine whether response variability was affected by the experimental condition, an ANOVA was performed on the mean intra-subjects standard deviations. A main effect of the experimental condition was found ($F_{(3,27)}=24.13$; $p<.001$). Post-hoc analyses (Newman-Keuls test) showed that the GREL$_{v+k}$ and GREL$_{v/k}$ conditions yielded a lower intra-subjects’ variability than the GREL$_{v}$ condition ($p<.05$), whereas the GREL$_{k}$ condition yielded a higher intra-subjects’ variability than all other conditions ($p<.001$; Fig. 4).

Experiment 2

GREL settings performed in upright body orientation appeared also lower than the physical reference for both conditions (mean position: −2.2 deg). No significant difference was found between the conditions in this vertical body orientation.

The linear regression analysis, applied to the mean individual GREL estimates recorded in the six body orientations for each experimental condition, showed a significant linear influence of the angle of tilt on GREL$_{v}$ ($F_{(1,58)}=5.62$; $p<.05$), and GREL$_{v/p}$($F_{(1,58)}=70.63$; $p<.001$; Table 2). GREL estimates were again lowered with forward tilts and elevated with backward tilts (Fig. 5).

A *t*-test, between the slope coefficients calculated for each individual regression trend line in the two experimental conditions, showed that these were statistically different, reflecting a difference in the magnitude of the body tilt influence ($t(9)=-3.90$; $p<.01$; Fig. 6). This indicates that using the outstretched arm to assess visual estimates of GREL (GREL$_{v/p}$) increased the “body tilt effect”.

Table 1 Results of the linear regression analysis between the mean individual GREL estimates and the different body orientations in pitch (Experiment 1)

Experimental conditions	β	R^2	*p*<	*Slope coefficient*
GREL$_{k}$	.57	.32	.001	.34
GREL$_{v}$	.31	.09	.01	.07
GREL$_{v+k}$	.44	.19	.001	.11
GREL$_{v/k}$	.56	.31	.001	.18

Table 2 Results of the linear regression analysis between the mean individual GREL estimates and the different body orientations in pitch (Experiment 2)

Experimental conditions	β	R^2	*p*<	*Slope coefficient*
GREL$_{v}$	.30	.09	.05	.07
GREL$_{v/p}$	.74	.55	.001	.19

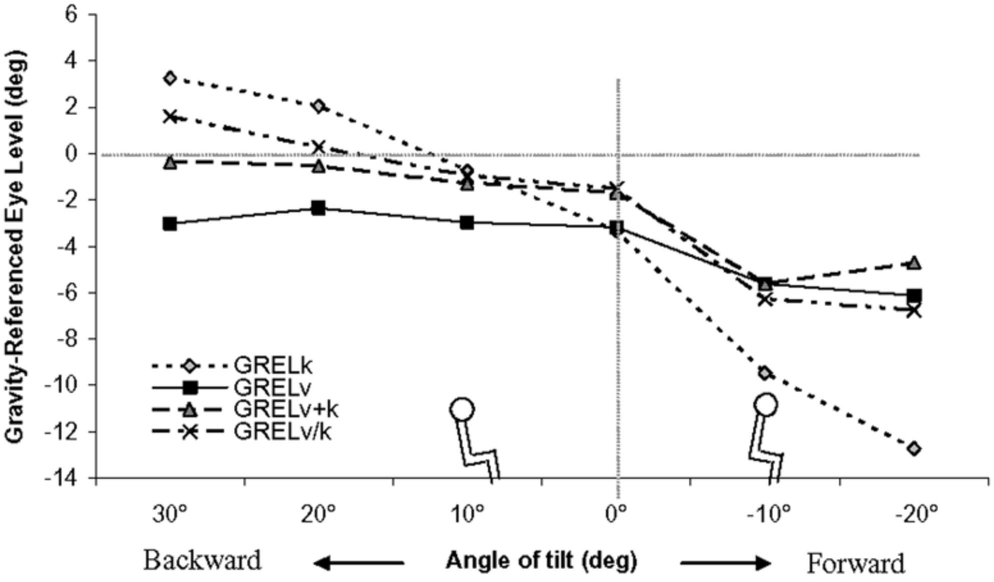
A *t*-test was conducted on the mean intra-subjects standard deviations of the GREL estimates for the two experimental conditions to analyse the variability of subject’s performance. It revealed that intra-subject variability was lower when visual GREL was assessed through arm pointing movements ($t(9)=5.20$; $p<.001$; Fig. 7).

Discussion

In the present experiments, all GREL estimates recorded in upright body orientation were consistently lower than the physical reference (i.e. below the earth-referenced horizon or “true” horizontal eye level), in agreement with the data reported in the literature (Raphel and Barraud 1994; Stoper and Cohen 1986). In addition, our study shows the existence of a main effect of body orientation on the perceived GREL, namely a linear attraction of the GREL estimates towards the tilted body, at our stimulus parameters. More strikingly, this influence extended to perceptual judgements involving different sensory modalities and/or different levels of motor activity. The second main finding of this study is the absence of perceptual improvement in GREL judgements (i.e. in terms of a lower dependency on body orientation) when arm movements were used (motor-kinesthetic involvement). Even adding a kinesthetic component to a visual assessment (GREL$_{v/k}$) led to an increasing influence of body tilt, compared with a passive visual task (GREL$_{v}$).

Regarding the first aim of the present study, our results confirm that GREL perception is not invariant in total darkness, but appears to be dependent on body orientation. Bourdin et al. (2001) showed a similar linear shift of GREL estimates towards the tilted body for rotations well below semicircular canals threshold rotations and small pitch angles. Our results indicate that it is possible to generalize this influence to larger body tilts induced by suprathreshold rotations. Taken together, the findings have important consequences for the manner observers judge the height of an object with respect to external space. For instance, the concomitant elevation of GREL with backward tilts found in this study would imply a relative lowering of the perceived location of an immobile target in a dark environment. Schöne (1964) has already suggested

Fig. 2 Mean perceived GREL with respect to whole-body tilt for the four experimental conditions (Experiment 1)

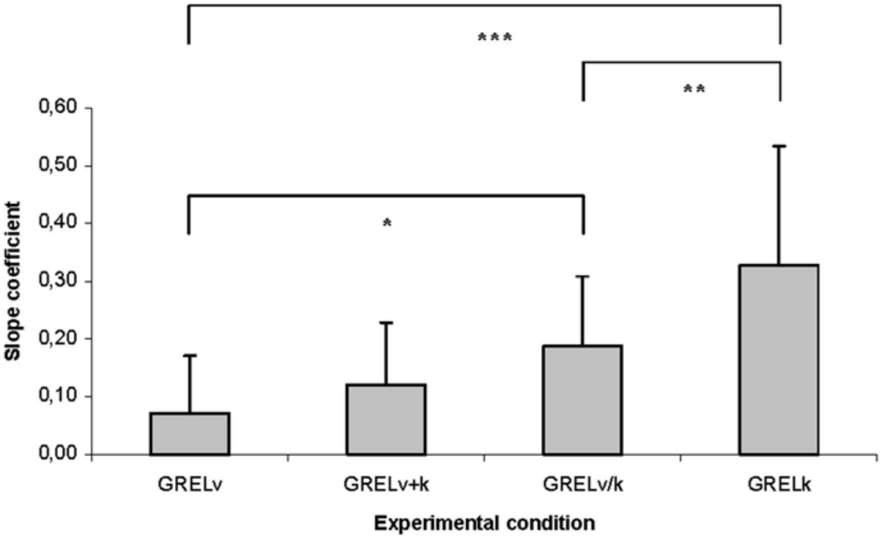


that "under the influence of increased field strength, the space appears to shift in the same direction as the movement of the head". Our findings enable us to extend the influence of head and body orientation, in a smaller scale but consistently, to a normogravity environment.

Such results can be interpreted in terms of body tilt underestimation. Subjects would adjust the spatial reference as if they were less tilted than they actually were, suggestive of a failure of the graviceptive sensory systems needed to correctly perform the necessary transformation of coordinates required by the task (Schöne 1964). This hypothesis is comparable to explanations of the Aubert-effect for subjective visual vertical estimates (Lechner-Steinleitner 1978). However, several studies showed that there is no direct link between the estimated body orientation and the perception of geographical directions such as vertical or horizontal (van Beuzekom and van Gisbergen 2000; Bronstein 1999; Ebenholtz 1970; Mast and Jarchow 1996; Mittelstaedt 1995).

An alternative to the tilt underestimation hypothesis could emerge from the analysis of the task constraints of the present experiments. Since estimating the GREL consists of selecting, amongst all the horizontal planes (geocentric component), the one which passes through the eyes (egocentric component), the task involves a semi-geocentric frame of reference. The effect of tilting the body on GREL estimates could then be interpreted as a bias induced by the egocentric component of the task. This interpretation is in line with the idiotropic vector hypothesis formulated for subjective visual vertical estimates (Mittelstaedt 1983; 1999), that is, a central tendency to shift judgements towards the subjects' own longitudinal axis. A comparable "egocentric attraction" was also reported in previous reports involving geocentric judgements, showing that head or body tilt can affect the hand orientation with respect to earth-fixed horizontal (Chelette et al. 1995) or the forearm orientation relative to earth fixed vertical (Darling and Hondzinski 1999).

Fig. 3 Mean slope coefficient of the linear regression trend lines between the mean individual GREL estimates and the different body orientations, and inter-subjects standard deviation for the four experimental conditions (Experiment 1). The slope coefficient represents the weight of the "body tilt effect", i.e the shift of GREL estimates towards the body tilt



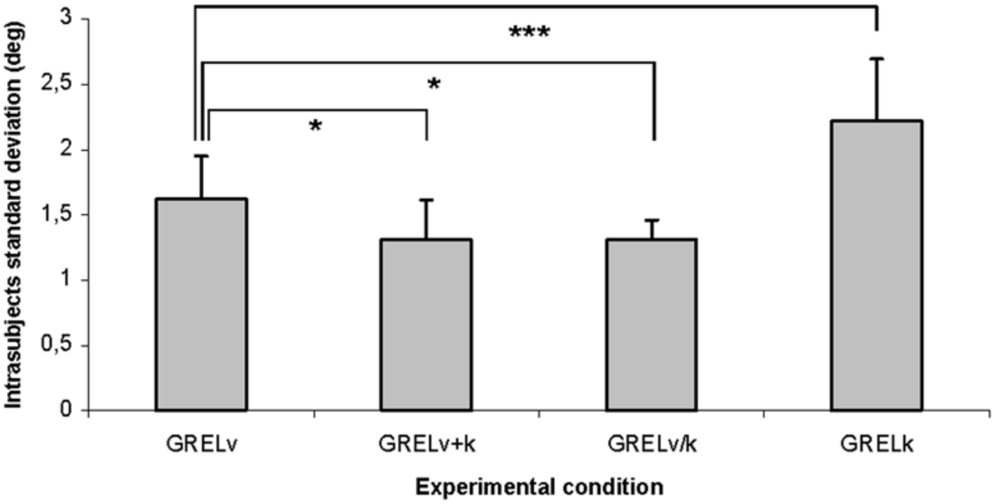


Fig. 4 Mean intra-subject variability and inter-subjects standard deviation for the four experimental conditions (Experiment 1)

The second major finding of this study is the influence of experimental condition upon the general tilt effect discussed above. GREL estimates performed through arm movement only ($GREL_k$) or visually performed with non goal-directed arm movement ($GREL_{v/k}$ or $GREL_{v/p}$) were more dependent on body orientation than purely visual settings ($GREL_v$). Therefore, the results do not support the hypothesis that arm movements against gravity should reduce the tilt-based shift in GREL settings.

Bock (1994) and Gooey et al. (2000) showed that arm position sense was significantly improved or became less variable when gravity cues were not disturbed compared with weightless environments or when adjustable loads were added to the arm. These observations suggested that lifting the arm in normal circumstances on earth might provide additional positional information about arm orientation in space. Although still under discussion, several studies have shown that the gravitationally generated torque around the shoulder of an extended arm could be involved in arm position sense (Darling and Miller 1995; Worringham and Stelmach 1985) and also in a more general perception about the direction of gravity (Fitger 1976; Gentaz and Hatwell 1996; Luyat et al. 2001). Considering these findings, we expected that any additional gravitational cues would help the subjects in perceiving their own body orientation better, and would thus lead to reduce the tilt effect on GREL estimates. However, our data suggested that there is no direct link between the perception of body orientation and the judgement of a semi-geocentric reference such as GREL. If arm movements provide any additional input for perceiving body position in space, they nevertheless seem to enhance the GREL shift towards the subjects' longitudinal axis. These findings indicate that active motor involvement and/or the addition of kinesthetic input to the GREL estimates acts as a perturbing factor, inducing a switch towards a more egocentric frame of reference. This calls into question the assumption that summing non-conflicting multiple sensory inputs (Howard 1997) or using intermodal information arising from action (Fouque et al. 1999) should systematically improve perceptual performance. For tasks defined in a purely geocentric

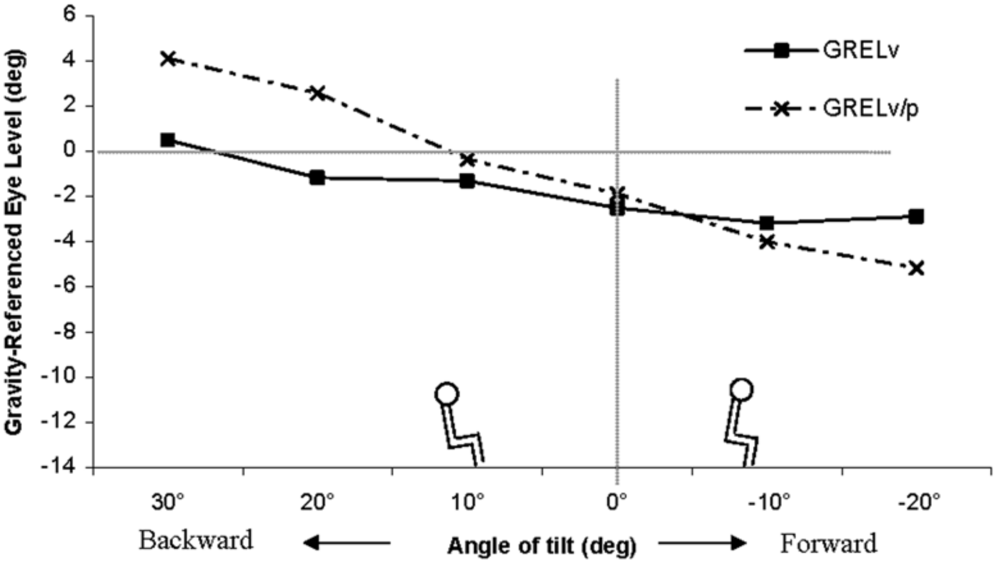


Fig. 5 Mean perceived GREL with respect to whole-body tilt for the two experimental conditions (Experiment 2)

Fig. 6 Mean slope coefficient of the linear regression trend lines between the mean individual GREL estimates and the different body orientations, and inter-subjects standard deviation for the two experimental conditions (Experiment 2)

frame of reference such as the subjective vertical (Luyat et al. 2001) or the subjective zenith (Mittelstaedt 1983) assessed haptically, additional arm gravitational cues offered by arm lifting can be helpful. However, in the present semi-geocentric tasks, the movement of the arm can reinforce the egocentric component of the frame of reference used.

One might argue nevertheless that lifting a rod against gravity with a bent arm (Experiment 1) could require a more complicated transformation of coordinates, providing less precise or relevant kinesthetic information than would be obtained from reaching an outstretched arm through a more natural pointing movement (Experiment 2). As proposed by Gooey et al. (2000), the brain could assign a particular significance to kinesthetic cues when movements are performed through natural patterns often experienced. However, both experiments led to the same increase of the tilt effect on visual GREL estimates when using an additional arm movement ($GREL_{v/k}$ or $GREL_{v/p}$). Therefore, whether the movement was natural or not, adding a motor-kinesthetic component to the task interfered with the subjects' perception. On the other hand, analysis of the intra-subject standard deviations showed that combining visual and kinesthetic information ($GREL_{v+k}$; $GREL_{v/k}$; $GREL_{v/p}$) reduced the perceptual variability with respect to that measured for estimates involving a single sensory channel ($GREL_v$ $GREL_k$), as predicted by Bayes' law (Ernst and Banks 2002). This finding also has a correlate in the visual vertical. Whereas the tilt-induced bias known as "A-effect" disappears when a hemi-anesthetic patient lies on the anesthetic side, variability and inconsistency of visual vertical estimates rise significantly (Anastasopoulos and Bronstein 1999).

In conclusion, the present study demonstrates that the perception of the Gravity-Referenced Eye Level can be modified by body tilt and motor-kinesthetic involvement. These two factors might depend on the same cognitive process consisting in a more or less pronounced shift from a semi-geocentric frame of reference to a more egocentric frame of reference. This interpretation is supported by recent work, suggesting that egocentric and geocentric frames of reference are pre-existing neurophysiological structures between which subjects could switch easily, depending on the task demand (Ghafouri et al. 2002). These findings could be of value in man-machine interfaces where subjects have to accurately locate their perceptual horizon and related objects in a visually impoverished environment.

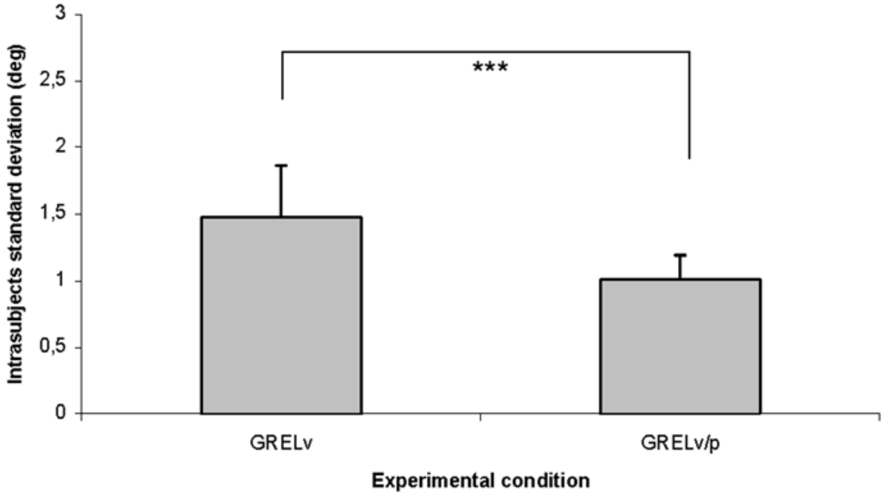


Fig. 7 Mean intra-subject variability and inter-subjects standard deviation for the two experimental conditions (Experiment 2)

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Impact d'un déficit vestibulaire bilatéral

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Influence of pitch tilts on the perception of gravity-referenced eye level in labyrinthine defective subjects

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Abstract

We investigate the role of vestibular information in judging the gravity-referenced eye level (i.e., earth-referenced horizon or GREL) during sagittal body tilt whilst seated. Ten bilateral labyrinthine-defective subjects (LDS) and 10 age-matched controls set a luminous dot to their perception of GREL in darkness, with and without arm pointing. Although judgements were linearly influenced by the magnitude of whole-body tilt, results showed no significant difference between LDS and age-matched controls in the subjective GREL accuracy or in the intra-subject variability of judgement. However, LDS performance without arm pointing was related to the degree of vestibular compensation inferred from another postural study performed with the same patients. LDS did not utilize upper limb input during arm pointing movements as a source of graviceptive information to compensate for the vestibular loss. The data suggest that vestibular cues are not of prime importance in GREL estimates in static conditions. The absence of difference between controls and LDS GREL performance, and the correlation between the postural task and GREL accuracy, indicate that somatosensory input may convey as much graviceptive information required for GREL judgements as the vestibular system.

Keywords: Vestibular defect; Body orientation; Frame of reference; Egocentric; Geocentric

1. Introduction

The vestibular system is a key sensor for the perception of head and body orientation in space (Green & Angelaki, 2004; Schöne, 1964). Nevertheless, previous studies showed that the perception of body orientation was not impaired in labyrinthine-defective subjects (LDS) (Bringoux et al., 2002; Bronstein, 1999). Mean estimates of the subjective postural vertical (SPV) in LDS were identical to those performed by normal subjects, although a decreased sensitivity in the judgements was noted. On the other hand, artificial removal of gravity-based somatosensory information or pathological somatosensory impairment yielded strong modifications in SPV or body tilt judgements (Anastasopoulos, Bronstein, Haslwanter, Fetter, & Dichgans, 1999; Bringoux, Nougier, Barraud, Marin, & Raphel, 2003). The present study investigates whether vestibular cues are of prime importance in an estimation task for which body orientation must be taken into account, namely judging the gravity-referenced eye level (GREL).

GREL can be defined as the "earth horizon", that is the trans-ocular plane normal to the direction of gravity (Bringoux, Tamura, Faldon, Gresty, & Bronstein, 2004; Stoper & Cohen, 1989). It is known to be involved in distance (Ooi, Wu, & He, 2001) and location (Li, Dallal, & Matin, 2001) specification of visual targets seen in otherwise darkness, and its false perception may have critical repercussions in modern transportation (e.g., aeronautics). In a GREL estimation task, one must perceive an external gravity-referred direction (geocentric component), which has to be linked with eye level (egocentric component). Therefore it can be considered a "semi-geocentric" task.

GREL estimates are linearly dependent on pitch body tilt angle, that is lowered with forward tilt and elevated with backward tilt (Bringoux et al., 2004). Although this "body tilt effect" can be interpreted in terms of body tilt underestimation (according to classical explanations of the Aubert effect for

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the subjective visual vertical or SVV; Lechner-Steinleitner, 1978), the difference between SVV and SPV settings reported in the literature may suggest another interpretation, based on an egocentric shift (Bringoux et al., 2004). According to this hypothesis, subjects tend to rely more on an egocentric component when tilted (in line with the idiotropic vector hypothesis; Mittelstaedt, 1983, 1999), and thus shift GREL judgements towards the head-referenced eye level (HREL), namely the trans-ocular plane normal to the transverse plane of the head (i.e., a purely egocentric reference; Stoper & Cohen, 1989).

As this egocentric shift can be only counteracted by geocentric cues, one might expect a more pronounced egocentric shift for LDS, since the vestibular apparatus is involved in the perception of the direction of gravity. On the other hand, if LDS and normal subjects both used predominantly non-vestibular cues to estimate the geocentric component, then there should be no difference in GREL judgements for the two groups.

Additional gravitational cues, e.g., from the generation of gravitational torques around the arm joints when using arm movements (Gentaz & Hatwell, 1996), could also assist subjects in perceiving their orientation with respect to gravity (Fitger, 1976; Luyat, Gentaz, Regia-Corte, & Guerraz, 2001). However, the ‘body tilt effect’ on GREL in normals is increased when arm-pointing movements are used in addition to visual cues (Bringoux et al., 2004). This incoherence has been explained as an increased egocentric shift associated with the use of arm movements, which obscures any graviceptive function of arm inputs for normal subjects (Bringoux et al., 2004). However, in LDS, the graviceptive sensitivity of arm lifting could be increased in order to compensate for the lack of vestibular information.

Two experimental sessions involving LDS and age-matched controls (AMC) were carried out in order to test these hypotheses. The first one required subjects to estimate their GREL visually, without performing any arm movements. The second session, based on visual GREL settings performed through arm pointing movements, investigated the putative role of dynamic graviceptive signals arising from arm movement (i.e., dynamic gravitational torque; Fitger, 1976; Luyat et al., 2001) after loss of labyrinthine function.

2. Materials and methods

2.1. Subjects

Ten bilateral LDS (six males and four females, mean age: 56 ± 9.2 y.o.) and 10 AMC (5 males and 5 females, mean age: 57 ± 9.8 y.o.) gave informed consent to participate in the study, according to local ethic committee guidance and ethical standards laid down in the Declaration of Helsinki. Absence of vestibular function was documented with bithermal caloric ear irrigation (30 and 44 °C) and horizontal rotational in the dark (velocity steps of ±60° s^{-1}). Patients were tested in their chronic phase in order to avoid the influence of any disturbing manifestations such as vertigo or dizziness inherent to the acute phase. Table 1 summarizes the LDS’ clinical data.

2.2. Apparatus

A fully detailed description of the experimental materials and methods can be found in a previous paper (Bringoux et al., 2004). The subjects were seated and tightly restrained in a padded chair which could be rotated in pitch, about a horizontal axis. The height of the chair could be adjusted so that the subjects’ trans-ocular axis coincided with the axis of rotation. The velocity of the pitch rotation was set at 1.5° s^{-1}, with initial accelerations and final decelerations (1.5° s^{-2}) above the semi-circular canals’ thresholds for rotation perception (Fitzpatrick & McCloskey, 1994). The subject’s head was firmly restrained by a headrest and a chinrest fixed to the chair frame, in order to keep it in line with the body at all times (Fig. 1).

GREL judgements were performed under two conditions: vision alone (GREL-V) and vision with pointing (GREL-VP). In ‘GREL-V’, a laser pointer was mounted on an earth-fixed motorized support and the height of the projected laser beam was adjusted via a hand-held dial. In the ‘GREL-VP’ condition, the laser pointer was fixed onto the subject’s index finger with adhesive tape and they used arm pointing movements to indicate their visual perception of GREL. In both conditions the laser beam was projected onto a vertical board in front of the subject. This board was marked with a grid in Fick coordinates (i.e., angular projections onto the plane surface) and the position of the dot on the grid was recorded by the experimenter. In the ‘GREL-V’ condition, a potentiometer independently recorded the laser position, thus, providing confirmation of the reliability and validity of the experimenter’s observations. A dim blue light diffused in the experimental room allowed recordings of the dot position relative to the grid. Subjects wore blue filter goggles, so they could not see anything else except the adjustable dot. The resolution of the apparatus enabled a measurement accuracy ranging from 0.05° with the potentiometer to 0.2° with experimenter’s observations.

2.3. Task and procedure

The subject’s task was to judge their subjective GREL in darkness. This was defined as the plane passing through the eyes, which is always normal to

Table 1
Information about the bilateral labyrinthine-defective patients tested

Patient ID	Age/sex	Time since presentation (years)	Aetiology	Testing	
				Calorics[a]	Rotation[b]
P1	67/F	5	Idiopathic	Not done	No response
P2	59/F	>12	Idiopathic	Not done	No response
P3	48/M	12	Idiopathic	No response	No response
P4	47/M	10	Idiopathic	No response	No response
P5	51/F	16	Idiopathic	Not done	No response
P6	59/M	>10	Meningitis	Not done	No response
P7	42/F	6	Idiopathic	No response	No response
P8	70/M	>3	Gentamicin[c]	Not done	No response
P9	52/M	>1	Idiopathic	Not done	No response
P10	63/M	8 weeks	Gentamicin[c]	Not done	No response

[a] Bilateral caloric irrigation (30 and 44 °C) with and without visual fixation.

[b] Electro-oculography during velocity step rotations in the dark of at least ±60° s^{-1}.

[c] Gentamicin ototoxicity.

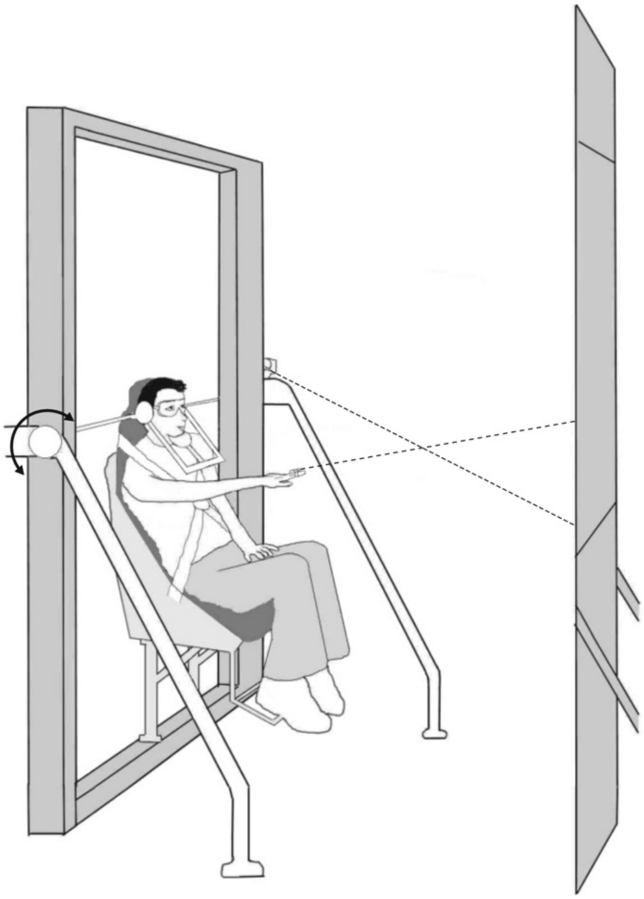

Fig. 1. Illustration of the setup with the two experimental conditions tested. The motorized chair rotated around the subjects' inter-ocular axis. The dotted lines illustrate the laser beam projected from an earth-fixed position for GREL-V and from the subject's index finger for GREL-VP.

gravity (i.e., parallel to the floor) and explained in lay terms as the perceived horizon, which could be thought of as "where the sky meets the sea". Drawings illustrating the experimental conditions and the objective GREL plane with tilted subjects were shown to avoid any ambiguity.

The experimental conditions were presented in two separate sessions and the order of the sessions was randomized. In Session 1, the subjects had to perform the task under purely visual control, without arm movements, by setting the height of the laser dot via a remote control dial (GREL-V). In Session 2, subjects used natural arm pointing movements to project the laser dot towards their perceived GREL (GREL-VP). Subjects were asked to concentrate on the visual dot location rather than on arm position. Six whole-body pitch orientations were deployed (upright; backward tilts of 10°, 20°, 30°; forward tilts of −10°, −20°). A session began and ended in the "upright" position. During the session, the sequence of pitch orientations was randomized, and subjects were returned to upright for 20 s before each new tilt angle. Once tilted, the subjects waited 20 s (allowing semi-circular canal effects to settle down) before being asked to perform their first setting. Six GREL estimates were obtained for each orientation (within a time period of 1 min). Subjects were told to close their eyes before and after each setting and, in the GREL-VP condition, to lower their arm to a resting position. In the GREL-V condition, the experimenter repositioned the visual target to a random location before each GREL-V setting, while the subject's eyes were closed.

2.4. Data analysis

Mean comparisons between groups or experimental conditions were performed with analyses of variance (ANOVAs), when data were distributed normally with comparable variance. Non-parametric analyses (Mann–Whitney *U*-tests for independent samples and Wilcoxon tests for dependant samples) were conducted when the assumption of normality and homogeneity of variance among groups was violated (see Table 2 for details). Statistical power of all parametric comparisons of means was also calculated. Distribution of GREL settings relative to the angle of body tilt was analysed through simple linear regression analyses. The relationship between LDS postural stability, reflecting the degree of vestibular compensation (Szturm, Ireland, & Lessing-Turner, 1994), and LDS performance in the GREL judgement task was also investigated. Postural sway data from an independent study was available for seven of our patients (Bunday & Bronstein, 2004). Postural sway (trunk displacement) had been recorded while the subjects stood on a moving platform (the MOVING condition in the "broken escalator" paradigm, Reynolds & Bronstein, 2003, 2004). The relationship between variables was assessed using a Pearson's correlation coefficient analysis.

3. Results

3.1. GREL estimates in upright orientation

Subjective GREL estimates performed in an upright orientation were lower than the physical GREL for both groups and conditions (mean position: −2.2°). A two groups (AMC versus LDS) × two conditions (GREL-V versus GREL-VP) ANOVA revealed no significant difference between groups ($F_{1,18} = 0.14$; $p > 0.05$, n.s.) or conditions ($F_{1,18} = 0.53$; $p > 0.05$, n.s.), and no

Table 2
Test of normality (Shapiro–Wilk test) and variance homogeneity (Levene's test) for subsequent mean comparison analyses

Normality	GREL estimates when upright		Slope coefficients		Intercept values		Intra-subjects variability	
	W	*p*	*W*	*p*	*W*	*p*	*W*	*p*
GREL-V: AMC	0.96	0.78	0.95	0.63	0.97	0.85	0.94	0.58
GREL-VP: AMC	0.96	0.74	0.96	0.73	0.93	0.45	0.95	0.72
GREL-V: LDS	0.88	0.15	0.95	0.69	0.99	0.99	*0.82*	*0.03*[*]
GREL-VP: LDS	0.92	0.33	0.96	0.76	0.96	0.81	0.87	0.11

Variance homogeneity	GREL estimates when upright		Slope coefficients		Intercept values		Intra-subjects variability	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
GREL-V: AMC vs. LDS	0.08	0.78	0.76	0.40	0.53	0.48	*6.94*	*0.02*[*]
GREL-VP: AMC vs. LDS	0.00	0.96	0.17	0.68	0.24	0.63	*11.04*	*0.004*[*]

[*] Significance ($p < 0.05$) means violation of normality or variance homogeneity assumption required for parametric analyses.

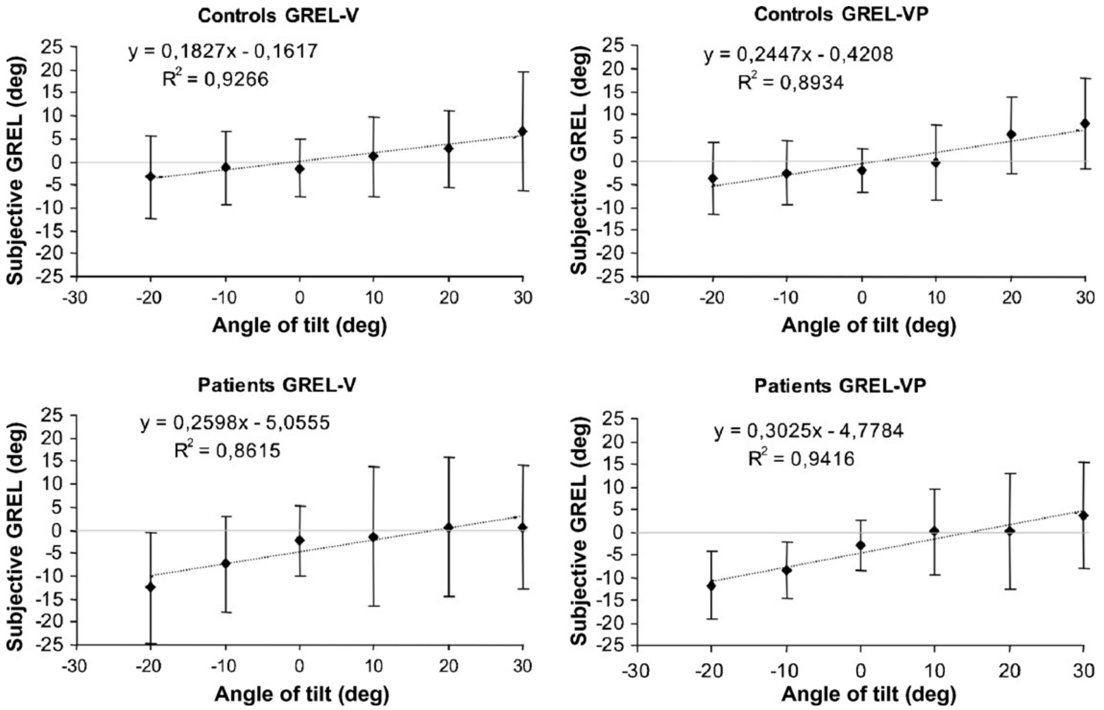

Fig. 2. Mean perceived GREL as a linear function of whole-body tilt for both groups of subjects and both experimental conditions. Negative angles of tilt correspond to forward tilts, whereas positive angles of tilt correspond to backward tilts. Negative GREL values indicate settings below physical GREL whereas positive GREL values indicate settings above physical GREL. Error bars represent standard deviation from the mean. The slope coefficients of the linear regression trend lines, representing the strength of the "body tilt effect", i.e., the shift of GREL estimates towards the body tilt, were not statistically different between groups and conditions.

interaction between these two factors ($F_{1,18} = 0.001$; $p > 0.05$, n.s.) in the absence of whole body tilt.

3.2. GREL estimates when tilted

In order to examine whether there was a linear relationship between subjective GREL and the angle of whole-body pitch tilt, a linear regression analysis was applied to the mean individual GREL estimates recorded in the six body orientations for both experimental conditions. The results showed a significant linear influence of the angle of tilt in both experimental conditions for AMC (GREL-V [$F_{1,58} = 7.54$; $p < 0.01$]; GREL-VP [$F_{1,58} = 17.95$; $p < 0.001$]) as well as for LDS (GREL-V [$F_{1,58} = 7.81$; $p < 0.01$]; GREL-VP [$F_{1,58} = 19.69$; $p < 0.001$]). GREL estimates were lowered with forward tilts and elevated with backward tilts (Fig. 2).

In order to study the magnitude of the linear body tilt influence upon GREL estimates, a two groups (AMC versus LDS) × two conditions (GREL-V versus GREL-VP) ANOVA was applied to the slope coefficients calculated for each individual regression line. This revealed no significant difference between groups ($F_{1,18} = 0.41$; $p > 0.05$, n.s.) and conditions ($F_{1,18} = 1.81$; $p > 0.05$, n.s.) and no interaction between these two factors ($F_{1,18} = 0.06$; $p > 0.05$, n.s.). The magnitude of the "body tilt effect" seemed then not to differ between AMC and LDS and between estimates assessed by vision alone or by vision with pointing movements (Fig. 2). In addition, we compared the mean intercepts obtained from each linear regression lines by a two groups (AMC versus LDS) × two conditions (GREL-V versus GREL-VP) ANOVA. It showed no significant difference between groups ($F_{1,18} = 2.36$; $p > 0.05$, n.s.) and conditions ($F_{1,18} = 0.03$; $p > 0.05$, n.s.) and no interaction between these two factors ($F_{1,18} = 0.19$; $p > 0.05$, n.s.). The mean "baseline" of the effect was not different between AMC and LDS and was not affected by the condition of assessment (Fig. 2). Nevertheless, results presented above were characterized by weak statistical power indices, mainly due to high variability in subjective responses between subjects. Table 3 summarizes the main statis-

Table 3
Level of significance (p) and statistical power ($1-\beta$) for parametric mean comparison analyses

Factor	GREL estimates when upright		Slope coefficients		Intercept values	
	p	$1-\beta$	p	$1-\beta$	p	$1-\beta$
Group (AMC vs. LDS)	0.72	0.06	0.53	0.09	0.14	0.31
Condition (GREL-V vs. GREL-VP)	0.47	0.11	0.20	0.25	0.86	0.05
Group × condition	0.98	0.05	0.80	0.06	0.67	0.07

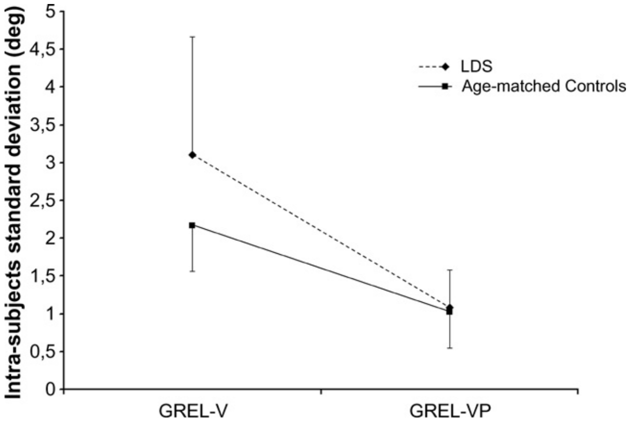

Fig. 3. Mean intra-subject variability for both groups of subjects and both experimental conditions. Error bars represent standard deviation from the mean.

tical outputs from parametric statistics about mean comparisons conducted in this study.

3.3. Intra-subjects variability on GREL estimates

Non-parametric statistics were used to analyse the intra-subjects variability, as preliminary tests revealed a violation of the assumption of normality and variance homogeneity between groups (Table 2). Mann–Withney *U*-test (comparing AMC versus LDS) and Wilcoxon test (comparing GREL-V versus GREL-VP conditions) were conducted on the mean intra-subjects standard deviations of individual GREL estimates. The results showed a main effect of the experimental condition for AMC ($T = 0$; $p < 0.01$) as well as for LDS ($T = 3$; $p < 0.05$) but no main effect of group, neither in GREL-V condition ($U = 32$; $p = 0.17$) nor in GREL-VP condition ($U = 37$; $p = 0.33$). Intra-subject variability was lower when visual GREL was assessed through arm pointing movements (Fig. 3).

3.4. Relationship between vestibular compensation and GREL estimates for LDS

Preliminary analyses did not show any relationship between the “body tilt effect” on GREL estimates and the time since presentation of all the patients tested ($r = -0.10$, $p = 0.78$ in GREL-V condition; $r = -0.09$, $p = 0.80$ in GREL-VP condition). Nevertheless, we aimed at investigating the influence of vestibular compensation and GREL perception. The relationship between LDS performance in the GREL task and in a postural condition reflecting an indice of their vestibular compensation was then tested in seven patients (see Section 2). A Pearson’s correlation coefficient analysis revealed a significant negative correlation between body sway amplitude and the GREL-V slope coefficients ($r = -0.78$, $p < 0.05$). The more the patients swayed after walking onto a moving platform, the less they were influenced by body tilt when assessing GREL by vision alone (Fig. 4A). No significant linear relationship was found between body sway amplitude and the GREL-VP slope coefficients ($r = 0.29$, $p = 0.52$; Fig. 4B).

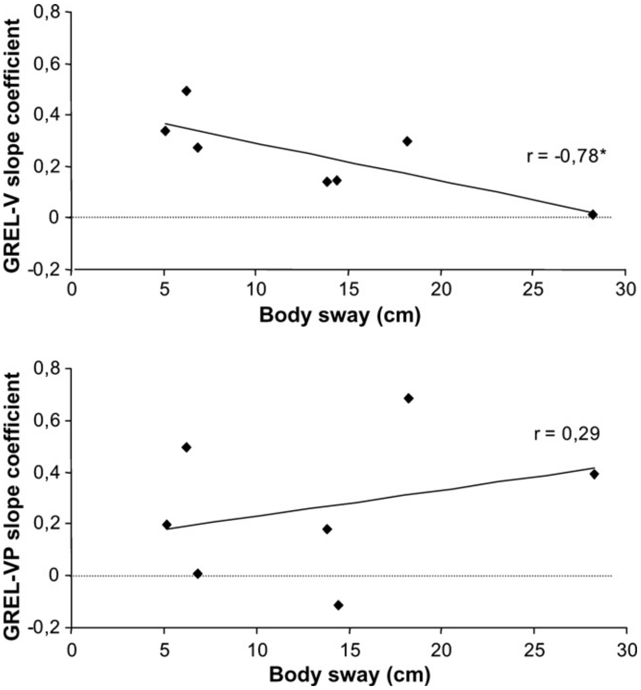

Fig. 4. Relationship between the GREL slope coefficients, i.e. the magnitude of the “body tilt effect” upon GREL estimates, in seven LDS and the maximum body (trunk) sway when walking on a moving platform (Reynolds & Bronstein, 2003, 2004). (A) Significant linear negative correlation between body sway and GREL settings performed with vision alone; (B) non-significant relationship between body sway and GREL settings performed through arm movements.

4. Discussion

The main purpose of the present study was to address the question of vestibular influence in the judgement of a semi-geocentric reference, such as the gravity-referenced eye level (GREL), for which the head orientation with respect to gravity must be taken into account (Bringoux et al., 2004; Stoper & Cohen, 1989). The otoliths are known to be the relevant vestibular organs for gravity sensing. Although the otoliths were not examined directly in our subjects (as otolith tests are cumbersome and often inconclusive), available clinical and pathological data indicates that disorders seriously involving the semi-circular canals regularly cause serious damage to the otoliths as well (Lempert, Gianna, Gresty, & Bronstein, 1997). This is confirmed by our previous study investigating body tilt effects on the subjective visual vertical in a similar group of LDS, which showed large differences between LDS and normal controls (Bronstein, Yardley, Moore, & Cleeves, 1996).

The results obtained in the upright position, both in patients with complete vestibular failure (LDS) and age-matched controls (AMC), are in line with previous reports of judgements of GREL being lower than the physical GREL (Raphel & Barraud, 1994; Stoper & Cohen, 1986). For body tilts between 30° backward and 20° forward, our results also confirm the linear relationship between the angle of tilt and GREL estimates, called the “body tilt effect” (Bourdin et al., 2001; Bringoux et al., 2004). GREL settings are lowered with forward tilts and elevated with backward tilts, a finding which may have repercussions on spatial orientation when subjects are tilted in an impoverished visual environment (Bringoux et al., 2004; Schöne, 1964). An explanation for this phenomenon invokes the presence of an "egocentric shift" towards the subjects' own longitudinal axis (for further details, see Bringoux et al., 2004), in line with the idiotropic vector hypothesis for roll tilts in visual vertical settings (Mittelstaedt, 1983, 1999). The magnitude of this egocentric shift is reflected in the mean slope coefficients calculated from each individual linear regression lines.

4.1. Vestibular defect and GREL judgement

The major finding of the present study is the unexpected lack of a significant difference in the mean slope coefficients between age-matched controls and LDS (Fig. 2). Intact otolith organs would be expected to counterbalance, to some extent, the egocentric shift exerted by pitch body tilt (the "body tilt effect"). This type of effect has been shown when visual vertical measurements during large roll body tilts have been compared in normal controls and LDS (large increase in 'A' effect seen in LDS, Bronstein et al., 1996). The range of body tilt in our study was anatomically limited (e.g. eyebrows restrict the visual range for perceiving the physical horizon). It is then possible that larger tilts could yield different results, like those obtained in the visual vertical experiments (Bronstein et al., 1996). Moreover, the weak power of our statistical analyses (Table 3) makes us remain cautious about the hypothesis of a strict equivalence between the LDS and AMC groups.

Nevertheless, the present finding puts into question a major vestibular contribution to the perception of static head and body tilts when other sensory cues are available. Earlier studies have already reported no difference in the perception of the subjective postural vertical (SPV) between normal subjects and LDS, after a very short adaptive period (Clark & Graybiel, 1963a, 1963b). This was recently confirmed by Bronstein (1999) who showed that the mean position of SPV was normal in LDS, despite a decreased sensitivity of judgement. In the same vein, Ito and Gresty (1997) found that LDS performed similarly to normals in estimating postural orientations in the pitch plane and Bringoux et al. (2002) showed that mean thresholds for the detection of body tilt for LDS and normals do not differ.

One might explain these results by a sensory reweighting process taking place after the vestibular deficit (Creath, Kiemel, Horak, & Jeka, 2002). As patients compensate, they progressively rely more on somatosensory inputs to ensure graviceptive function (Clark & Graybiel, 1966). This interpretation is supported by the finding of a significant negative correlation between LDS' body sway in a challenging postural task (the MOVING condition in the "broken escalator paradigm" (Reynolds & Bronstein, 2003, 2004), and visual GREL judgements (Fig. 4A). The patients who sway less might have learned to use mainly somatosensory cues for postural equilibrium. These more "somatosensory" patients would be more influenced by somatosensory adaptation when tilted (Bisdorff, Wolsley, Anastasopoulos, Bronstein, & Gresty, 1996); Clark & Graybiel, 1966; Higashiyama & Koga, 1998), in turn leading to an enhanced egocentric shift in GREL estimates. More work is needed in order to confirm this differential GREL behaviour depending on the recovery status of the patients, although important differences in visual and somatosensory dependence in patients with vestibular lesions are well documented (Guerraz et al., 2001).

The intra-subjects variability (i.e., the level of consistency in settings for a given subject), was also found to be similar between LDS and age-matched controls (Fig. 3). This result further confirmed the limited role of the vestibular system in GREL judgements, for which the "reproducibility" of estimates seemed not to be affected by the lack of vestibular information. In agreement, Clark and Graybiel (1967) have previously reported no significant difference between normals and LDS for "average errors" (i.e., variable errors) in a visual horizontal task during roll body tilts.

4.2. Influence of arm movements in GREL judgement

The second important result of the present study is the absence of influence of the experimental condition upon GREL judgements as well as the absence of interaction between the group of subjects and the experimental condition. Setting GREL via arm pointing movements neither diminished nor increased the "body tilt effect", and LDS responded similarly to age-matched controls whatever the method of assessment (Fig. 2).

Additional arm gravitational cues offered by arm lifting have been found to be helpful for tasks defined in a purely geocentric frame of reference such as the haptic assessment of the subjective vertical (Luyat et al., 2001) or the subjective zenith (Mittelstaedt, 1983). Our GREL-VP task differs from the former ones in that it also involves an egocentric component (i.e., eye level). Contrary to our previous findings in younger adults (Bringoux et al., 2004), we did not find an increased egocentric shift when judgements were performed via arm pointing movements. The higher mean slope coefficient and increased inter-subject variability recorded in GREL-V condition for the older LDS and age-matched controls tested in this study might explain this apparent contradiction. In view of the weak power of our statistics, here again, it is more prudent to report an absence of significant differences rather than absolute similarity between the LDS and AMC data sets.

In line with our previous study, however, analysis of the intra-subjects standard deviations in both groups confirmed Bayes' law (Ernst & Banks, 2002), namely that merging multiple sensory cues such as visual and kinesthetic information for GREL estimates reduced the perceptual variability with respect to that measured when a single sensory channel (i.e., visual) is used (Fig. 4).

Interestingly, no relationship was found between the amount of body sway and the strength of the body tilt effect upon GREL estimates performed by arm movements (GREL-VP, Fig. 4B), in contrast to the significant correlation with GREL settings performed with vision alone (GREL-V, Fig. 4A). This might suggest that the experimental condition could nevertheless influence GREL perception among patients differently; the better compensated LDS (i.e., with lower body sway) showed a decreased GREL slope, whereas the less compensated showed an increased

GREL slope, when using the arm. Hence, only the former might have access to graviceptive cues from arm movement to counteract the body tilt effect in their GREL perception. Further results need to be obtained to validate this hypothesis, since our mean results showed no effect of the experimental condition across groups.

In conclusion, the present study demonstrates that the perception of the gravity-referenced eye level is not drastically affected in patients with long standing vestibular loss. Other sensory inputs such as somatosensory cues appear sufficient to provide as much information about gravity as the vestibular system for elaborating the geocentric component required in GREL judgements. This graviceptive information – in addition to that potentially arising from arm lifting movements (Gentaz & Hatwell, 1996) – cannot completely counterbalance the "body tilt effect" reported for both normals and LDS when judging the "Earth horizon". Nevertheless, our results illustrate the capability of patients with vestibular defect to correctly use alternative sensory information such as somatosensory cues in spatial judgement tasks.

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Absence de gravité et indices somesthésiques

Carriot, J., **Bringoux**, L., Charles, C., Mars, F., Nougier, V., Cian, C. (2004). Perceived body orientation in microgravity: effects of prior experience and pressure under the feet. Aviation Space & Environmental Medicine, 75, 795-799.

SHORT COMMUNICATION

Perceived Body Orientation in Microgravity: Effects of Prior Experience and Pressure Under the Feet

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CARRIOT J, BRINGOUX L, CHARLES C, MARS F, NOUGIER V, CIAN C. *Perceived body orientation in microgravity: effects of prior experience and pressure under the feet.* **Aviat Space Environ Med 2004; 75: 795–9.**

Human activities often involve sensing body orientation using cues from gravity. Astronauts in microgravity are deprived of those cues and may have difficulty with certain tasks. We theorized that experience in microgravity combined with mechanically induced pressure under the feet (foot pressure) would improve the accuracy of a subject's perception of the body's z-axis as indicated by pointing to the subjective horizon (SH). ***Method:*** Experiments were conducted during parabolic flights using five experienced subjects and five novices. Subjects were required to raise their arm to point to their SH with eyes closed. Measurements were made on Earth and in microgravity, with or without foot pressure. Both pointing accuracy and the kinetics of the movement were analyzed. ***Results:*** Performance by experts was stable under all conditions. However, novices in microgravity pointed to a significantly lower SH (16.5° below the 1-G SH) and slowed their movements (mean angular velocity of movement: $16.8° \cdot s^{-1}$ less than in 1 G). Foot pressure improved the performance of the novices so that it was closer to that observed at 1 G (8.9° below the 1-G SH). ***Discussion:*** These results suggest that pressure cues under the feet activated the internal model of gravity in the novices, and thus improved the accuracy of their perception of their z-axis. Subjects with prior experience in microgravity correctly perceived their z-axis without the supplementary input.

Keywords: arm movements, adaptation, frame of reference, expertise.

GRAVITY IS A CONSTANT, pervasive, and significant feature by which humans orient themselves to the environment; it affects practically every aspect of overt behavior. However, astronauts working in space must perform all kinds of tasks without gravity. They may lose their sense of body orientation or even develop a false sense of position relative to their environment.

A subject on Earth can point precisely to memorized targets without any visual information during the movement, even when the body's z-axis (head-to-foot) is tilted with respect to gravity. Such an egocentric task does not require knowledge of z-axis orientation relative to the environment, only the localization of the target and the position of the arm. However, when subjects are asked to use their arm to point to their subjective horizon (SH), tilting their z-axis systematically shifts the results (1). Because this geocentric task requires taking into account body orientation, it is a strong indicator of the perception of z-axis orientation with respect to the gravity vector (9).

This study was designed to investigate how perturbations of gravity influence perception of body orientation. We used a microgravity environment in which, without visual cues, the perceived z-axis remained the only available reference for body orientation. Lackner and DiZio found that free-floating subjects can feel disoriented (7). They hypothesized that perception of SH in microgravity was impaired due to misperception of the z-axis, but noted that a modification of the SH could also result from degradation of limb proprioception in microgravity (7). Otolith-spinal mechanisms normally regulate spindle sensitivity in the anti-gravity musculature; microgravity affects this system through modulation of excitatory control on the alpha and/or gamma motoneurons. The z-axis is then correctly perceived, but control of movement can be disrupted. This hypothesis implies modifications at the level of movement control, whereas misperception of the z-axis works at the level of central command.

In microgravity, somatosensory cues (touch and pressure) appear to be of great importance in spatial orientation (7). Applying pressure to the top of the head makes subjects feel upside down, confirming the increased weighting of localized somatosensory cues during spaceflight (11). The structural polarity of "up" or "down" cued by touch and pressure seems to be based on cognitive factors (7). Localized somatosensory cues may be centrally interpreted as reaction forces against gravity, leading subjects to perceive a virtual gravity vector and a specific body orientation with respect to that vector. We hypothesized that the mechanical application of pressure to the bottom of the feet (foot pressure) in microgravity would provide a virtual gravity vector and enable subjects to bring their SH closer to that measured in 1 G.

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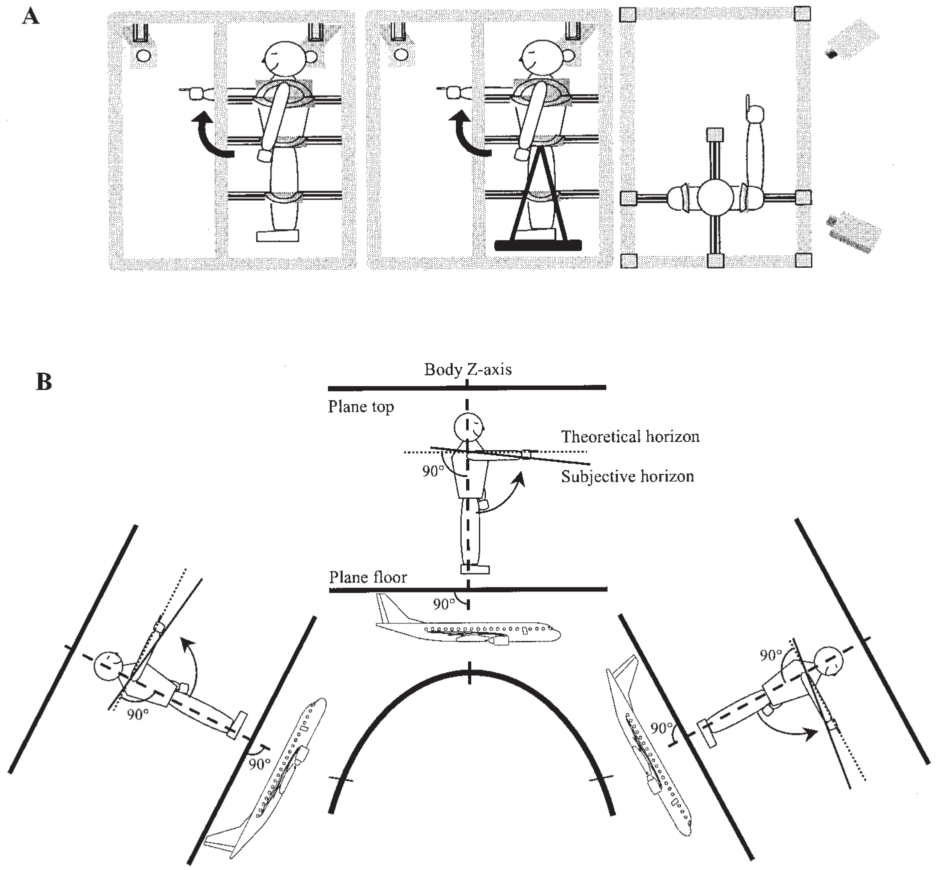

Fig. 1. A. Schematic representation of the experimental set-up. The left and center panels show side views of the set-up for microgravity without foot pressure and with, respectively. The right panel shows a top-view of the set-up including the cameras. B. Schematic representation of the movement used to indicate subjective horizon with respect to the body position inside the airplane at three different times during a parabola. The z-axis remained steady and perpendicular to the floor of the airplane. The arm position parallel to the floor of the airplane was the reference value.

An additional question concerned learning effects. It has been shown that in microgravity, when a repertoire of strategies used on the ground does not result in effective motor outputs, the central nervous system creates new strategies by means of a slow learning process (10). The dependence on non-inertial tactile and visual cues decreases after 1 wk in space, when the subjects manage to use their body frame of reference (11). Within this context, microgravity expertise through repeated experience of parabolic flights may induce an adaptive behavior that reduces or avoids the feeling of spatial disorientation. Therefore, we further hypothesized that z-axis perception would be less disrupted by microgravity in experts than in novices.

METHODS

The experiments were carried out during five parabolic flights aboard an Airbus A300 based in Bordeaux, France. Four conditions were studied: 1) 1 G on the ground 30 min before and 30 min after flight; 2) 1 G during level flight between parabolas; 3) microgravity without foot pressure (μG); and 4) microgravity with foot pressure (μG+FP). Each parabola started from level flight at 1 G and consisted of a 20-s pull-up at 1.8 G during which the aircraft climbed from 6000 to 8500 m, 20 s of microgravity obtained over the top of the trajectory, and then a symmetrical 20-s pull-out at 1.8 G to bring the aircraft back to horizontal flight at the original altitude. There was an interval of approximately 2 min between successive parabolas.

Subjects

There were 10 healthy right-handed volunteers (mean age 33 yr) who participated in the experiment. The novice group (4 men and 1 woman) had experienced a maximum of 62 parabolas (20 min maximum of microgravity) before this experiment. The expert group (also 4 men and 1 woman) had experienced about 3000 parabolas (mean 3087, range from 2697 to 3627), more than 1000 min of microgravity, during the past 5 yr. All subjects were naive about the purpose of the experiment and gave signed informed consent in compliance with the Huriet Law (i.e., Helsinki Convention) which governs and regulates human experimentation in France.

Apparatus

Subjects without shoes stood in a box approximately 140 cm long x 80 cm wide x 190 cm high. They were held in place by means of bungee cords attached to wide belts wrapped around the body at the level of the chest, hips, and knees. The cords exerted a distributed tension so that the subjects were held steady in the box during microgravity with their z-axis perpendicular to the floor of the airplane without contacting any surface (**Fig. 1A**, left panel). Foot pressure was generated by pulling a rigid plate up under the subject's feet by means of bungee cords adjusted to the subject's leg length and attached to the hip belt (Fig. 1A, middle panel).

To record kinematics, reflective markers were placed on the right side of the body at the hand (first phalanx of the index finger), shoulder (acromion), hip (iliac crest), and head (zygomatic process). Two digital cameras (DCR-TRV900E, Sony, Clichy, France), separated by an angle of 60° (Fig. 1A, right panel), recorded the pointing movements with a sampling frequency of 25 Hz. The recorded sequences were then digitized by means of a conversion card (Pinnacle DV500, Pinnacle Systems GMbH, Braunschweig, Germany) and the software Adobe Première (Version 6.1). The video sequences were analyzed with the Ariel Performance Analysis System (APAS 2000, v1.1, Ariel Dynamics Inc., San Diego, CA) to process the kinematics data associated with the markers. Data were filtered with a Butterworth filter (10 Hz cutoff frequency).

Procedure

Each trial consisted of five consecutive pointing movements performed with eyes closed during a 20-s period. The subject began with the right arm hanging down along the body, then raised the extended arm to point to the SH as quickly and as accurately as possible. Subjects were instructed to indicate the horizon defined on Earth as "where the sun rises in the sea at the level of the shoulder." They were further told to adjust the arm's level to coincide with the plane they perceived as perpendicular to gravity passing throughout their shoulder. In flight, this geocentric task was referenced to the interior of the aircraft so that the "horizontal plane" was parallel to the floor of the aircraft (**Fig. 1B**). Subjects indicated that they had reached their final arm position by pushing a button held in the left hand that activated a red light; further corrections were not allowed. The arm was then returned to the starting position for the next trial. Subjects performed the task on three 1-G phases (before, during, and after flight) and on eight successive parabolas, four each for μG and μG+FP in mixed order.

Data Collection

The stability of the body and of head position with respect to the body were confirmed by calculating the mean positions of the markers at the hip, shoulder, and head for each subject in each condition. Analysis of variance (ANOVA) was applied to these data for the x-, y-, and z-axes. Results showed no significant effect of condition ($p > 0.05$), indicating that body position was stable throughout all trials and conditions. We could, therefore, measure the angular movement between the axis of the trunk (markers of the hip and shoulder) and the axis of the arm (markers of the shoulder and index), where 90° represented the arm perpendicular to the body's z-axis and parallel to the floor. The final pointing position or SH for each condition was calculated in degrees averaged across all trials.

For technical reasons, movement kinematics were recorded for only six subjects (three experts and three novices). The analyzed variables were: 1) mean angular velocity of movement (VM), a better temporal indication than movement duration when amplitude varies, where slower movement is thought to be associated with more consistent control; 2) peak acceleration of the movement (PAM), representing the central command programmed before movement onset; and 3) time to peak acceleration of the movement (T-PAM) as a percentage of movement time, which indicates the extent to which the movement is controlled.

RESULTS

In order to verify that there was no systematic difference among the different 1-G phases, we analyzed all variables using ANOVA for group (expert vs. novice) × the three 1-G phases (before, during, and after flight) with repeated measures for phase. Results showed no significant effect of phase; we, therefore, pooled the 1-G data to form a single reference value for each dependent variable. No effect of group was found at 1 G for SH [$F(1,8) = 0.2$; $p > 0.05$; **Fig. 2A**] or for the PAM [$F(1,8) = 2.5$; $p > 0.05$; **Fig. 2C**]. However, compared with the novices, the experts showed a significantly higher VM [$F(1,8) = 105.7$; $p < 0.05$] and a longer T-PAM [$F(1,8) = 25.5$; $p < 0.05$; **Fig. 2B and 2D**, respectively].

To find out whether microgravity and foot pressure affected perception of the z-axis, all variables were analyzed using ANOVA for group × condition with repeated measures on the latter. A post hoc (Newman-Keuls) analysis was performed for variables where $p < 0.05$. SH showed no main effect for group [$F(1,8) = 2.08$; $p > 0.05$], but did show a significant effect of condition [$F(2,16) = 6.78$; $p < 0.05$] as well as a significant interaction of group × condition [$F(2,16) = 7.05$; $p < 0.05$]. As shown in Fig. 2A, novices indicated a lower SH in both microgravity conditions but were closer to their 1-G baseline with foot pressure, whereas experts indicated the same SH for both 1 G, μG, and μG+FP.

The VM for both groups was slower in microgravity compared with 1 G [$F(2,8) = 73.69$; $p < 0.05$], but was always faster for experts than for novices [$F(1,4) = 7.85$; $p < 0.05$; Fig. 2B]. Foot pressure increased VM for novices but did not influence experts (Fig. 2B). Novices showed a lower PAM than did experts [$F(1,4) = 7.41$; $p < 0.05$; Fig. 2C], and an effect of condition was observed [$F(2,8) = 18.34$; $p < 0.05$] as well as an interaction for group × condition [$F(2,8) = 18.91$; $p < 0.05$]. For novices, PAM was significantly smaller for μG and was closer to the 1-G value for μG+FP, whereas experts showed no change with condition. Finally, T-PAM was longer in microgravity than at 1 G [$F(2,8) = 6.95$; $p < 0.05$] with no difference between μG and μG+FP (Fig. 2D). No difference was observed for group [$F(1,4) = 4.70$; $p > 0.05$]. The interaction of the two factors [$F(2,8) = 7.24$; $p < 0.05$] showed that T-PAM for the experts remained stable throughout all conditions. For the novices, it was shorter in 1 G than in the other two conditions ($p < 0.05$) which remained similar ($p > 0.05$, Fig. 2D).

DISCUSSION

One aim of this study was to investigate how prior experience with microgravity might influence percep-

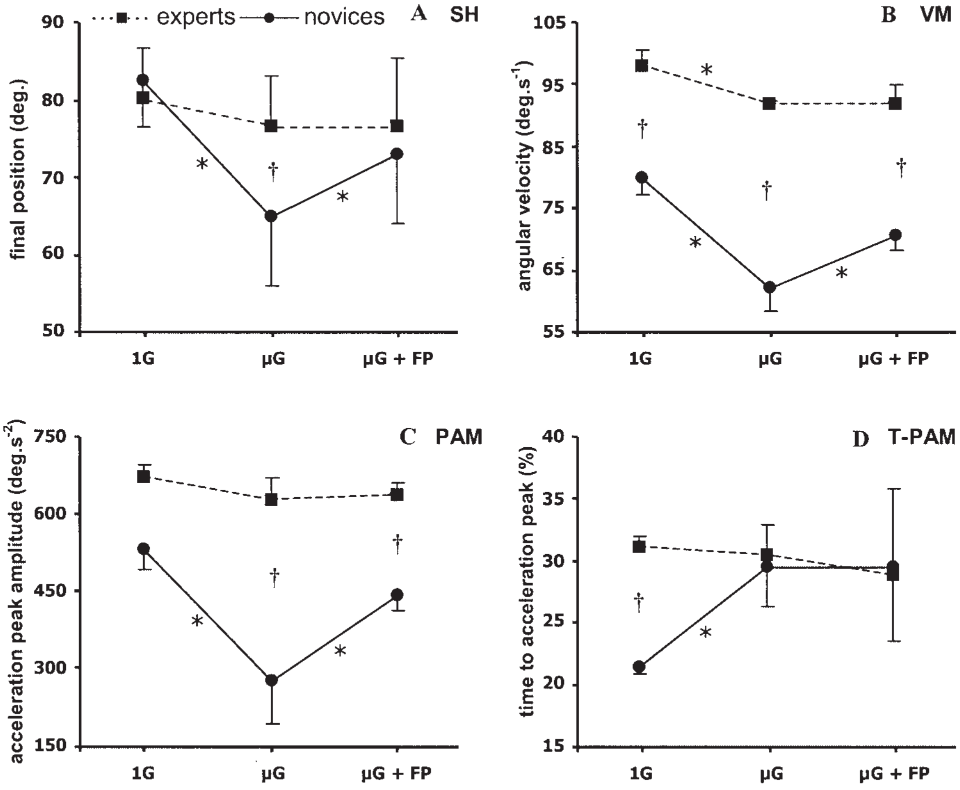

Fig. 2. Mean values and standard deviations for measured variables under three experimental conditions [1 G, microgravity (μG), and microgravity with foot pressure (μG+FP)]: A.) Final pointing position, indicating the subjective horizon (SH); B.) velocity of movement (VM); C.) peak acceleration of the movement (PAM); and D.) time to peak acceleration of the movement (T-PAM). The novices are shown by circles with solid lines and the experts by squares with dashed lines. Statistical significance ($p < 0.05$) is shown by † for differences between groups and * for differences among conditions.

tion of the z-axis during perturbations of gravity (absent or virtual). Results showed a lower SH in microgravity for novices, whereas experts retained stable perceptions. This difference cannot be related to ability to point to the horizon per se, as pointing accuracy in 1 G was similar for both groups. Moreover, it cannot be explained by an effect of frequent, rapid changes of condition (i.e., the parabola's succession of 1 G, 1.8 G, and microgravity) as the movements executed at 1 G in flight were similar to those executed on the ground before and after the flight.

Moving the arm toward the "horizontal," that is perpendicular to the body, requires the subject to take into account their z-axis. The presence of normal gravity allows an accurate perception of this axis. However, in microgravity the novice subjects were disoriented (7) and unable to use their z-axis as a frame of reference (5,11). As a result, their SH was less accurate and their movement kinematics differed. Adding pressure under the feet allowed novices to improve their performance. These pressure cues may have been interpreted as a force reaction against "virtual gravity" (6), perhaps by allowing central activation of a model of gravity that improved perception of the z-axis (9). This central hypothesis was supported by the observed modification of movement kinematics. The decrease of PAM and the increase of T-PAM in microgravity suggested that the central nervous system initialized the body frame of reference on the basis of available sensory information before starting the movement. For novices, this initial sensory state, modified by the exposure to microgravity, may have induced an incorrect prediction of the effect of microgravity on their motor behavior; by relying on both modified proprioceptive feedback and a misperception of their z-axis with respect to the floor of the airplane, novices may have overestimated the "muscle unloading effect" of microgravity (13). Such an overestimation would induce a movement of smaller amplitude and thus a lower SH, as shown by our data. A complementary hypothesis is suggested by studies of adaptation of postural control to microgravity (3,8), where subjects leaned forward with respect to the "vertical" even though they felt their posture to be normal. Adaptation to the absence of gravity was suggested to involve two mechanisms: a short-term operative process and a long-term conservative one. In our experiment, only the former could have been activated. Since subjects were held perpendicular to the floor of the airplane, they may have perceived themselves as leaning backward with respect to the reference position, causing them to undershoot their pointing movement.

Providing pressure under the feet would not improve proprioceptive feedback, but probably did allow the novices to make a more precise identification of their z-axis with respect to the airplane, resulting in a more accurate SH. In contrast, the experts showed no change in movement kinematics whatever the gravity condition. Although one might expect that producing the same movement in the absence of gravity would induce greater movement amplitude and speed, it is consistent with previous data showing stability of movement kinematics in 1 G (12). The only observed differences in 1 G were localized at the level of the muscles with an increase of the co-contraction when the movement was performed in the direction of gravity (12). A similar EMG pattern may also be observed in microgravity to reach the same movement accuracy with rather constant movement kinematics. Furthermore, the experts' movement was more ballistic, exhibiting higher VM and higher PAM, suggesting that the movement was preprogrammed and less dependent on the presence or absence of gravity. The experts, who were used to working without the frame of reference provided by gravity, may have developed an adaptive behavior that takes altered gravity into account. They would, then, be better at extracting and associating those relevant cues from the sensory systems that are still useful (2) in order to create a frame of reference for their body which remains stable, despite changes in external conditions, with respect to the airplane (5,11). This would explain why their performance did not change with our three conditions.

In conclusion, the removal of gravity as a frame of reference prevented novices from developing an accurate perception of the exocentric space, probably because they misperceived the orientation of their z-axis. As already shown in the literature (7), the central activation of an internal model of gravity, by means of pressure cues under the feet, improved the perception of the z-axis. Moreover, people with more prior experience of parabolic flight may have learned to use their z-axis as a strong frame of reference to avoid spatial disorientation.

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Influences cognitives

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Effects of external feedback about body tilt: Influence on the Subjective Proprioceptive Horizon

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Abstract

The present study investigated a cognitive aspect upon spatial perception, namely the impact of a true or false verbal feedback (FB) about the magnitude of body tilt on Subjective Proprioceptive Horizon (SPH) estimates. Subjects were asked to set their extended arm normal to gravity for different pitch body tilts up to 9°. True FB were provided at all body tilt angles, whereas false FB were provided only at 6° backward and 6° forward body tilts for half of the trials. Our data confirmed previous results about the egocentric influence of body tilt itself upon SPH: estimates were linearly lowered with forward tilts and elevated with backward tilts. In addition, results showed a significant effect of the nature of the external FB provided to the subjects. When subjects received a false FB inducing a 3° forward bias relative to physical body tilt, they set their SPH consequently higher than when they received a false FB inducing a 3° backward bias. These findings clearly indicated that false cognitive information about body tilt might significantly modify the judgement of a geocentric direction of space, such as the SPH. This may have deleterious repercussions in aeronautics when pilots have to localize external objects relative to earth-based directions in darkened environments.

Keywords: Spatial perception; Body orientation; Geocentric; Egocentric; Cognitive information

The perception of spatial orientation has been studied for decades, mainly through the influence of multiple sensory information, such as visual, vestibular and somatosensory cues available to the observer. However, recent literature provided growing evidence that cognitive factors may have a significant implication in spatial perception.

In this context, several studies focused on the role of subjective expectations in perceptual judgements about orientation in space. For instance, Lackner and DiZio [11] showed that sensations of body inversion in microgravity seem to depend on cognitive factors including anticipated or expected orientation with respect to the aircraft cabin. On earth, when subjects have prior knowledge of the type of linear motion to which they are exposed in darkness, they never exhibit any sensation of body tilt, contrary to what can happen when subjects are unaware of how they are moved [19]. This observation might be due to a cognitive suppression of tilt sensation when the displacement is known and expected. Conversely, mental imagery of a visual motion is able to facilitate the perception of a roll-vection displacement [12]. The perception of a geocentric direction, such as the subjective visual vertical has also been found to be significantly influenced by mental imagery [13,14] and by other cognitive components, such as the presence of a meaningful visual frame (e.g., a circular clock whose numbers were displaced [7]).

Not only subjective expectations but also external feedback (FB) provided by the experimenter can modify spatial perception. Earlier studies investigating factors of adaptation to prismatic displacements emphasized the influence of conscious correction strategies based on the relevant given information [18]. For instance, making subjects aware of the visual space shift by providing them explicit information about prisms distortion led to reduced levels of adaptation [10,17]. However, by investigating the effect of erroneous FB in a spatial context, Brosvic and Finizio [5] showed that if accurate FB may markedly reduce the magnitude of the Müller-Lyer illusion, inaccurate FB does not necessarily deteriorate judgements by the same amount of the FB itself.

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The following experiment aimed at investigating whether an external erroneous FB about body tilt magnitude can modify the perception of the Subjective Proprioceptive horizon, compared to a condition in which an accurate feedback is provided. The SPH can be considered an estimated geocentric direction as subjects have to set their extended arm normal to gravity for achieving the task [2,3,9]. The originality of the present study was then to question the influence of different types of external conscious information about body orientation upon the judgement of a geocentric direction of space.

Eight right-handed healthy subjects (four males and four females; mean age: 25 ± 3.6 years) took part in the experimental sessions. None of the subjects had any known history of vestibular or somatosensory disorders and they all provided informed consent prior to testing according to the local ethic committee guidance and to the Helsinki convention.

Subjects were seated on a tilting servo-controlled apparatus allowing slow rotations in pitch (Fig. 1; for a more detailed description, see Bourdin et al. [2]). The axis of rotation was located 60 cm behind subjects' back, 20 cm lower than their hip level. Position signals from the tilting apparatus were sampled at 20 Hz (12 bit A/D converter). An enslaved position and velocity system enabled to reach an accuracy of ±0.005°. Subjects were tightly restrained with harness-type safety belts and their head was firmly stabilized by means of strap restrains. A rigid gutter placed around the elbow joint with straps maintained subjects' right arm extended. The SPH measurements were performed using an inclinometer (Accustar© no. 0211002), which was held at the level of the lateral epicondyle of the humerus to record arm position with respect to gravity. It reached a range of ±60° and a resolution of ±0.001° for a response frequency of 0.5 Hz.

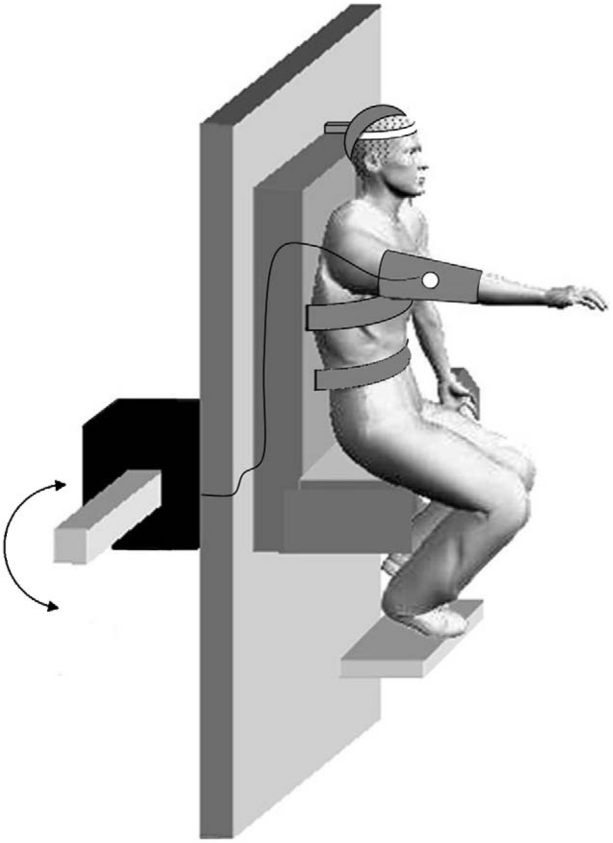


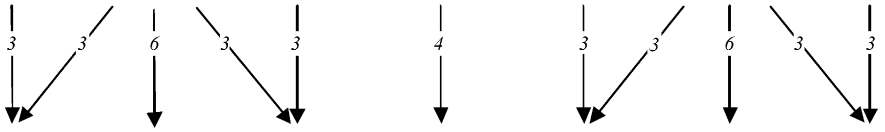
Fig. 1. Schematic representation of the experimental setup. The tilting apparatus enables to perform backward and forward body tilts at several velocities. Subjects were strongly attached with head, shoulders, hips and feet belts, to prevent any movement.

Two experimental sessions were randomly presented to the subjects. Both involved two successive episodes, a familiarization phase and a testing phase. During the familiarization phase, subjects were oriented at each angle of tilt manipulated during the subsequent testing phase. A constant velocity of 2° s^{-1} was used to reach, respectively, 3°, 6°, 9° forward (FOR) and 3°, 6°, 9° backward (BACK) tilts, at which the tilting apparatus stopped for 10 s. Subjects were informed about the real tilt magnitude at each angle of tilt. They were told to concentrate on the conscious sensations they would feel in the final static tilt rather than on the dynamics of tilt (as different patterns of rotation were manipulated in the subsequent testing phase). During the testing phase, each trial proceeded as follows: subjects were first positioned at a desired body orientation; then, they received an external FB about their body orientation, and finally, they were asked to judge their SPH by setting their right extended arm normal to the direction of gravity. Forty judgments were collected per subjects in the experiment. Seven body orientations (0°; 3° FOR, 6° FOR, 9° FOR and 3° BACK, 6° BACK, 9° BACK tilts) were presented and three tilt velocities (0.1°, 0.5°, 4° s^{-1}, with initial accelerations above the semi-circular canal threshold for rotation perception [1]) were randomly manipulated to avoid time cues for tilt perception. Verbal external FB about the magnitude of body tilt was provided by the experimenter once subjects' tilt was stabilized. This FB was either true or false. In case of false FB, provided only at 6° FOR and 6° BACK physical body tilts for half of the trials, a "directional bias" was induced, with a magnitude of either 3° *forward* or 3° *backward.* A *forward* bias corresponded to a 6° BACK physical tilt announced "3° BACK" or to a 6° FOR physical tilt announced "9° FOR". A *backward* bias corresponded to a 6° BACK physical tilt announced "9° BACK", or to a 6° FOR physical tilt announced "3° FOR". True FB was provided for the other half of the trials at 6° FOR and 6° BACK of physical body tilt and for the rest of tilts manipulated in the testing phase. Table 1 summarizes the organization of trials presented in the experiment. Once the physical tilt was reached, subjects were kept immobile during 20 s, allowing the semi-circular canal effects to settle down [8], with their right arm aligned with the trunk. Then, they were asked to adjust their SPH by setting their right extended arm horizontally (i.e., normal to gravity) and to keep it in position for 3 s before turning back to the starting position. The tilting apparatus was brought back to the vertical after each SPH judgement at random constant velocities (0.1°, 0.5°, 4° $s^{-}1$) and the room was enlightened until the next trial. Throughout the experiment, none of the subject consciously perceived any bias in the given external FB.

A six body tilts (3° FOR, 6° FOR, 9° FOR, 3° BACK, 6° BACK, 9° BACK tilts) × three velocities (0.1°, 0.5°, 4° s^{-1}) analysis of variance (ANOVA) with repeated measures on all factors was performed on SPH estimates when true FB about body orientation was provided. It showed a main effect of the angle

Table 1
Number of trials (SPH estimates) for each body orientation

Body orientation	9 deg FOR	6 deg FOR	3 deg FOR	0 deg	3 deg BACK	6 deg BACK	9 deg BACK
Number of trials relative to real tilt	3 3 velocities × 1 [true] FB × 1 repetition	12 3 velocities × 1 [true] FB × 2 repetitions + 3 velocities × 2 [false] FB × 1 repetition	3 3 velocities × 1 [true] FB × 1 repetition	4 1 [true] FB × 4 repetitions	3 3 velocities × 1 [true] FB × 1 repetition	12 3 velocities × 1 [true] FB × 2 repetitions + 3 velocities × 2 [false] FB × 1 repetition	3 3 velocities × 1 [true] FB × 1 repetition
Number of trials relative to announced tilt	6	6	6	4	6	6	6



The purpose of this repartition is to generate the same number of trials for each magnitude of *announced* tilt.

of tilt ($F(5,35) = 10.64$, $p < 0.001$), but no effect of tilt velocity ($p = 0.40$) and no interaction between the two factors ($p = 0.16$). Furthermore, a regression analysis yielded a significant linear relationship between the angle of tilt and SPH estimates when subjects received veridical information about the magnitude of their body tilt (Fig. 2). Indeed, when a true FB was provided, SPH settings appeared significantly lower when subjects tilted forward and conversely higher when subjects tilted backward than when they sat upright.

A second step consisted in comparing SPH judgements achieved under true and false FB conditions. A two body tilts (6° FOR and 6° BACK) × three conditions of external FB (no bias condition for which correct FB about body tilt magnitude was provided; false FB condition inducing a *forward* bias; false FB condition inducing a *backward* bias) ANOVA was performed on SPH estimates. Results showed a main effect of the angle of tilt ($F(1,7) = 14.30$, $p < 0.01$; Fig. 3). SPH estimates appeared significantly lower at 6° FOR physical body tilt than at 6° BACK physical body tilt, whatever the FB condition. In addition, the ANOVA yielded a main effect of FB condition ($F(2,14) = 4.59$, $p < 0.05$): SPH settings appeared significantly higher in the *forward* bias condition when compared to the *backward* bias condition ($p < 0.05$; Newman–Keuls post hoc test; Fig. 3). The interaction between the two factors was not significant ($p = 0.37$).

Two main findings emerged from the present experiment. First, we found a clear linear effect of body tilt on SPH estimates when true external FB about the magnitude of tilt was provided to the subjects. This influence of body orientation is in line with many studies involving geocentric judgements, such as

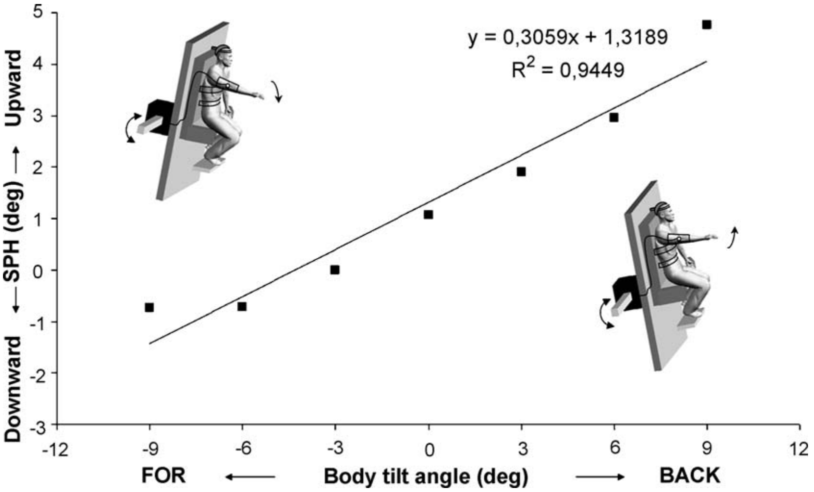


Fig. 2. Mean SPH as a linear function of whole-body tilt, when subjects received a true FB about the magnitude of their body tilt (i.e., no bias condition). Negative angles of tilt corresponded to forward tilts (FOR), whereas positive angles of tilt corresponded to backward tilts (BACK). Negative SPH values indicate settings below physical proprioceptive horizon whereas positive SPH values indicate settings above physical proprioceptive horizon. Sketches show the direction of the "body tilt effect".

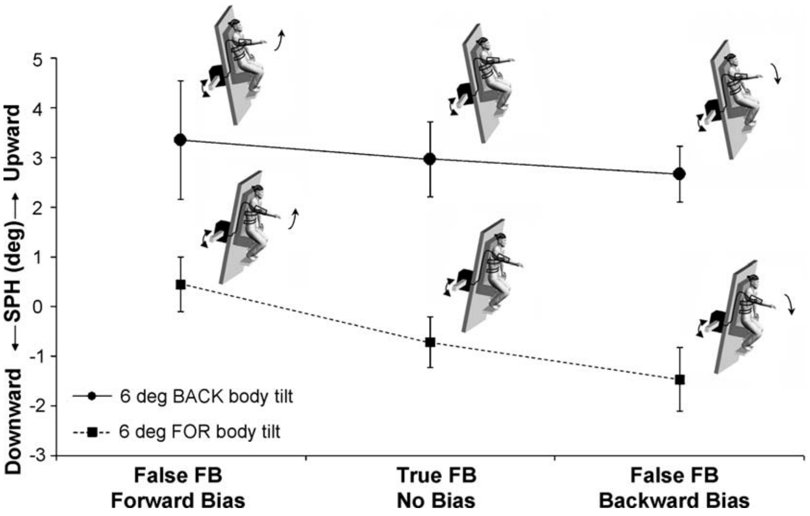


Fig. 3. Mean SPH estimates and standard errors recorded at 6° BACK and 6° FOR physical body tilts for different conditions of external feedback about body tilt magnitude. The *forward* bias condition corresponds to a false external information given by the experimenter about body orientation with a $-3°$ forward error (e.g., 6° BACK physical tilt announced "3° BACK", or 6° FOR physical tilt announced "9° FOR"). The *backward* bias condition corresponds to a false external feedback about body orientation with a $+3°$ backward error (e.g., "6° BACK" physical tilt announced "9° BACK", or 6° FOR physical tilt announced "3° FOR"). The no bias condition (which can be viewed as a baseline) corresponds to a true external feedback about body tilt. Sketches show the direction of the "Feedback effect".

the subjective visual vertical in roll tilts (i.e., A-Effect, [4,15,20]) or the gravity referenced eye level in pitch tilts [3]. This effect could be explained by an "egocentric attraction" upon geocentric estimates exerted by the longitudinal *Z*-axis as a reference for verticality (i.e., idiotropic vector hypothesis [15]). Bourdin et al. [2] already showed a similar effect of body tilt upon SPH estimates when up to 8° slow body tilts were achieved without external FB. Strikingly, the slope of the linear regression line, reflecting the importance of the body tilt effect, was almost comparable in both studies (0.31 versus 0.34 in Bourdin et al.'s study). This may indicate that the knowledge of the magnitude of body tilt, when veridical, does not help subjects to successfully compensate for the egocentric attraction exerted by a physical tilt.

The second main finding of the present experiment was that false cognitive information provided to the subjects about their body orientation may yield repercussions on their perception of the geocentric environmental space. We found indeed a significant effect of the nature of the external FB relative to the magnitude of body tilt on SPH settings. When a *forward* bias in external FB was induced (i.e., when the magnitude of body tilt was actually announced 3° forward relative to the physical tilt), SPH was consequently set higher than in the *backward* bias condition. Although subjects were totally unaware of the incongruence between physical tilt and external FB, they partially compensated for the externally induced over- or under-estimation of tilt in their SPH estimates. In other words, when subjects were "induced" to feel more tilted forward than they actually were, the upward arm movement they need to do for setting their SPH exceeded in magnitude the one they would perform if they were induced to feel less tilted. This demonstrates that subjects took into account erroneous cognitive information about body tilt in their SPH judgements. Previous works already emphasized the role of erroneous external FB in sensorimotor [6,16] or in spatial perception [5,21] tasks, but they manipulated sensory sources as biased information and the provided FB essentially related to the measured variable. In the present experiment, we demonstrated that a biased verbal FB about body orientation might indirectly affect the perceived geocentric space. However, one must notice that the "amount" of cognitive bias was not fully taken into account in the SPH judgement. For instance, a +3° *forward* bias did not induce a +3° *upward* SPH setting, the ratio between FB bias and its repercussions on SPH estimates being less than one third in average. This is in line with results from Brosvic and Finizio [5], who showed that inaccurate FB about the Müller-Lyer illusion is not fully taken into account by the central nervous system to reach the intended adaptation.

Nevertheless, the present study clearly showed that subjects can be deleteriously influenced by wrong cognitive information about body tilt in judging a geocentric direction of space, such as the SPH. This may have important repercussions in aeronautics when pilots have to judge the position of external objects relative to earth-based directions in darkened environments.

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Le paradigme du franchissement d'obstacles : Effet de l'inclinaison du corps en tangage

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RESEARCH ARTICLE

Judging beforehand the possibility of passing under obstacles without motion: the influence of egocentric and geocentric frames of reference

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Abstract Previous studies have shown that the perception of the earth-based visual horizon, also named Gravity Referenced Eye Level (GREL), is modified by body tilt around a trans-ocular axis. Here, we investigated whether estimates of the elevation of a luminous horizontal line presented on a screen in otherwise darkness and estimates of the possibility of passing under are identically related to body tilt in absence of motion. Results showed that subjects overestimated the elevation of the projected line, whatever their body orientation. In the same way, subjects also overestimated their capacity of passing under the line. Both estimates appeared as a linear function of body tilt, that is, forward body tilt yielded increased overestimations, and backward body tilt yielded decreased overestimations. More strikingly, the linear effect of body tilt upon these estimates is comparable to that previously observed for direct GREL judgements. Overall, these data strongly suggest that the perception of the elevation of a visible obstacle and the perception of the ability of passing under in otherwise darkness shared common processes which are intimately linked to the GREL perception. The effect of body tilt upon these perceptions may illustrate an egocentric influence upon the semi-geocentric frame of reference required to perform the task. Possible interactions between egocentric and geocentric frames of reference are discussed.

Keywords Spatial perception · Egocentric · Geocentric · Frame of reference · Gravity Referenced Eye Level · Body orientation

Introduction

Imagine you are stuck in your van, on a foggy day, waiting to enter a car park whose entrance is height restricted. You will probably ask yourself: “am I able to pass under the gate?” Perceiving the location of static obstacles in an impoverished visual environment is a complex task which is then crucial for avoiding collisions. The localization of an object in space may be achieved through different systems of coordinates named frames of reference (Howard 1982). Although visible surroundings may constitute a frame of reference for *allocentric* judgements, the body may define axes and planes relative to which *egocentric* judgements can be performed (Paillard 1991). For instance, the height of a gate may be either referred to some objects present in the visual field or to “eye level” (Matin and Li 1992). Although eye level is usually defined as a central norm for up and down egocentric localization in darkness (Matin and Li 1995), it may evoke two distinct spatial references, often undistinguished in the literature. One is the plane normal to the frontal plane of the head (Head-Referenced Eye Level or HREL) and the other is the plane normal to the direction of gravity (Gravity Referenced Eye Level or GREL; Stoper and Cohen 1989). Both references coincide when the observer stands stationary and erect but become different as soon as the observer is tilted. Although HREL judgements can be assessed in a pure egocentric frame of reference, GREL estimates must integrate a *geocentric* component (i.e., the horizontal plane). Therefore, GREL, also known as the earth-based visual horizon,

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can be considered a semi-geocentric reference (Bringoux et al. 2004, 2007).

The main purpose of the present experiment is to investigate whether the judgement of the elevation of an object (e.g., a horizontal line) and estimate of passing under in darkness share common mechanisms for which GREL constitutes the fundamental spatial reference.

Until recently, it was broadly accepted that specific sensory cues, mainly issued from vestibular and somatosensory inputs, were able to inform accurately about some geocentric directions of space (Benson 1990; Pozzo et al. 1990). This assumption mainly stems from the confusion between efficient postural control for stance conservation mediated by vestibulo-spinal pathways and higher perceptual graviceptive functions. Several experiments demonstrated, however, that the conscious estimation of the gravitational direction fundamentally differs from the perception and control of body orientation (Bringoux et al. 2003; Bronstein 1999). Nevertheless, as otolith organs and other somatic graviceptors were thought to provide accurate information about vertical and horizontal directions, GREL was assumed to be rather correctly estimated under normal circumstances (Schöne 1964; Tribukait and Eiken 2005).

In darkness, however, the subjective GREL appears slightly lower than the objective physical reference (MacDougall 1903; Stoper and Cohen 1986). It has also been shown that GREL perception is influenced by pitch tilts of the visual field (Li et al. 2001; Matin and Fox 1989; Matin and Li 1992; 1995; Stoper and Cohen 1989) and by modifications of the gravitoinertial force field strength (Cohen 1973; DiZio et al. 1997; Lackner and Graybiel 1980; Schöne 1964; Tribukait and Eiken 2005; Welch et al. 1996). More recently, GREL judgements in normogravity have been found linearly deviated towards body tilts ranging from 30° backward to 20° forward (Bringoux et al. 2004, 2007). The quantity of this deviation reached 20% of the body tilt magnitude. This phenomenon, named "egocentric attraction", has been interpreted as a perceptual shift, in line with the idiotropic vector hypothesis stated for vertical estimation (Mittelstaedt 1983). The latter postulates the existence of a central tendency to bias the subjective vertical towards the direction of the observer's body *Z*-axis. Similarly, the tendency to shift GREL estimates towards HREL may illustrate an egocentric influence upon the semi-geocentric frame of reference required to perform the task. Subjects with bilateral vestibular deficit exhibit a comparable effect (Bringoux et al. 2007), suggesting that vestibular inputs are not determinant in counteracting this egocentric attraction. Comparable shifts when tilted have been reported for judgements of hand orientation relative to earth-fixed horizontal (Chelette et al. 1995) or judgements of the forearm orientation relative to earth-fixed vertical (Darling and Hondzinski 1999). However, as shifts in GREL estimates correspond to a modification of the perceived visual space (Schöne 1964), this may yield important consequences in the manner to which observers visually localize objects in an otherwise dark environment.

Several studies have shown that the localization of objects with respect to head-centric fixed planes (e.g., the transverse plane or the mid-sagittal plane of the head) was influenced by eye position, in the direction opposite to the eccentric gaze (Bock 1993; Lewald and Ehrenstein 2000). Alternatively, Poljac et al. (2005) demonstrated that the perceived elevation of objects relative to the "plane of regard" (defined by the interocular axis and the fixation point) is accurate, irrespective of eye and head orientation. Moreover, the gaze orientation was also found correctly estimated (Poljac and van den Berg 2005). This strongly suggests that the plane of regard constitutes a useful reference for accurate egocentric perception of objects' elevation. Therefore, it may be stated that a correct representation of the objects' location relative to the plane of regard is necessary for the transformation into a geocentric reference frame (Poljac and van den Berg 2005).

Within the general reference frame research area, the present study aims firstly at investigating whether the perception of objects' elevation into a geocentric reference frame is referred to GREL in absence of visual allocentric cues. In such a case, one would expect that the perceived elevation of an obstacle is modified by whole-body orientation, because the related reference (i.e., GREL) is linearly influenced by pitch tilts.

Secondly, this work aims at determining whether the perceived possibility of passing under a visible obstacle is also related to GREL perception in otherwise darkness. Such projective judgements would encounter the same dependency on body orientation as elevation estimates if one considers that: (1) the distance separating the obstacle from the observer (i.e., depth cue) is correctly estimated, (2) the observer internally represents the virtual displacement as horizontal (i.e., perpendicular to gravity), and (3) that body scheme—and specifically the perceived distance separating the eyes from the top of the head—is unmodified during body tilt.

Methods

Subjects

Twelve subjects (six males and six females; mean age 28 ± 4.6 years) with normal or corrected to normal vision participated in the experiments. They had no previous history of vestibular or other neurological symptoms. All gave informed consent, in compliance with the ethical laws which govern and regulate human experimentation in France.

Apparatus

The subjects were seated and firmly secured on a padded tilting chair by means of a shoulder harness (Fig. 1). The subjects' head, restrained with a headrest, was positioned such that the naso-occipital axis was orthogonal to the direction of gravity when the chair was vertically oriented. The axis of rotation of the tilting chair was coincident with the trans-ocular axis. This allowed in keeping eye level at the same height independently of the tilt magnitude. The chair could be tilted in pitch through a range extending from +20° backward to -20° forward. The random patterns of tilt induced angular accelerations well above the semicircular canals' threshold for tilt perception (defined at $0.3°/s^2$ by Benson 1990).

A laser pointer mounted on a fixed structure, positioned above the tilting chair was used to project a thin horizontal beam on a mirror. The pitch orientation of the mirror was adjustable by means of a servo-controlled galvanometer. The reflected beam was projected on a flat vertical screen of 2 m in height × 2.5 m in width, placed in front of the subjects, 2.28 m away from their eyes. The height of the luminous horizontal line, 2 m in width and 0.001 m in thickness, could be adjusted with a precision of 0.001 m. Subjects held in hands a push button box for judgement settings. Galvanometer control and response recordings were performed by the ADwin-Pro system (Keithley®) piloted via the Docometre© software.

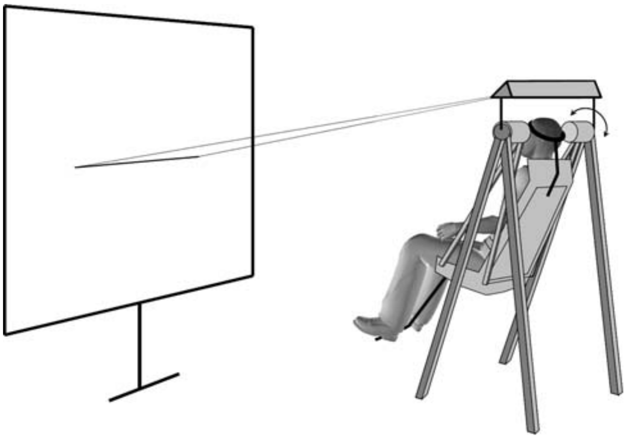

Fig. 1 Experimental set-up. The angular position of the platform could be set from +20° backward to −20° forward by rotation around the subjects' trans-ocular axis. The screen on which the thin luminous *horizontal line* was projected at different elevations was 2.28 m away from the observer's eyes

Procedure

The present experiment was divided into two counterbalanced sessions, lasting 45 min each. The first session required the subjects to judge the height of a luminous horizontal line relative to their earth-based visual horizon, presented as "*where the sky meets the sea*". Drawings and illustrations were also shown to avoid any confusion about the nature of the reference. In the second session, the subjects were asked to estimate whether they would be able to pass under the projected luminous line with their current body orientation. During this session, subjects were not told about any reference such as eye level or visual horizon for making their judgement. This clearly distinguishes the second perceptual task with respect to the former. For both sessions, five sagittal body orientations were randomly adjusted (0°; forward tilts: −10°, −20°; backward tilts: +10°, +20°). For each of these orientations, 10 luminous line elevations were randomly presented, ranging from +20 cm upward to −35 cm downward relative to eye level for session 1 and from +35 cm upward to −20 cm downward relative to eye level for session 2.

A typical sequence of judgements unrolled as follows: The subjects were first rotated to the desired angle of orientation. This was followed by a 15 s period of rest, allowing the post-rotational effects issued from the semicircular canals stimulation to fade away (Benson 1990). Then, the luminous line was projected at a set height in the otherwise dark room, and the subjects were allowed to open their eyes and stare at it for 4 s. Following this period of observation, subjects were asked to give a forced-choice response in a 3 s interval via the push buttons ("above the earth-based horizon" or "able to pass" with the right hand-held button and "below the earth-based horizon" or "not able to pass" with the left hand-held button). Then, the subjects were requested to close their eyes for about 5 s while the luminous line was adjusted to a new height. Ten judgements (corresponding to 10 line elevations) were collected within a sequence executed at a given body orientation. Each sequence ended by a rotation of the tilting chair back to the vertical position, and the room was turned on for 5 s before a new sequence was launched. Four similar sequences, for a total of 200 judgements, were recorded in each session.

Data processing

Judgements were converted in binary values. A score of 1 was attributed to positive estimates, that is, when a line elevation was perceived higher than the earth-based horizon (session 1) or higher than the minimal height for passing under (session 2). Conversely, a score of 0 was attributed to negative estimates. A Probit model, using a non-linear regression analysis for dichotomic variables, enabled us to determine the probability P that a line elevation be judged higher or lower than the considered reference. The Probit function (Eq. 1) was characterized by the following relation:

$$p_{\mathrm{i}} = 1/\left(1 + \left(\mathrm{C}\left(_{\mathrm{i,j}}\right)/\mathrm{C}_0\right)^{\mathrm{n}}\right) \qquad (1)$$

where "p_{i}" is the probability of perceiving a line elevation higher than the related reference, "i" corresponds to the line number in the sequence, "j" to the trial number, "C_0" the line number for $P = 0.5$ and "n" the slope of the tangent at the inflection point of the curve. The latter coefficient constitutes an estimation of the discrimination sensibility relative to the chosen increments. A repeated measures Analysis of Variance (ANOVA) was performed on "n" values, to test any differences between sessions and body orientation conditions.

Line elevations obtained at $P = 0.5$ via the psychometric function define thresholds for the perceived earth-based horizon, that is, the subjective GREL (session 1), and for the minimal height required for passing under obstacles (session 2). A repeated measures ANOVA was applied to these thresholds, calculated for each subject at each body orientation, to test any differences between sessions and body orientations. For convenience, thresholds were expressed as a vertical elevation (in cm) relative to eye level. Finally, a linear regression analysis was conducted on the mean thresholds relative to the magnitude of body tilt, to establish the presence of a linear effect of body orientation upon estimates.

Results

Probit analysis

A non-linear regression analysis (Probit function) applied to raw judgements was used on each subject's data to specify the thresholds around which a line elevation was perceived higher or lower than the related reference (see Methods). Figure 2 shows the psychometric functions obtained for a subject at different body orientations.

To assess the discrimination sensibility of the Probit processing, a 2 session × 5 body orientation (−20°; −10°; 0°, +10°; +20°) ANOVA was applied to the "n" values (i.e., the slopes calculated at the inflection point of each function). Results showed that the discrimination sensibility did not differ, whatever the session ($F_{(1,11)} = 0.45$, $P = 0.52$) or the body orientation ($F_{(4,44)} = 2.99$, $P = 0.11$). The interaction between both factors was also non-significant (($F_{(4,44)} = 0.36$, $P = 0.84$).

Mean threshold comparisons

The thresholds obtained via the Probit analysis were found notably lower than true eye level. In session 1, the mean line elevation perceived at earth-based horizon (i.e., the subjective GREL) was −10.5 cm relative to eye level, that is, subjects consistently overestimated the elevation of the projected line with respect to eye level. In session 2, the mean minimal height for passing under the line was −1.12 cm relative to eye level. This means, for instance,

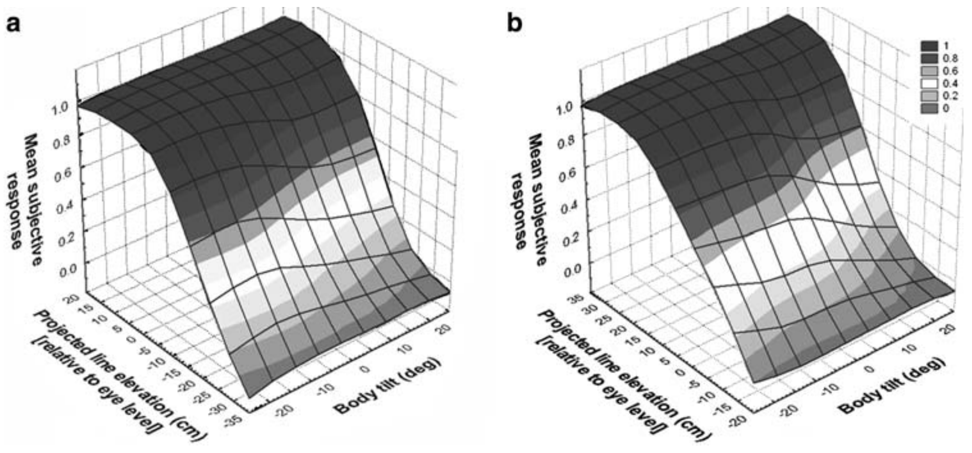

Fig. 2 Typical psychometric functions from a subject obtained via Probit non-linear regression analysis for the different body orientations in the two experimental sessions. The mean subjective responses corresponded to the mean perceptual scores obtained when the subject had to estimate that a particular line elevation was either higher (score = 1) or lower (score = 0) than Earth-based horizon (Session 1: **a**) or than the minimal height for passing under (Session 2: **b**). The values of subjective responses extracted at $P = 0.5$ from each Probit function correspond to the thresholds for Subjective GREL (session 1) and the perceived minimal height for passing under the line (session 2)

that subjects judged they could pass under a line projected at eye level. In other words, they overestimated their capacity of passing under an obstacle, whatever their body orientation.

A 2 session × 5 body orientation (−20°; −10°; 0°, +10°; +20°) ANOVA conducted on the calculated thresholds revealed a significant difference between sessions ($F_{(1,11)} = 20.56$; $P < 0.01$). The mean threshold corresponding to the perceived minimal height required for passing under obstacles was unsurprisingly higher than the subjective GREL. The mean difference between both thresholds (9.5 cm) was close to the physiological distance between eyes and upper head (11 cm).

The ANOVA also yielded a significant effect of body orientation ($F_{(4,44)} = 8.06$; $P < 0.01$). A post hoc analysis (Newman–Keuls test) showed that the thresholds obtained at +20° of body tilt were significantly higher than those calculated at 0, −10° and −20° ($P < 0.01$). In the same way, thresholds obtained at +10° were significantly higher than those calculated at −20° ($P < 0.05$). The interaction between both factors was non-significant ($F_{(4,44)} = 0.21$; $P = 0.93$), that is, the effect of body orientation was not different between sessions (Fig. 3).

Linear regression analysis on threshold estimates

The linear regression analysis applied to the thresholds obtained in both sessions with respect to body orientation (Fig. 3) showed a significant effect of body tilt upon the subjective GREL ($F_{(1,3)} = 22.11$; $P < 0.05$) and upon the perceived minimal height for passing under obstacles ($F_{(1,3)} = 65.85$; $P < 0.01$). The more the subjects were tilted forward (up to −20°), the lower the thresholds, that is, the more the subjects overestimated the elevation of an obstacle and their capacity of passing under. Conversely, the more the subjects were tilted backward (up to +20°), the higher the thresholds, that is, the less the subjects overestimated the elevation of an obstacle and their capacity of passing under. Non-significant individual linear regressions observed in three subjects unauthorized the statistical comparison of slopes calculated for each regression line between sessions. Nevertheless, observation of the data and absence of significant interaction in the threshold comparison ANOVA strongly suggest that the linear effect of body orientation was similar in both sessions.

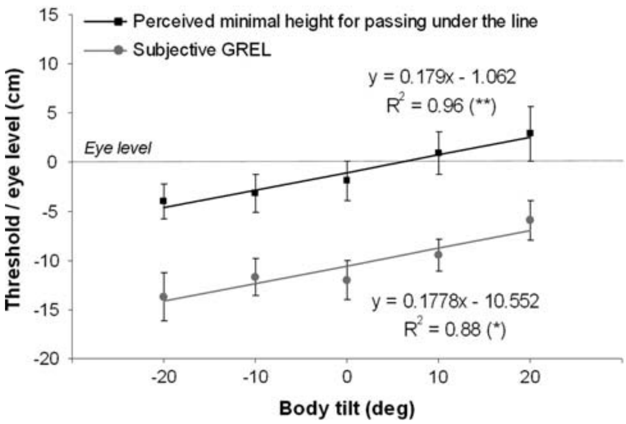

Fig. 3 Linear regression lines applied to the mean thresholds (plotted with ± SE) obtained for the different body orientations in the two experimental sessions. Subjective GREL and the perceived minimal height for passing under the line were found to be similarly and linearly related to body tilt

Discussion

The present study aimed at investigating whether the perceived elevation of a luminous obstacle in otherwise darkness and judgements of the capacity of passing under are identically influenced by body tilt. Both types of estimates were found inaccurate with respect to the true elevations—that is, subjects overestimated the elevations of the projected line relative to GREL and their ability of passing under, whatever their body orientation. More strikingly, we showed that body tilt exerted a comparable linear influence on both estimates. The latter observation may indicate the existence of a common reference for judging the elevation of obstacles in a dark environment and the capacity of passing under in absence of any displacement.

The GREL as a key reference

The main finding of the present experiment is that body tilt yields a comparable influence on the perceived ability of passing under a luminous horizontal line as on elevation judgements relative to GREL. This strongly suggests that GREL constitutes a fundamental reference for estimating, without motion, the possibility of avoiding above-head obstacles when allocentric cues are not available. Changes observed on the subjective GREL during body tilt may then have a direct effect on the perceived ability of passing under obstacles, even when GREL is not explicitly specified as the reference to be used for the judgement (e.g., as in session 2). Former results discussed in the frame of the ecological theory of affordances (Gibson 1979; Warren 1984) already suggested that intrinsic information about object’s elevation is scaled with reference to the perceivers’ eyeheight (Mark 1987; Van Der Meer 1997). Specifically, when manipulating the optical texture convergence which led to illusory rising of the floor, a decrease in subjective eyeheight was observed, that in turn yielded a modification of “passability” judgements of apertures (Warren and Whang 1987).

Similar eyeheight-scaled information was also found in the affordance of passing under a barrier for children and adults (Van Der Meer 1997).

However, such models of affordance were developed in presence of a structured visual field where information about environmental properties is naturally scaled in terms of some body dimensions of the observers (Mark 1987). Here, we demonstrate a similar effect of body tilt upon GREL judgements and estimations of the possibility of passing under obstacles without changing eyeheight-scaled information and in absence of structured visual field.

The fact that GREL perception is probably involved in the perceived ability of passing under obstacles implies three conditions to be fulfilled. The first one is that the distance separating the obstacle from the observer (i.e., depth cue) be correctly estimated. This is important, as an object located at a given angle above GREL will be perceived higher if its distance is overestimated. If fusional vergence (based on binocular disparity) is probably not a salient distance cue in the present study (involving a thin horizontal line projected on a screen), accommodation, in addition to the prior knowledge of the distance between the screen and the tilting chair, are good candidates to enable the perception of depth of the projected visual scene (Büttner and Büttner-Ennever 2005). The second required condition is that the observer internally represents the virtual displacement as horizontal. Once again, prior knowledge of the room configuration (e.g., horizontal floor) may facilitate the access to this information. A third condition implicitly underlies the direct link between the subjective GREL and the perceived ability of passing under obstacles. It requires that the perceived distance separating the eyes from the upper head be kept stable during body tilt. This assumption is supported by the constant gap between the two mean thresholds whatever body orientation, as illustrated by the parallel regression lines in Fig. 3. In addition, the mean difference between thresholds (9.42 ± 0.83 cm) is close to the mean physiological distance between eyes and upper head, calculated at various body orientations (11.3 ± 0.86 cm), suggesting an accurate and stable representation of body scheme for different body orientations or gravitational environments (Gurfinkel et al. 1993).

The idea that GREL may be regarded as a key reference in the perceived possibility of passing under obstacles is then mainly supported by the existence of a body tilt effect comparable to that observed for direct GREL estimates. The following part will discuss the potential origins of this body tilt effect.

Origins of the body tilt influence

Mittelstaedt (1983) postulates the existence of a central and idiosyncrasic tendency to shift the estimates towards the observer's own *Z* axis, named "idiotropic vector". This is obviously the expression of an egocentric influence upon a geocentric judgement, close to the effect observed in the present study. The remaining question is which body part constitutes the predominant source of this egocentric attraction.

A first candidate could be the retinal meridian planes of the eyes (Poljac et al. 2005). Following this interpretation, such a geocentric estimate could be drawn towards the longitudinal retinal meridian (Wade and Curthoys 1997). In the pitch dimension, Poljac et al. (2005) showed that the plane of regard, containing the interocular axis and the line of sight, is a fundamental reference for egocentrically judging the elevation of objects, irrespective of head orientation. Further experiments need to be carried out to investigate whether the plane of regard is also predominantly involved in earth-based elevation judgements.

As a second candidate, the head may also play a major role in the reported egocentric attraction. Head stabilization relative to gravity while walking is thought to provide a stable egocentric reference for spatial perception (Pozzo et al. 1990). In the sagittal plane, several studies emphasized the involvement of the transverse plane of the head at eye level (HREL) as a reference for egocentric judgements (Stoper and Cohen 1989; Matin and Li 1992; 1995). Nevertheless, the specific role of this reference remains to be investigated for geocentric estimates collected in the pitch dimension.

At a higher level, the longitudinal whole-body axis has often been evoked as the main reference for egocentric attraction in earth-based judgements (Mittelstaedt 1983). Observations in microgravity strongly suggest that astronauts rely on the virtual line running from the head to the feet to determine the direction of up and down and orientations of objects in the spacecraft (Clément et al. 2007). Ito and Gresty (1996) demonstrated that a rostrocaudal trunk-and-leg axis is predominantly used as a reference for SVV settings in the sagittal plane when the body is tilted backward. Changing the posture of a seated human subject (e.g., extended or bended legs) would help determine the relative weight of this reference in the perceptual process yielding earth-based spatial orientation and localization.

Whatever the main body axes involved in the body tilt effect, our results support the hypothesis of an interaction between egocentric and geocentric frames of reference. In this context, tasks and/or environmental requirements could not only produce switches between frames of references (Ghafouri et al. 2002), but also mutual influences and partial overlapping. Several studies indeed suggest the existence of an intermediate state where the frame of reference normally required to adequately perform the task is distorted by a concurrent one (Heath et al. 2007; Neggers et al. 2005). Neural correlates of interactions between egocentric and allocentric frames of reference have been found in the right posterior parietal and right ventral premotor cortex (Fink et al. 2003; Committeri et al. 2004). Still, further experiments need to be conducted to isolate the neurophysiological locus of the interaction between egocentric and geocentric frames of reference emphasized in the present work.

Conclusion

Our study strongly supports the idea of common perceptual processes for judging, without motion, the elevation of a luminous object in otherwise darkness and the possibility of passing under. Both estimates may be based on the perception of the subjective GREL, a semi-geocentric reference whose perception may be biased towards some egocentric components, as attested by the linear influence of body tilt upon these judgements. Overall, our results may be of value for preventing misperceptions regarding the judged elevation of objects one is to pass under. For instance, the global—and potentially damaging—overestimation of the perceived possibility of passing under obstacles reported in the present experiment may be reduced when tilting observers backward. At least, one must be aware of the influence of postural orientation when one is required to pass under a gate at the entrance of a car park in deteriorated weather conditions.

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Le paradigme du franchissement d'obstacles : Influence de l'orientation de regard

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RESEARCH ARTICLE

Influence of gaze elevation on estimating the possibility of passing under high obstacles during body tilt

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Abstract We investigated the influence of gaze elevation on judging the possibility of passing under high obstacles during pitch body tilts, while stationary, in absence of allocentric cues. Specifically, we aimed at studying the influence of egocentric references upon geocentric judgements. Seated subjects, orientated at various body orientations, were asked to perceptually estimate the possibility of passing under a projected horizontal line while keeping their gaze on a fixation target and imagining a horizontal body displacement. The results showed a global overestimation of the possibility of passing under the line, and confirmed the influence of body orientation reported by Bringoux et al. (Exp Brain Res 185(4):673–680, 2008). More strikingly, a linear influence of gaze elevation was found on perceptual estimates. Precisely, downward eye elevation yielded increased overestimations, and conversely upward gaze elevation yielded decreased overestimations. Furthermore, body and gaze orientation effects were independent and combined additively to yield a global egocentric influence with a weight of 45 and 54%, respectively. Overall, our data suggest that multiple egocentric references can jointly affect the estimated possibility of passing under high obstacles. These results are discussed in terms of "interpenetrability" between geocentric and egocentric reference frames and clearly demonstrate that gaze elevation is involved, as body orientation, in geocentric spatial localization.

Keywords Spatial localization · Reference frames · Gaze elevation · Body orientation · Egocentric · Geocentric

Introduction

Imagine you are visiting an old castle, walking towards an open door which seems rather low. You will doubtlessly ask yourself whether you are able to pass under or not without bending. Now, imagine that before you cross the door, you pay attention to an object located on the ground, or conversely above the top of the door; will your estimation of the possibility of passing under be the same for these different gaze elevations? This study deals with the influence of gaze elevation on the estimated possibility of passing under high obstacles with different body tilts.

Motor behaviour when crossing high obstacles has already been investigated, through a task in which observers walked and passed under a horizontal barrier (Van der Meer 1997). According to Gibson's theory of affordances (1979) which claims that the environment offers a collection of possibilities for action that organisms need to detect, Van der Meer (1997) found a body-scaled critical point at which subjects began to duck under a barrier. Specifically, their results showed that subjects used a non-negligible safety margin in presence of full visual reference (for instance, a 5.25 cm safe margin was observed for a subject whose height is 1.75 m). This cautious behaviour was also observed in full light when erect subjects had to estimate while stationary the possibility of walking under a barrier, but was not present when subjects

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sat on the floor (Wagman and Malek 2008). It was therefore suggested that intrinsic individual characteristics (body size, speed of locomotion and level of motor control) and the position of the point of observation may constitute important properties of the actor-environment fit. Other studies have demonstrated that judgements of “passability” through apertures (Mark 1987; Warren and Whang 1987) and “climbability” of objects (Warren 1984) were based on affordances for which body-scaled information were also important. As a main reference for this body-scaled information, the observers’ eye level appeared determinant in estimating these possibilities of action (Marcilly and Luyat 2008; Mark 1987; Wagman and Malek 2008).

Nevertheless, although processes ruling the possibility of passing under obstacles in full vision may radically differ from those involved in complete darkness, Bringoux et al. (2008) showed that estimating the possibility of passing under a horizontal line in absence of motion at various body tilts was also referred to the estimated eye level. Interestingly, in their study, direct eye level estimates (i.e. judgements of the subjective visual horizon, that is the plane normal to gravity crossing eye level), clearly distinguished from estimates of subjective “passability”. Both judgements were indeed separated by the distance between the top of the head and the physical eye level, although the slight modifications of this distance at different body orientations have not been shown to be integrated in the subjective estimates. Moreover, Bringoux et al. (2008) found a similar effect of body orientation on the subjective estimation of the height of an obstacle with respect to eye level and the possibility of passing under. Specifically, the more the subjects were tilted forward, the more they overestimated the possibility of passing under the projected line. These findings questioned the role of the vestibular system regarding the accuracy of perception of gravity-specified axes. Bringoux et al. (2007) found a similar performance in both labyrinthine-defective subjects and control subjects when judging the visual horizon in static conditions. They concluded that somatosensory inputs can convey as much graviceptive information as the vestibular system for visual horizon estimates. The observed linear relation between body orientation and the estimated possibility of passing under high obstacles was explained in terms of egocentric attraction induced by body tilt. Mittelstaedt (1983, 1986) has already explained similar phenomena by the existence of an idiotropic vector which “attracts” judgements of verticality along the longitudinal body axis. It has since been suggested that different body parts might be involved in the elaboration of the idiotropic vector (Ito and Gresty 1997). For instance, the head axis (Guerraz et al. 1998) as well as other body segments (Ito and Gresty 1997) could be involved in the egocentric influences reported in verticality judgements.

Another possible source of egocentric “attraction” may be the plane of regard. The plane of regard, containing the interocular axis and the line of sight, has been considered an important reference in egocentric spatial localization (Poljac et al. 2005; Poljac and van den Berg 2005). Specifically, the elevation of objects relative to this plane is perceived accurately, irrespective of eye or head orientation. However, the question remains whether the orientation of the plane of regard, that is, gaze elevation, is also crucial in judging the location of objects relative to some geocentric (i.e. earth-based) systems of coordinates, including the direction of gravity and the physical horizon (Howard 1982). Gaze elevation may have an influence on geocentric estimates because information about the position of the target on the retina and information about the position of the eye in the head are required for such perceptual tasks (Matin and Li 1992; Stoper and Cohen 1989). By successive transformations of coordinates, a stable map can be maintained between spatial localization, spatial orientation, and physical space (Matin and Li 1995).

The following experiment aimed first at investigating the influence of gaze elevation on estimating the possibility of passing under high obstacles during whole-body tilt, with subjects motionless, and in the absence of visual allocentric cues. The second purpose of this work was to question the relation between the influence of gaze elevation and body orientation on these judgments. A linear effect of gaze orientation was expected on the estimates since a linear body orientation influence has been previously observed by Bringoux et al. (2008).

Methods

Subjects

Twelve subjects (6 males and 6 females; mean age 27.5 ± 9.8 years) with normal or corrected to normal vision (by lens correction), participated in the experiment. They had no previous history of vestibular and neurological symptoms. All gave informed consent, in compliance with the ethical committee which regulates human experimentation in France.

Apparatus

The subjects were seated in complete darkness on a padded tilting chair, and restrained by means of a shoulder harness (Fig. 1). The head was strapped to a headrest which was adjusted so that the naso-occipital axis was orthogonal to the direction of the gravity when the chair was vertically oriented. The axis of rotation of the chair coincided with the trans-ocular axis. Thus, eye level remained at the same

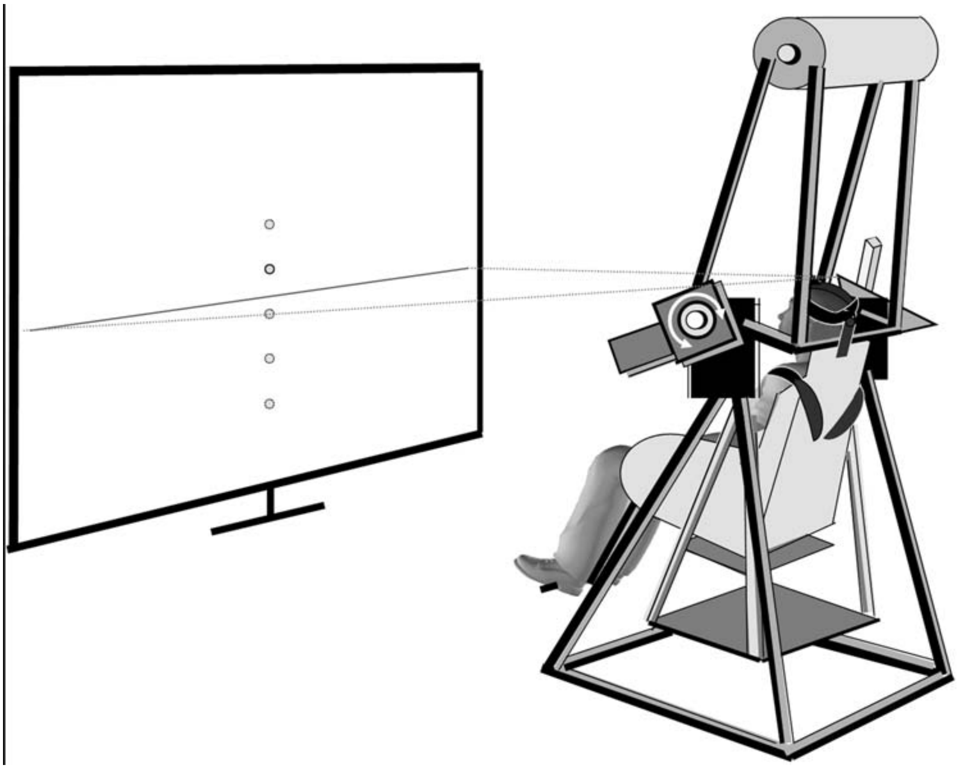

Fig. 1 Illustration of the experimental set-up. The motorized chair rotating around the subjects' trans-ocular axis could be rotated from +10° backward to −10° forward. The screen, 2.28 m away from the observers' eye supported five luminous targets (LEDs). The luminous horizontal line was projected from a laser beam at different elevations on the screen. Subjects had to rigorously fix the lighted target on the screen and to estimate whether they would be able to pass under the luminous horizontal line, imagining a horizontal displacement

height (1.34 m) from the floor reference, regardless of the tilt magnitude. The motorized tilting chair, servo-controlled in speed, enabled backward and forward rotations ranging from +10° backward to −10° forward. The chair was first tilted during a 2 s period of initial acceleration ($a = 0.5° \text{ s}^{-2}$) before reaching a constant velocity ($1° \text{ s}^{-1}$ for −10° and +10° of tilt; $v = 0.375° \text{ s}^{-1}$ for −5° and +5° of tilt) during 8 s, followed by a 2 s period of final deceleration ($0.5° \text{ s}^{-2}$). Finally, irrespective of the angle of tilt the total duration of tilting was 12 s.

Compliance with gaze elevation instructions was controlled online by recording subjects' eye movements (vertical DC electro-oculography, EOG). A flat vertical semi-opaque screen 2 m height × 2.5 m wide was placed in front of the subjects, at a distance of 2.28 m from the eyes. Behind the screen, five luminous targets were vertically aligned in order to define five gaze elevations (+10°, +5°, 0°, −5°, −10° elevations from eye level). A laser pointer mounted on a fixed structure positioned beside the tilting chair projected a thin horizontal beam on a tilting mirror. The pitch orientation of the mirror was adjustable by means of a galvanometer (Scanner Control CCX 100), so that the reflected beam was projected on the screen at the desired elevation. The resulting luminous horizontal line was 2 m long and 0.01 m thick and adjustable in height with a precision of 0.01 m. Subjects held in both hands the digital response push buttons for judgement settings. Galvanometer control and response recordings were performed by the ADwin-Gold system (Keithley©) piloted via our in-house Docometer software. Throughout the experiment, subjects were placed in darkness without any allocentric cue to influence their judgement.

Procedure

Five body orientations (+10°, +5°, 0°, −5°, −10°, respectively, backward and forward), five gaze elevations (+10°, +5°, 0°, −5°, −10° elevations from eye level) and ten line elevations (+25, +20, +15, +10, +5, −5, −10, −15, −20, −25 cm from eye level; i.e., respectively, +1.3°, +2.5°, +3.8°, +5.0°, +6.3°, −6.3°, −5.0°, −3.8°, −2.5°, −1.3°, elevations from eye level) were manipulated in a counterbalanced pseudo-random order to prevent the possibility of any order effect. Subjects were neither informed about the number and angular values of body and gaze orientations nor about the number and height of line elevations. They were asked to answer the following question: "Do you think that you would pass under the line, in the present body orientation, imagining a virtual horizontal displacement of your body?".

A typical sequence of judgements happened as follows: the subjects were first tilted at the desired angle of orientation. This was followed by a 15 s period of rest, allowing the post-rotational effects issued from semi-circular canals stimulation to disappear (Benson 1990; Goldberg and Fernandez 1977). A loudspeaker, positioned in the subjects' median plane, 1 m behind the chair and elevated at eye level, emitted a first auditory signal indicating the trial onset, at which a luminous target appeared ($t = 0$ s). Subjects had to keep their gaze on the target during all the visual presentation. At $t = 2$ s, a luminous line appeared. Subjects were then required to orient their attention towards the luminous line projected in the peripheral field of vision and to estimate the possibility of passing under the line. At $t = 6$ s, the luminous target and the line disappeared and a second auditory signal indicated it was time to respond via the push buttons ("able to pass" with the right hand-held button and "not able to pass" with the left hand-held button). The instructions were frequently repeated to keep subjects alert and concentrated on the task throughout the experiment. We assume that auditory signals did not affect visual localization, as no attentional focus on the spatial location of the sound was required (Bertelson and Radeau 1981; Pick et al. 1969; Warren 1979).

Eye movements were controlled online by means of a vertical EOG recording of the subjects' dominant eye. A consistent shift of the EOG signal indicated a change in gaze elevation whereas a sustained signal indicated a stabilization of gaze elevation. The signal polarity indicated the direction of vertical gaze displacement. Overall, subjects adequately performed the task. Nevertheless, if the DC signal indicated a change during the fixation task (e.g. a blink or an eye movement), the trial was immediately cancelled by the experimenter and presented again later in the session.

Finally, ten judgements (corresponding to ten line elevations randomly presented for different gaze elevations) were obtained within a sequence executed at the same body orientation. Each sequence ended by a rotation of the tilting chair back to the vertical and the room was lit for 15 s before a new sequence was launched. To limit the time spent on the experiment, a specific trial was presented only once for a total of 250 judgments. This design was chosen in accordance to the previous observations of Bringoux et al. (2008) who found high intrasubject judgment reliability after several trial repetitions in a similar perceptual task.

Data processing

Judgements were converted into binary values. A score of 1 was attributed when the subjects estimated they could pass under the line (in other words, when the line elevation was perceived higher than the minimal height for passing under). Conversely, a score of 0 was attributed when the subjects estimated they could not pass under the line. A Probit model, using a non-linear regression analysis for dichotomic variables, enabled us to determine the probability P that subjects estimated at 50% that they could pass under the line. The Probit function was defined by the following relation:

$$P_i = 1/\left(1 + \left(C_{i,j}/C_0\right)^n\right) \qquad (1)$$

where "P_i" is the probability that subjects estimated they can pass under the line. "i" corresponds to the line number in the sequence, "j" to the trial number, "C_0" the line number for $P = 0.5$ and "n" the slope of the tangent at the inflection point of the curve. The latter coefficient constitutes an estimation of the discrimination sensibility relative to the chosen increments. An analysis of variance (ANOVA) with repeated measures was performed on "n" values, to test any differences between the discrimination sensibility calculated for each experimental condition. Line elevations obtained at $P = 0.5$ via the psychometric function defined judgements of subjective "passability", that is, estimates of the minimal height relative to eye level required for passing under obstacles. The estimates of subjective "passability", initially referred to eye-level for convenience, were subsequently reported to the top of the head, defined as the highest physical point of the head from the horizontal floor of the room measured for each subject in each body orientation. Hence, the data were expressed as a vertical elevation (in cm) relative to the top of the head in order to define a true level of "passability". A repeated measures ANOVA was applied to the estimates of subjective "passability" relative to the top of the head in order to test any differences between body and gaze orientation angles and to investigate a possible interaction between the two factors. The influence of the egocentric position of the eyes was also investigated by a one way ANOVA applied to the estimates of subjective "passability" relative to eye-in-head orientation. Finally, a multiple linear regression analysis was conducted on the mean estimates of subjective "passability" for each condition (i.e. for a specific body orientation associated to a particular gaze elevation) in order to investigate the presence of linear and independent effects of body and gaze orientation upon estimates and to characterize the magnitude of these effects.

Results

All the subjects stated that the required task was easy to perform and overall exhibited no hesitation when giving their response. Figure 2 illustrates the mean raw responses obtained for the different line elevations, relative to (a) body orientation and (b) gaze elevation. Overall, observation of the data showed that the higher the line relative to eye level, the more the subjects tended to answer that they could pass under, independently of their body orientation or their gaze elevation. Furthermore, these raw data also

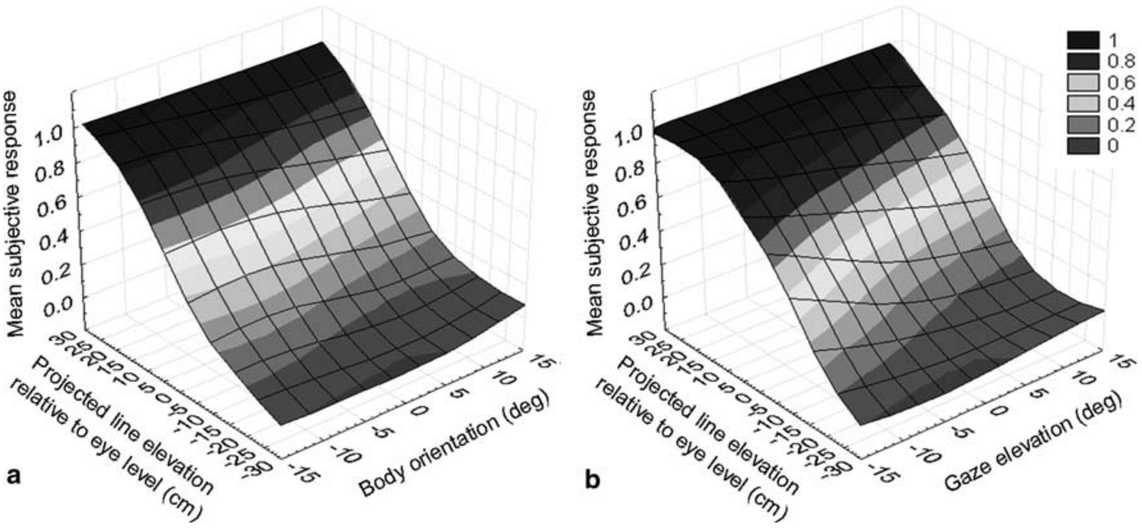

Fig. 2 Typical psychometric functions from all the subjects obtained via Probit non-linear regression analysis for **a** the different body orientations or **b** different gaze elevations. The mean subjective responses corresponded to the mean perceptual scores obtained when subjects had to estimate the minimal height for passing under. The value extracted at $P = 0.5$ from each Probit function corresponds to the subjective "passability", that is, the perceived minimal height for passing under the line

suggested specific effects of body and gaze orientation upon estimates.

Probit analysis

A non-linear regression analysis (Probit function) was performed to determine the subjective "passability" for each subject in each experimental condition (see "Methods"). To assess the discrimination sensibility of the Probit processing, a five body orientations (−10°; −5°; 0°; +5°; +10°) × five gaze elevations (−10°; −5°; 0°; +5°; +10°) repeated measures ANOVA was performed on the "*n*" values (i.e. the slopes calculated at the inflection point of each function). Results showed there was no significant difference between body orientation angles [$F_{(4,44)} = 1.75$; $P = 0.16$] or gaze elevation angles [$F_{(4,44)} = 0.91$; $P = 0.47$]. The interaction between both factors was also non-significant [$F_{(16,176)} = 1.31$; $P = 0.2$]. These results showed that the sensibility to discriminate the subjective "passability" for subjects did not differ between the experimental conditions.

Mean comparisons of subjective "passability"

The subjective "passability" relative to eye level obtained via the Probit analysis was reported to the true level of "passability", that is, relative to the top of the head for each subject at each body orientation angle. Overall, the subjective "passability" reported to the top of the head was found notably lower (8.24 cm) than the minimal physical height required for passing under the line. This denotes a significant over-estimation of the "passability" under obstacles.

A five body orientations (−10°; −5°; 0°; +5°; +10°) × five gaze elevations (−10°; −5°; 0°; +5°; +10°) ANOVA conducted on the mean estimates of subjective "passability" revealed a significant effect of body orientation [$F_{(4,44)} = 7.5636$; $P < 0.001$] and gaze elevation [$F_{(4,44)} = 9.5481$; $P < 0.001$] on the estimated possibility of passing under the line. The interaction between both factors was not significant [$F_{(16,176)} = 0.74$; $P = 0.75$]. This means that the main effect of body orientation was not affected by gaze elevation and vice versa. Post hoc analyses (Newman–Keuls test) showed significant differences between body orientation angles (Fig. 3).

A nine eye-in-head orientations (−20°; −15°; −10°; −5°; 0°; +5°; +10°; +15°; +20°) ANOVA conducted on the mean estimates of subjective "passability" showed non-significant differences between eye-in-head orientation conditions [$F_{(8,88)} = 1.21$; $P = 0.30$]. Then, the judgement of subjective "possibility" was not affected by the egocentric position of the eyes relative to the head.

Multiple linear regression analysis

A multiple regression analysis, applied to the mean estimates of subjective "passability" obtained for all the subjects in all experimental conditions, showed a linear effect of body orientation and an independent linear effect of gaze elevation on the estimated possibility of passing under high obstacles [$F_{(2,22)} = 81.84$; $P < 0.001$]. Figure 4 shows that most of the data fit on a simple plane when plotted as a function of body and gaze orientation.

These results showed that the error on estimating the possibility of passing under high obstacles is both

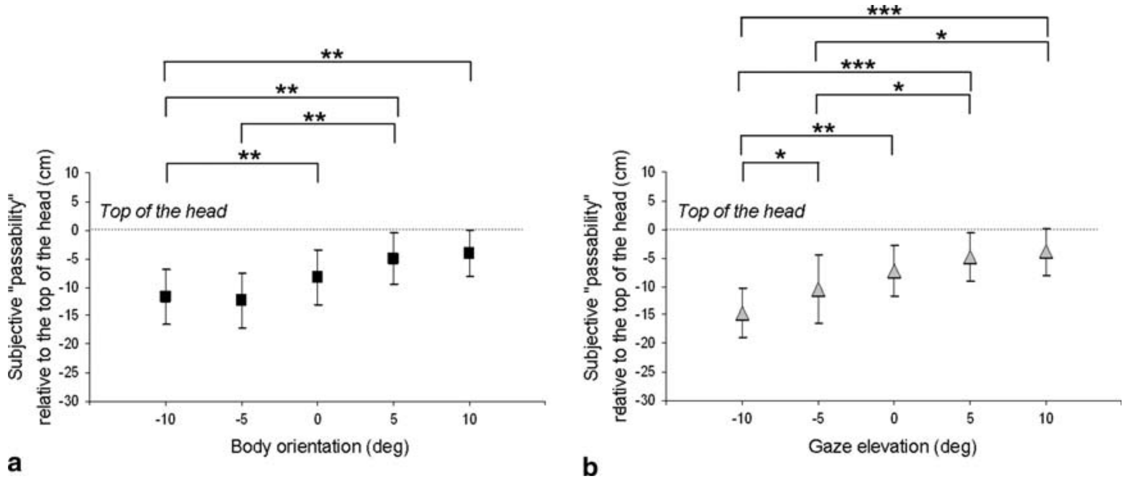

Fig. 3 Mean subjective "passability" relative to the top of the head (plotted with ± confidence intervals) obtained for **a** the different body orientations or **b** for the different gaze elevations. The zero corresponds to the top of the head reference (i.e. the highest point of the head irrespective of head orientation). Significant differences between body and gaze orientation angles (Newman–Keuls test) are also shown (***$P < 0.001$; **$P < 0.01$; *$P < 0.05$)

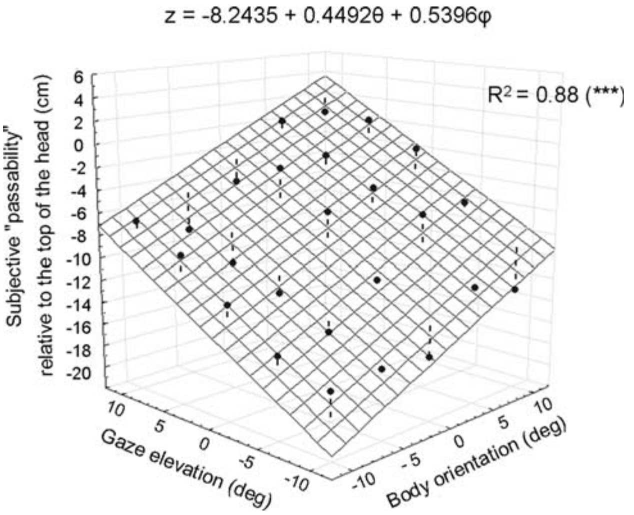

Fig. 4 Multiple regression function fitted to the mean estimates of subjective "passability". Mean estimates of subjective "passability" relative to the top of the head (*black circles*) are plotted against body orientation and gaze elevation. The *hatched area* represents the multiple regression plane, whose regression equation is given above the graph: "z" corresponds to the subjective "passability" relative to the top of the head, "θ" to the body orientation angle, and "φ" to the gaze elevation angle. The length of the segments joining the *black circles* to the plane represents the deviation of the subjective "passability" from the plane. The R^2 indicates the significance level of the fit

proportional to the body orientation angle and to the gaze elevation angle. They also showed that the independent effects of body and gaze orientation combined additively. The multiple linear regression analysis is characterized by the following function:

$$z = 0.45\theta + 0.54\varphi - 8.24 \qquad (2)$$

where "z" corresponds to the subjective "passability" relative to the top of the head, "θ" to the body orientation angle, "φ" to the gaze elevation angle. The coefficient associated to the weight of the body orientation influence is 0.45; 0.54 is the coefficient associated to the weight of the gaze orientation influence and −8.24 corresponds to the mean calculated subjective "passability" relative to the top of the head.

Discussion

The main purpose of this study was to investigate the influence of gaze elevation on estimating the possibility of passing under high obstacles during whole-body tilt, while stationary, and in absence of visual allocentric cues. Specifically, the question was to determine whether gaze elevation could constitute an egocentric influence which may in turn affect geocentric estimates. The second objective of this work was to question the relation between body orientation and gaze elevation on these perceptual judgements.

Overall, our results showed that the mean subjective "passability" is −8.24 cm (i.e. −2.07°) lower than the physical minimal height required to adequately perform the task. In other words, subjects estimated they were able to pass under obstacles which were actually located below the top of their head. These results highlighted a global overestimation of the possibility of passing under obstacles. Recently, Bringoux et al. (2008), using the same experimental setup as the one designed in the present study, found a similar overestimation of the subjective "passability" during body tilt. This result has been related to the perceived visual horizon, which was found globally lower than the physical reference in darkness (Bringoux et al., 2008). For instance, the measured offset was −3° in the same experimental setup. Although the subjective visual horizon was not recorded in the present experiment, the occurrence of such a phenomenon is clearly assumed in this study. Other previous works also reported that the subjective visual horizon is lower in darkness (Bringoux et al. 2004, 2008; MacDougall 1903; Raphel and Barraud 1994; Sharp 1934; Stoper and Cohen 1986). This phenomenon may be related to the 30° backward orientation of the saccular and utricular maculae relative to the head (Rosenhal 1972; Bortolami et al. 2006). As a consequence, obstacles, whose elevation is referred to the subjective visual horizon, will be considered higher than they actually are, since the visual horizon is perceived lower than its true location in darkness.

Gaze elevation effect on geocentric judgments

Our results showed a significant effect of gaze elevation on estimating the possibility of passing under high obstacles. Specifically, the more the gaze was orientated downward, the more the possibility of passing under high obstacles was overestimated. Conversely, this overestimation was reduced when the gaze was orientated upward. According to many studies, gaze constitutes an egocentric reference that may be advanced as a potential source of egocentric attraction reported on geocentric judgments.

Numerous authors have stressed the importance of eye level in height and distance judgments (Li et al. 2001; Matin and Li 1995; Ooi et al. 2001). Specifically, eye level is commonly considered as a central reference in egocentric (Matin and Li 1995) and geocentric spatial localization in darkness (Bringoux et al. 2004, 2008; Stoper and Cohen 1989). In parallel, Poljac and van den Berg (2005) and Poljac et al. (2005) have investigated the importance of the plane of regard in egocentric spatial localization. In a first study, subjects were asked to point with their supported arm to their plane of regard (Poljac and van den Berg 2005). The results showed a correct localization of this plane in space. In a second study, subjects were asked to perceptually estimate the elevation of flashed probe points relative to their plane of regard during eccentric viewing (Poljac et al. 2005). These results showed that the elevation of objects relative to this plane was perceived accurately, irrespective of eye or head orientation. These findings suggest that passive object localization relative to an egocentric reference is correctly achieved along the vertical dimension, contrary to what has been reported for judgements of object lateral eccentricity in the peripheral field assessed via pointing movements (Bock 1993). In the latter case, the necessary transformation of sensory coordinates into an appropriate motor output could explain the errors reported in pointing judgments (McIntyre et al. 1997).

In line with the conclusion of Poljac et al. (2005), stating that "*the plane of regard is a good starting point for representing objects in head-centric coordinates*", our results demonstrated that the plane of regard is also involved in judging the location of objects with respect to a geocentric reference frame (i.e. including the horizontal plane passing through the eyes). The linear effect of gaze elevation on estimating the possibility of passing under high obstacles observed in our study implies that gaze elevation influence is not magnified for the maximal gaze elevation angles tested in this experiment. In other words, gaze elevation exerted a linear egocentric attraction upon geocentric judgments in a range from −10° to +10° (a range limited by some morphological constrains at extreme body tilts such as the curvature of the brow).

Additive independent effects of body and gaze orientation

The results did not reveal any interaction between body and gaze orientation. Specifically, in the range of the tested orientations, body orientation effect is not influenced by gaze elevation angle, and conversely, gaze elevation effect is not affected by body orientation angle. Additive effects of body and gaze orientation were also shown. Moreover, our results showed that several egocentric references may have additive effects and participate, each independently, in the construction of a resultant egocentric influence upon geocentric judgments.

Some previous studies suggested that multiple body parts could constitute egocentric references which additively combine to yield main effects on geocentric judgments. For instance, Guerraz et al. (1998) showed that lateral head tilt alone and lateral trunk tilt alone generated single effects on subjective visual vertical estimates, which could merge into a cumulative main egocentric effect when head and trunk are tilted together. Moreover, some authors (Becker et al. 2000; Ito and Gresty 1997) suggested that multiple body parts could be involved in the elaboration of the idiotropic vector influencing verticality perception. Consequently, one might expect that the whole-body configuration in space (sitting or upright posture) could modify the perception of some geocentric directions of space involved in the judgement of "passability" under obstacles.

Interpenetrability between reference frames

The extent to which reference frames are implicated in spatial cognition tasks is still widely discussed. Several hypotheses have been proposed in the literature.

The first hypothesis suggests that subjects can rapidly adapt their behaviour by switching from a specific reference frame to another while performing their task. For instance, Ghafouri et al. (2002) identified a radical switch between allocentric and egocentric references frames during fast arm pointing movements. In this task, subjects had to point either to a motionless target or to a target moving synchronously with the trunk. In this context, reference frames could be considered as pre-existing neurophysiological structures, some exclusive from others (Galati et al. 2000).

The second hypothesis supports the existence of intermediate states, in which egocentric, allocentric and geocentric cues would merge into a hybrid reference frame (Flanders and Soechting 1995; Kappers 2003, 2004; Paillard 1991; Soechting and Flanders 1992). For instance, Kappers (2004) found a combined contribution of allocentric and egocentric cues in the haptic judgment of parallelism. Blindfolded subjects exhibited systematic deviations when manually rotating a test bar in such a way that they felt it as parallel relative to a reference bar in the midsagittal plane. In the same vein, Coello and Iwanow (2006) found an influence of allocentric cues (given by a structured background) on an egocentric pointing task (i.e. pointing movements towards a visual target located at various distances along the sagittal axis). Finally, according to Bringoux et al. (2004, 2007, 2008), the present findings illustrate the "interpenetrability" between reference frames.

Two cases of "interpenetrability" have been described in the literature. The first relates to the existence of a dynamic intermediate state, where the weight attributed to each reference frame evolved during the task. Specifically, this phenomenon has been observed on the rod-and-frame effect during head tilt (DiLorenzo and Rock 1982) or whole-body tilt (Bishof 1974; Goodenough et al. 1985; Zoccolotti et al. 1992). For instance, it was shown that a 45° head tilt increased the influence of a 20° tilted frame upon visual vertical estimates, compared to a head upright condition (DiLorenzo and Rock 1982). The greater rod-and-frame effect was explained by the decreased efficiency of available gravity cues during head tilt, but might also be understood as an increased weight of the allocentric (visual) frame of reference when the head is no longer aligned with gravity.

The second case refers to the existence of an intermediate reference frame in which the contribution of each egocentric, allocentric or geocentric cues is kept constant and stable throughout the task (Bringoux et al. 2004, 2007, 2008; Kappers 2003, 2004; Neggers et al. 2005). For instance, Bringoux et al. (2008), showed that egocentric references could influence the perceived location of objects relative to some geocentric references, each with a constant weight, whatever the tilt magnitude. In the same perspective, Neggers et al. (2005) showed that allocentric cues, given by a structured visual background placed behind a target, biased judgements of the target's location relative to the body with a constant weight.

According to the latter hypothesis, our study strongly suggests that perceptual shifts in judging the "passability" under obstacles may result from the "interpenetrability" between egocentric and geocentric reference frames. This finding might lead to a new and hybrid reference frame, corresponding to a sustained intermediate state between a geocentric reference frame normally required to adequately perform the task, and a disturbing egocentric reference frame. Successive transformations of coordinates required to perform the task (Matin and Li 1992; Stoper and Cohen 1989) may account for the influence of one reference frame to another.

Conclusion

To our knowledge, the present study is the first to show an independent, linear influence of gaze elevation on estimating the possibility of passing under high obstacles, while stationary and in the absence of allocentric cues. Furthermore, our results suggest that gaze elevation is additively combined to body orientation to yield a resultant egocentric effect that modifies geocentric estimates. The present work also supports the hypothesis of "interpenetrability" between egocentric and geocentric reference frames to explain how judgements of "passability" under obstacles are attracted towards body orientation and gaze elevation. Further experiments investigating the orientation of different body segments in space should be particularly interesting to better understand the egocentric influences upon judgements of subjective "passability" under obstacles.

Finally, our study may have important repercussions in aeronautics where pilots are usually seated 30° backward (Roumes and Grau 2003). Comparable egocentric attraction upon spatial estimates may arise when pilots have to elevate their gaze towards a vertical visual display, while controlling the pitch of their aircraft. Mars et al. (2004, 2005) showed that head and body orientation are of importance in judging the pitch of aircrafts. Our study suggests that gaze elevation should also be taken into account in the conception of visual displays to prevent pilots from risks of spatial disorientation, specifically under visually poor flight conditions (Braithwaite et al. 1998; Kirkham et al. 1978).

In addition, because gaze orientation and attentional focus are often congruent in everyday life, further experiments dissociating gaze orientation and attentional location might also be investigated to reduce the risks of accidents in aeronautics. Specifically, in accordance with the paradigm of Posner et al. (1980), it could be valuable to determine whether priming cues orienting attention would affect geocentric estimates in the same way as gaze elevation.

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Le paradigme du franchissement d’obstacles : Effet de la configuration posturale

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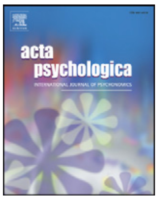

Postural configuration affects the perception of earth-based space during pitch tilt

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ABSTRACT

This study investigates the relative contribution of body parts in the elaboration of a whole-body egocentric attraction phenomenon previously observed during earth-based judgments. This was addressed through a particular earth-based task requiring estimating the possibility of passing under a projected line, imagining a forward horizontal displacement. Different postural configurations were tested, involving whole-body tilt, trunk tilt alone or head tilt alone. Two legs positions relative to the trunk were manipulated. Results showed systematic deviations of the subjective "passability" toward the tilt, linearly related to the tilt magnitude. For each postural configuration, the egocentric influence appeared to be highly dependent on the position of trunk and head axes, whereas the legs position appeared not relevant. When compared to the whole-body tilt condition, tilting the trunk alone consistently reduced the amount of the deviation toward the tilt, whereas tilting the head alone consistently increased it. Our results suggest that several specific effects from multiple body parts can account for the global deviation of the estimates observed during whole-body tilt. Most importantly, we support that the relative contribution of the body segments could mainly depend on a reweighting process, probably based on the reliability of sensory information available for a particular postural set.

1. Introduction

The visual horizon, defined as the plane normal to gravity crossing eye level (Stopper & Cohen, 1989) has been found critically involved in the perception of earth-based space. Several studies have shown that estimating distance (Ooi, Wu, & He, 2001), elevation (Matin & Li, 1995), and the possibility of passing under high obstacles (Bringoux, Robic, Gauthier, & Vercher, 2008) relies on this reference. Most of the time, the visual horizon is fully accessible, or can be derived from the contextual lines of a structured visual environment if not directly available (Wu, He, & Ooi, 2005). However, in absence of vision (during night or foggy day), the spatial judgments mentioned above must rely on an implicit horizontal reference named the subjective visual horizon (SVH).

Numerous studies indicated that the visual horizon was generally perceived $-2°$ below the physical reference, when measured in darkness for erect subjects (e.g., McDougall, 1903; Howard, 1986). They also showed that the SVH could be influenced by numerous environmental factors such as the orientation of the visual scene (Matin & Li, 1995), and the gravitational flow field (Tribukait & Einken, 2005). Interestingly, body orientation was also found to significantly influence the SVH (about 20% of body tilt magnitude in the direction of pitch body tilt, and in a range from $\pm 20°$), stressing the importance of taking into account the whole-body position in space when making earth-based spatial judgements (Bourrelly, Bringoux, & Vercher, 2009; Bourrelly, Vercher, & Bringoux, 2010; Bringoux, Tamura, Faldon, Gresty, & Bronstein, 2004; Bringoux et al., 2008). Nevertheless, the origin of this whole-body tilt influence remains unclear.

The main effect of body tilt upon SVH was initially interpreted as a decreased sensitivity of the vestibular system during tilt, leading to a diminished sensation of tilt (Lechner-Steinleitner, 1978; Shöne, 1964; Young, 1984). Similar interpretation could be given considering the phenomenon of somatosensory adaptation observed after prolonged tilt (Higashiyama & Koga, 1998; Wade, 1970). However, this hypothesis was inconsistent with other studies which found no relationship between the estimated body orientation and the perception of earth-based references (Mast & Jarchow, 1996, Mittelstaedt, 1996; Trousselard, Barraud, Nougier, Raphel, & Cian, 2004). Another interpretation of the relationship observed between body orientation and SVH has been recently suggested in terms of egocentric attraction induced by body tilt (Bringoux et al., 2004, 2008).

Here, we addressed the issue of the possible link between this latter interpretation and the idiotropic vector hypothesis previously formulated by Mittelstaedt (1983). This hypothesis considers that the

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longitudinal *Z*-body axis could serve as a strong reference in estimating some relevant earth-based directions such as the subjective visual vertical and the SVH. According to the previous explanation, geocentric judgements would be attracted towards the whole *Z*-body axis, regardless of the perception of tilt (Carriot, DiZio, & Nougier, 2008). This whole-body attraction has been reported more or less important, however, depending on the dimension of body tilt (roll vs. pitch; Ebenholtz, 1970) or the direction to be estimated (vertical vs. horizontal; Betts & Curthoys, 1998; Carriot et al., 2008; Lejeune, Thouvarecq, Anderson, Caston, & Jouen, 2009). Alternatively, the *Z*-trunk axis and the *Z*-head axis were also shown to constitute relevant egocentric references influencing the perception of earth-based directions (Guerraz, Poquin, Luyat, & Ohlmann, 1998; Wade, 1969, 1970; Wetzig & Baumgarten, 1990). For instance, Wetzig and Baumgarten (1990) and Guerraz et al. (1998) showed a specific effect of roll head tilt on judgments of verticality which was smaller than during whole-body tilt, supporting the assumption that multiple body parts could be taken into account in the elaboration of a whole-body egocentric attraction. Moreover, Guerraz et al. (1998) suggested that the single effects relative to the tilt of the *Z*-trunk axis and the *Z*-head axis could be additively combined into a main egocentric effect when the head and trunk were tilted together. However, this hypothesis of additivity between independent body parts has not been systematically accepted. Ito and Gresty (1996) supported the theory of a dynamic combination of multiple body parts such as legs, trunk and head position in the elaboration of a main egocentric effect. Specifically, they suggested that the weight attributed to each single body part could evolve during the task such as the more the subjects are tilted backward, the more the weight attributed to the trunk–leg axis is important. In addition, the egocentric attraction during tilt was found greater for erect subjects (with the head to trunk–leg axis in alignment) than for seated subjects. These results strongly suggested that the postural configuration in space could affect a large number of spatial tasks relied on earth-based directions.

The aim of the present study was to determine the origin of the egocentric attraction previously observed on earth-based judgments during whole-body tilt. The question was addressed by testing the influence of postural configuration on a particular earth-based task which requires to estimate the possibility of passing under high obstacles (Bourrelly et al., 2009; Bringoux et al., 2008). Indeed, it has been previously demonstrated that the perceived ability of passing under obstacles in otherwise darkness is related to the perceived earth-based horizon at eye level, acting as a reference for height judgements (Bringoux et al., 2008; Marcilly & Luyat, 2008). In Experiment 1, we examined the contribution of head, trunk and leg positions in the elaboration of the whole-body egocentric attraction previously observed in the judgements of "passability" under a projected horizontal line. In Experiment 2, we focused on the influence of active head orientation in the same task to further investigate the contribution of somatosensory and vestibular inputs in the elaboration of the main egocentric attraction effect.

2. General methods

2.1. Apparatus

In the subsequent experiments reported here, subjects were seated on a padded tilting chair allowing body rotations in pitch within a range from +20° backward to −20° forward with accelerations above the vestibular threshold for rotation perception. Prior to any condition, subjects were restrained by means of a shoulder harness with their head strapped on a head-and-chinrest so that the naso-occipital axis was orthogonal to the direction of gravity when the chair was vertically oriented. Eye level was positioned so that the trans-ocular axis coincided to the axis of rotation of the chair. Consequently, eye level was kept at the same height relative to the floor reference (1.34 m) whatever the body tilt magnitude. Depending on the experimental condition, the head could be kept either vertical while the trunk was tilted, aligned with the trunk during whole-body tilts, or tilted alone while the trunk was kept vertical. The feet were strapped onto an adjustable foot-rest which permitted to reach specific legs positions (flexed vs. extended) relative to the body.

Subjects were placed in front of a flat vertical screen 2 m height × 2.5 wide at a distance of 2.28 m from the eyes. A laser pointer located behind the screen projected a thin horizontal beam on a tilting mirror. The luminous line was reflected on the screen. The elevation of the projected line was adjustable in height by means of a galvanometer (Scanner Control CCX 100) which allowed the rotation of the mirror in pitch. The resulting luminous horizontal line was 2 m long and 0.01 m thick and adjustable in height with a precision of 0.01 m. Subjects held in both hands the digital response push buttons for judgment settings. Galvanometer control and response recordings were performed by the ADwin-Pro system (Keithley©) piloted via our in-house software (Docometre). All the judgments were performed in a dark room to avoid external visual cues (Fig. 1).

2.2. General procedure

Nine angles of tilt were manipulated in the present study. For each body orientation, 10 line elevations were randomly presented. Subjects were asked to answer the following question: "Do you think you could pass under the line in the present body orientation, imagining a forward horizontal displacement of your body?". To make sure that the subjects clearly understood the task, sketches were presented, illustrating a forward horizontal displacement (always normal to gravity) and passable or impassable obstacles for different postural configurations. Subjects were first positioned at the desired body angle relative to gravity in complete darkness. The chair was rotated at a constant velocity during 11 s, with a period of initial acceleration and final deceleration of 2 s (0.4° s^{-1} and 0.2° s^{-2} for ±5° tilt, 0.8° s^{-1} and 0.4° s^{-2} for ±10° tilt, 1.2° s^{-1} and 0.6° s^{-2} for ±15° tilt, 1.6° s^{-1} and 0.8° s^{-2} for ±20° tilt). This was followed by 15 s of rest. This specific duration was chosen as a compromise between the weakest vestibular resting discharge allowing to consider post-rotational effects as negligible and limited somatosensory adaptation due to the subsequent period of static tilt (Benson, 1990; Goldberg & Fernandez, 1977). Stationary subjects were then asked to open their eyes and to gaze at the horizontal line which appeared on the screen during 4 s. At the end of the visual presentation, the line was switch off and subjects were asked to respond about the possibility of passing under the line, via a forced-choice judgment by means of two hand-held buttons. Judgment settings were recorded via the ADwin-Pro system (Keithley©) piloted via our in-house software (Docometre). At the end of the sequence (i.e., a successive presentation of 10 line elevations in a same body orientation), the chair was brought back to the vertical and the room lights were turned on for 10 s before a new sequence was launched. The instructions were frequently repeated to keep subjects alert and concentrated on the task throughout the experiment. Subjects were neither informed about the number and height of line elevations.

2.3. Data processing

Judgment settings were first converted into binary values. A score of 1 was attributed when the subjects estimated they could pass under the line, that is, when the line elevation was perceived higher than the minimal height for passing under. Conversely, a score of 0 was attributed when the subjects estimated they could not pass under the line. A subsequent "Probit" model, using a non-linear regression analysis for dichotomic variables, was used to determine the probability *p* that subjects estimated at 50% that they

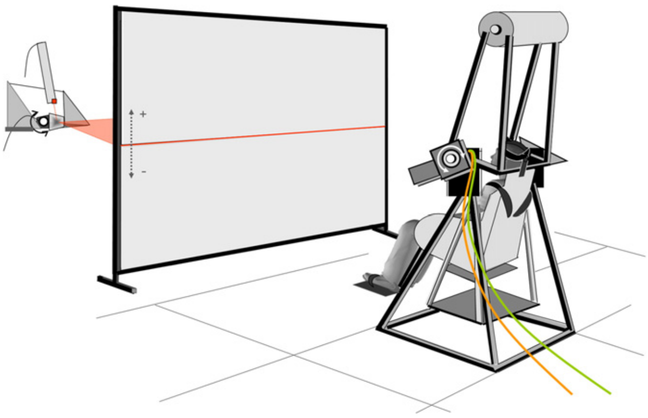

Fig. 1. Illustration of the experimental set-up. The motorized chair rotating around the subjects' trans-ocular axis could be rotated from +20° backward to −20° forward. Depending on the experimental condition, subjects head could be either kept vertical while the trunk was tilted, aligned with the trunk during whole-body tilts, or tilted alone while the trunk was kept vertical. The feet were strapped onto an adjustable footrest which permitted to reach flexed or extended legs positions relative to the body. The luminous horizontal line was projected from a laser beam at different elevations on the screen. Subjects had to fix the line on the screen and estimate whether they could pass under, imagining a forward horizontal displacement.

could pass under the line. Line elevations obtained at $p = 0.5$ via the psychometric function defined judgements of subjective "passability", that is, estimates of the minimal height relative to eye level required for passing under obstacles (see Bourrelly et al., 2009). The slope of the tangent at the inflection point of the Probit curve gave an indication about the discrimination sensitivity of the so-called subjective "passability" relative to the chosen increments. The sharper the slope, the higher the discrimination sensitivity. Analyses of variance (ANOVA) with repeated measures were performed on the slopes of the Probit function to ensure there was no difference in the discrimination sensitivity whatever the experimental condition. The estimates of subjective "passability" initially referred to eye-level for convenience, were subsequently referred to the top of the head (the highest physical point of the head from the horizontal floor reference) measured for each subject in each body orientation. Hence, the data were expressed as a vertical elevation (in cm) relative to the top of the head in order to define a true level of "passability" Repeated measures ANOVAs were performed on the data to test the presence of a specific egocentric influence in each postural configuration at the different angles of tilt. Linear regression lines were then applied to the estimates of subjective "passability" for each subject in each postural configuration to characterize the nature of the egocentric influence. Differences between postural configurations were tested by comparing the slopes of the regression lines obtained for each subject. Newman–Keuls post-hoc tests were used to characterize the effects.

3. Experiment 1

The purpose of the Experiment 1 was to investigate the contribution of head, trunk and legs position in the elaboration of the whole-body egocentric attraction previously reported in the judgments of "passability" under high obstacles.

3.1. Methods

3.1.1. Subjects

Eight subjects (four males and four females; mean age 23.4 ± 4.2 year) with normal or corrected to normal vision (by lens correction) gave informed consent to participate in the study, in compliance with the ethical committee which regulates human experimentation in France. They had no previous history of vestibular and neurological symptoms. All were naive as to the hypothesis under study.

3.1.2. Experimental conditions

Four postural configurations were tested in the present experiment (Fig. 2). The effects of the whole-body orientation, trunk orientation, and legs position were investigated. The experimental conditions were named as following: B (whole-body tilt with extended legs), B-Lflex (whole-body tilt with flexed legs), T (trunk tilt alone with the extended legs), and T-Lflex (trunk tilt alone with flexed legs). For each condition, the head was secured by means of a head-and-chinrest, either mounted on the tilting display (so that head-and-trunk was tilted as a whole during whole-body rotation) or fixed in space (so that the trunk was tilted alone with the head remaining fixed). The feet were secured to an adjustable footrest. The position of the legs, flexed or extended, was determined so that the axis from the malleolus to the eye axis respectively reaches an angle of

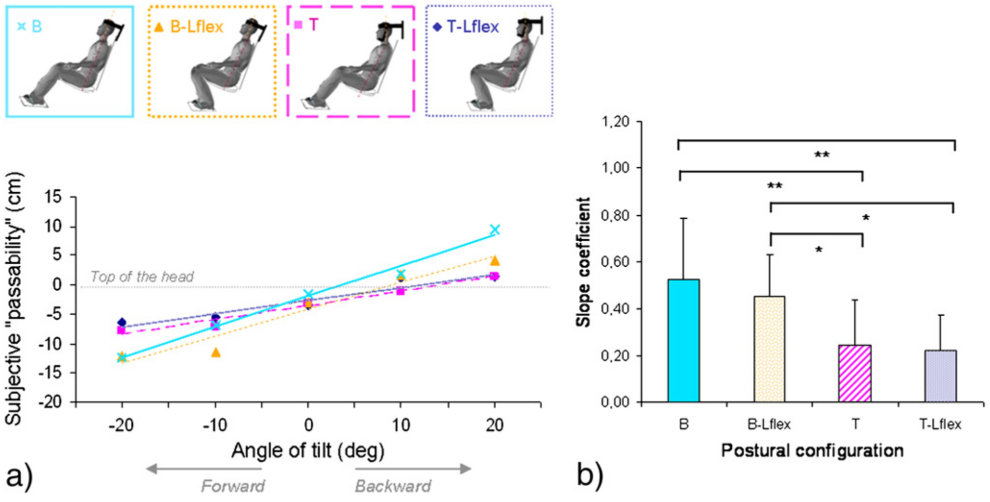

Fig. 2. (a) Linear regression analysis applied to the mean estimates of the subjective "passability" under obstacles relative to the angle of tilt obtained for the four postural configurations (Experiment 1). (b) Mean slope coefficient of the linear regression lines between the mean subjective "passability" and the angle of tilt, and the inter-subjects standard deviation for the four postural configurations (Experiment 1; *** = $p<0.001$; ** = $p<0.01$; * = $p<0.05$). The slope coefficient corresponds to the weight of the orientation influence.

35° or 45° relative to gravity. The order of the tested different body positions was initially randomized and then counterbalanced for half of the subjects (i.e., strict inverse order in the presentation of the postural configurations for two sub-groups).

3.1.3. Procedure

Five angles of tilt relative to gravity (i.e. whole-body tilt or trunk tilt alone; 0°; −10°, −20° forward; and +10°, +20° backward) were manipulated in the present experiment. For each body orientation, 10 line elevations (+5, +10, +15, +20, +25 cm upward elevations; and −5, −10, −15, −20, −25 cm downward elevations cm from eye level; i.e., respectively, ±1.3°, ±2.5°, ±3.8°, ±5.0°, ±6.3° elevations from eye level) were pseudo-randomly presented. To avoid any order effects, the order of presentation was strictly counterbalanced for half of the subjects. The total number of judgments was 400 ($4 \times 5 \times 10$) for a total session duration of 90 min.

3.2. Results and discussion

A non-linear regression analysis (Probit function) was performed to determine the subjective "passability" for each subject in each experimental condition (see "General methods"). A one-way ANOVA with repeated measures on the slopes of the Probit function curve was performed for each body orientation. The analysis showed no significant difference in the discrimination sensitivity of the subjective "passability" whatever the body orientation ($F(3,12) = 0.79$, $p = 0.52$). A 4 postural configurations × 5 angles of tilt ANOVA with repeated measures on each factor was then conducted on the estimates of subjective "passability" Results showed a significant difference between the manipulated angles of tilt on the subjective "passability" ($F(4,28) = 30$, $p < 0.001$) but no significant main difference between the postural configurations ($F(3,21) = 0.65$, $p = 0.59$). Nevertheless, the interaction between the angle of tilt and the postural configuration was highly significant ($F(12,84) = 3.59$; $p < 0.001$). This suggested that the tilt effect was clearly dependant on the postural configuration.

In order to further characterize the influence of body orientation upon the judgements, linear regression analyses were applied to the estimates of subjective "passability" obtained for each subject in each experimental condition (Fig. 2-a). Results, summarized in Table 1, showed a significant linear influence of body orientation on the estimated possibility of passing under high obstacles in the four postural configurations. Specifically, the level of subjective "passability" was systematically deviated in the direction of tilt, that is, the more the subjects were tilted backward, the more they felt possible to pass under a given obstacle. Equations of the regression lines performed on the mean subjective estimates for the four experimental conditions are expressed in the following terms $Y = a\theta - b$, where the slope coefficient "a" corresponds to the weight of the orientation influence, "θ" to angle of tilt, "Y" to the subjective "passability" and "b" to a negative offset characterizing the general lowering of the subjective estimates relative to the true level of "passability"

In order to compare the magnitude of the "tilt influence" (i.e., the deviation of the subjective "passability" in the direction of tilt) between the different postural configurations, a one-way ANOVA with repeated measures was conducted on the slope coefficients derived from the individual regression lines for each postural configuration (Fig. 2-b). Results showed significant differences between postural configurations ($F(3,21) = 7.99$, $p < 0.001$). Specifically, post-hoc analyses (Newman–Keuls test) showed a significant influence of the head position in space (i.e., significant differences between B and T condition; $p < 0.01$) but no significant differences in the legs position relative to the trunk (i.e., no differences between the B and B-Lflex condition, and between the T and T-Lflex condition).

Table 1
Results of the linear regression analysis between the mean subjective "passability" and the angle of tilt (Experiment 1).

Experimental conditions		Equation of the regression lines	R2	p
B	(Whole-body)	$Y = 0.53\theta - 1.90$	$R2 = 0.99$	$p < .001$
B-Lflex	(Whole-body – legs flexed)	$Y = 0.46\theta - 4.18$	$R2 = 0.94$	$p < .05$
T	(Trunk alone)	$Y = 0.24\theta - 3.55$	$R2 = 0.97$	$p < .01$
T-Lflex	(Trunk alone – legs flexed)	$Y = 0.22\theta - 2.59$	$R2 = 0.92$	$p < .01$

The egocentric effect for the B and B-Lflex condition was about 46 and 53% of the tilt magnitude, respectively. Noteworthily, the weight obtained for the whole-body orientation influence is fully comparable with the one previously described in the literature for similar judgments of "passability" under obstacles (45%; Bourrelly et al., 2009). Interestingly, fixing the head in space appears to notably reduce the weight of the egocentric attraction observed on perceptual judgments of "passability" under obstacles. This can be explained by the fact that the head-Z axis, which is kept aligned with gravity, constitutes a stabilizing reference for earth-based judgments (Pozzo, Papaxanthis, Stapley, & Berthoz, 1998). Nevertheless, regarding the weight of the egocentric attraction obtained for each experimental condition, the results showed that the trunk orientation influence (between 22 and 24% of the tilt magnitude) can account for almost half of the whole-body egocentric attraction in both legs positions. However, no direct conclusion can be done about the relative contribution of head orientation in the elaboration of the whole-body egocentric attraction. This is precisely the aim of Experiment 2 to question this point.

4. Experiment 2

The purpose of the Experiment 2 was to further investigate the influence of head orientation in the egocentric attraction effect previously reported in literature. Active head orientation, rather than passive head orientation, was manipulated with the assumption that active head movements could improve the subjective "passability" under obstacles (Fouque, Bardy, Stoffregen, & Bootsma, 1999; Viviani, 1990). Particularly, active head orientation could contribute to diminish the effect of egocentric attraction from the head tilt by providing additional information of the head position relative to gravity (Gooey, Bradfield, Talbot, Morgan, & Proske, 2000; Luyat, Gentaz, Regia Corte, & Guerraz, 2001). Specific effects of head and trunk orientation were evaluated separately and compared to the whole-body egocentric effect obtained in a range of ±20° pitch tilts.

4.1. Methods

4.1.1. Subjects

Eight new subjects (three males and five females; mean age 25.25 ± 2.9 year) with normal or corrected to normal vision (by lens correction) participated in this second experiment. They had no previous history of vestibular and neurological symptoms. None of them took part in the previous experiment to avoid any prior knowledge relative to the hypotheses under study.

4.1.2. Experimental conditions

Three postural configurations were tested to address the influence of the whole-body tilt (B), the trunk tilt alone (T), and the head tilt alone (H) on the subjective "passability" under obstacles (Fig. 3). To allow comparisons with the Experiment 1, the B and T conditions were the same as previously described. In the H condition, the head was tilted alone relative to gravity while the chair was kept vertically oriented.

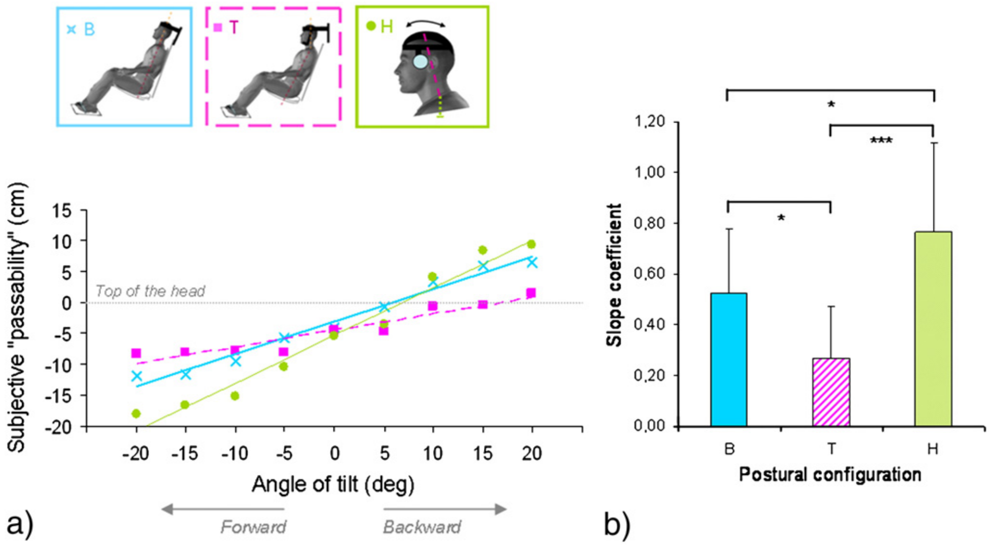

Fig. 3. (a) Linear regression analysis applied to the mean estimates of the subjective "passability" under obstacles relative to the angle of tilt obtained for the three postural configurations (Experiment 2). (b) Mean slope coefficient of the linear regression lines between the mean subjective "passability" and the angle of tilt, and the inter-subjects standard deviation for the three postural configurations (Experiment 2; *** = $p<0.001$; ** = $p<0.01$; * = $p<0.05$). The slope coefficient corresponds to the weight of the orientation influence.

4.1.3. Procedure

Subjects' head was first positioned at the desired angle. The orientation was controlled on line by the experimenter by means of an inclinometer (AccuStar®). Eye level was positioned at a constant height (1.34 m relative to the floor reference, and 2.28 relative to the screen) by adjusting the chair in height and depth. Subjects were asked to keep the head orientation still until the end of the trial. If the signal of head position changed during the judgments by more than 1 degree, the trial was canceled and presented again later in the session.

Nine angles of tilt relative to gravity (0°; −5°, −10°, −15°, −20° forward; and +5°, +10°, +15°, +20° backward) were manipulated in the present experiment. For each body or head orientation, twelve visual stimuli (0; +5, +10, +15, +20, +25, +35 cm upward elevations; and −5, −10, −15, −20, −25 cm downward elevations cm from eye level; i.e., respectively, 0, ±1.3°, ±2.5°, ±3.8°, ±5.0°, ±6.3° and +7.5° elevations from eye level) were presented to the subjects in a pseudo-randomized order. For a given body or head orientation, each visual stimulus was repeated 3 times in a pseudo-randomized order. This order was strictly counterbalanced for half of the subjects. Finally, the total number of judgments was 324 ($3 \times 9 \times 12$) for a total session duration of 60 min. Except for the previous points, the experimental set-up and procedure were the same as in the Experiment 1.

4.2. Results and discussion

As for Experiment 1, no significant difference was found in the discrimination sensitivity of the Probit function whatever the body orientation magnitude ($F(2,16) = 0.15$, $p = 0.86$). A 3 postural configurations × 9 angles of tilt ANOVA with repeated measures on each factor was then conducted on the mean estimates of subjective "passability" Results showed a significant difference between the manipulated angles of tilt ($F(8,56) = 31.65$, $p<0.0001$) but no significant main difference between the postural configurations ($F(2,14) = 0.23$, $p = 0.8$). Nevertheless, the interaction between the angle of tilt and the postural configuration was highly significant ($F(16,112) = 4.94$; $p<0.0001$). Here again, this clearly suggested that the tilt effect appeared dependant on the postural configuration.

Linear regression analyses were performed on the subjective "passability" obtained for each subject in each experimental condition (Fig. 3-a). Results confirmed a linear effect of the whole-body tilt (B) and the trunk tilt alone (T) on estimating the possibility of passing under high obstacles, as observed in Experiment 1. In addition, results showed a linear effect of head tilt alone (H) on the perceptual estimates. The equations of the regression lines calculated on the mean subjective estimates were summarized in Table 2.

In order to compare the linear influences between the different postural configurations, a one-way ANOVA with repeated measures was conducted on the slope coefficients derived from the regression lines for each postural configuration. Results, summarized in Fig. 3-b showed significant differences between the three postural configurations ($F(2,14) = 12.77$, $p<0.001$). Post-hoc analyses (Newman–Keuls test) are reported in Fig. 3-b.

Regarding the slope coefficients of the regression lines obtained for each postural configuration, the "whole-body tilt" (B) condition and the "trunk tilt alone" (T) condition show comparable weights in both Experiments 1 and 2. As for Experiment 1, the weight of the egocentric attraction seems to be half of the whole-body egocentric attraction when the head is fixed in space. Conversely, tilting the head alone induced a greater egocentric attraction than when the whole-body is tilted. In this latter (H) condition, one must acknowledge the presence of supplementary motor information resulting from the active support of the head (i.e., efference copy). While further investigations need to be conducted to disambiguate the role of "active" vs. "passive" proprioception, our data strongly suggest a relevant implication of the combined vestibular and neck proprioceptive information in the observed egocentric attraction.

5. General discussion

The aim of the present study was to determine the origin of the egocentric attraction previously observed on earth-based judgments.

Table 2
Results of the linear regression analysis between the mean subjective "passability" and the angle of tilt (Experiment 2).

Experimental conditions	Equation of the regression lines	R2	p
B (Whole-body)	$Y = 0.52\theta - 3.10$	R2 = 0.98	$p<.001$
T (Trunk alone)	$Y = 0.27\theta - 4.60$	R2 = 0.90	$p<.001$
H (Head alone)	$Y = 0.77\theta - 5.34$	R2 = 0.97	$p<.001$

To address this question, we investigated the contribution of head, trunk and legs position, in the elaboration of the whole-body egocentric attraction previously reported on estimating the possibility of passing under high obstacles during pitch body tilt. The main finding of this study was that the estimated possibility of passing under high obstacles depends on both the magnitude of tilt and the postural configuration in space. Whole-body, trunk and head orientations were found to exert a significant linear effect on perceptual judgments in a range of $\pm 20°$ of tilt. In other words, systematic deviations of the subjective "passability" were observed toward the tilt, and were proportional to the tilt magnitude. For each postural configuration, the egocentric influence appeared also to be highly dependent on the position of trunk and head axis in space. For instance, when compared to the whole-body tilt condition, tilting the trunk alone was found to consistently reduce the amount of the deviation toward the tilt, whereas tilting the head alone was found to consistently increase the deviation toward the tilt.

Previous studies suggested that specific egocentric effects from several body parts could merge together to influence earth-based judgments (Bourrelly et al., 2009; Guerraz et al., 1998; Ito & Gresty, 1996; Mittelstaedt, 1983). However, the way this combination would be achieved remains unclear. Two main interpretations can be advanced from the literature. A first hypothesis suggested that trunk and head specific effects may originate from independent egocentric influences, which could additively combine to yield a main egocentric attraction on earth-based judgments. In line with this hypothesis, Bourrelly et al. (2009) showed that, in a range of $\pm 10°$ of tilt, gaze and body orientation participated each with a constant weight in the elaboration of the main egocentric attraction by a simple summation process. This hypothesis of additivity was also supported by the work of Guerraz et al. (1998) and Wetzig and Baumgarten (1990). Both studies suggested that specific head roll influence could account for the whole-body egocentric attraction in a main part, the remaining part being due to the trunk influence. Our data showed that the weight corresponding to the effect of the trunk orientation alone is half of that obtained for the whole-body orientation. If such an additive process is at work in the elaboration of the main egocentric attraction, the effect of head orientation should account for the other half in the elaboration of the main whole-body egocentric effect. However, the sum of the single effects observed in our study when the head and the trunk are tilted independently gives rise to a larger egocentric influence than when the whole-body is tilted. This suggests that the egocentric attraction may stem from a more complicated process than a simple summation of single and independent effects related to the orientation of different body parts. In other words, our results did not support the idea of an "absolute" and invariant weight attributed to each body segment, irrespective of the postural configuration.

Hence, a second hypothesis may be advanced to explain how the body segments may combine to yield a main egocentric influence on earth-based judgments. The main assumption is that a reweighting process may occur between the different body parts and their respective egocentric influence, depending on the reliability of sensory cues available for a given postural configuration. By reweighting process, we name the interaction between several agents (e.g., sensory inputs, body parts, reference frames) whose influence (i.e., weight) may combine and evolve over time. By allocating a higher weight to reliable cues and a lower weight to unreliable ones, the central nervous system may optimize sensory integration and resolve sensory ambiguities about space representation for a given task (Ernst & Banks, 2002; Ernst & Bülthoff, 2004; Mars, Vercher, & Popov, 2005). For instance, Mars et al. (2005) demonstrated that the respective weight attributed to vestibular and somatosensory cues were inversed, depending on whether the observers had to judge their self-orientation in space or objects orientation relative to gravity. In our study, the difference in sensory reliability may be related for a part to the nature of somatosensory and motor information involved in both tasks, that is information from trunk graviceptors, pressure cues from the skin, neck proprioceptive information or even efference copy during active tilt. For instance, trunk tilt alone induces neck proprioceptive changes, but no vestibular changes, which tends to confirm that vestibular cues are more reliable than somatosensory cues for the assessment of earth-based judgments when the head is vertically oriented (Wade, 1970). Conversely, a decreased vestibular reliability may occur during whole-body tilt (Schöne, 1964; Bringoux et al., 2004), hence explaining the increasing influence of tilt upon earth-based judgements. Furthermore, tilting the head alone induces neck proprioceptive and vestibular changes, as well as efferent information issued from active motor involvement (see 4.2 Results and discussion). Additional information from neck proprioception during head tilt alone, may it be actively maintained, could then provide ambiguous signals about whether the head is moving relative to the trunk or the trunk is moving relative to the head. In this condition, when available sensory cues are modified during tilt and may express different postural configurations, we hypothesized that the central nervous system may cautiously select the head orientation as a main reference for verticality during earth-based judgments. This point is supported by previous works indicating that the head constitutes a stabilized platform for numerous spatial tasks (Berthoz, 1997; Pozzo et al., 1998). Finally, one may summarize the latter interpretation by considering that the egocentric weight attributed to the *Z*-head axis is increased in case of head-and-trunk orientation dissociation.

This strongly challenges the assumption that active head movement could reduce the amount of errors in subjective "passability" by providing additional information about head position relative to gravity (Luyat et al., 2001). Previously, Bringoux et al. (2004) made a similar observation regarding the effect of active arm lifting on SVH judgements. Although arm lifting was supposed to provide additional information about gravity, the authors found that the SVH became more dependent on the whole-body tilt when judgements were performed through active arm movements. These observations stressed once again that estimating limb or body orientation in space and judging the location of earth-based references are likely based on different perceptual processes (Bronstein, 1999).

6. Conclusion

The present study demonstrates that estimating the subjective "passability" under high obstacles depends not only on the whole-body tilt magnitude, but also on the postural configuration in space. Head and trunk tilts were found to mainly attract the subjective "passability" toward their direction. Our results suggest that head and trunk influence could be reweighted to yield a main egocentric attraction, depending on the postural configuration. Special care should be addressed to the orientation of the head, as its egocentric weight may drastically increase when the head axis is not aligned with the trunk axis. The origin of such a reweighting process may probably stem from the reliability of the sensory information available for a particular postural set. Further investigations about the effect of passive vs. active head orientation alone may help to better understand the influence of motor involvement upon the whole-body egocentric attraction during static pitch tilt. In parallel, regarding the findings of Bringoux et al. (2009) who showed a dynamic evolution of the subjective vertical settings toward a tilted visual background, further experiments should be done to investigate how specific egocentric effects could evolve and merge over time. Finally, these findings could be of value in aeronautics where pilots, seated under different postural configurations depending on the type of aircraft, must achieve earth-based judgments in absence of a structured visual background, such as during night or foggy day.

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Le paradigme du franchissement d'obstacles : Conflit entre orientation du flux visuel et orientation du corps

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To pass or not to pass: More a question of body orientation than visual cues

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This study investigated the influence of pitch body tilt on judging the possibility of passing under high obstacles in the presence of an illusory horizontal self-motion. Seated subjects tilted at various body orientations were asked to estimate the possibility of passing under a projected bar (i.e., a parking barrier), while imagining a forward whole-body displacement normal to gravity. This task was performed under two visual conditions, providing either no visual surroundings or a translational horizontal optic flow that stopped just before the barrier appeared. The results showed a main overestimation of the possibility of passing under the bar in both cases and most importantly revealed a strong influence of body orientation despite the visual specification of horizontal self-motion by optic flow (i.e., both visual conditions yielded a comparable body tilt effect). Specifically, the subjective passability was proportionally deviated towards the body tilt by 46% of its magnitude when facing a horizontal optic flow and 43% without visual surroundings. This suggests that the egocentric attraction exerted by body tilt when referring the subjective passability to horizontal self-motion still persists even when anchoring horizontally related visual cues are displayed. These findings are discussed in terms of interaction between spatial references. The link between the reliability of available sensory inputs and the weight attributed to each reference is also addressed.

Keywords: Spatial perception; Body tilt; Vision; Self-motion; Optic flow; Reference frame; Geocentric; Egocentric; Allocentric.

Passing under high obstacles, like the upper part of a door, a tree branch, or a motorway toll height level, is a very natural and successful task daily experienced. In usual situations, such a skill seems easy to perform without any doubts about the effectiveness of action. Nevertheless, in some particular cases, estimating this possibility of action may not be so obvious, leading one to wonder: “Do I pass or not under this obstacle?”

The question raised here concerns the multisensory influence on spatial perceptuomotor skills. This issue has been addressed from two different, complementary approaches, one focusing on the nature of the information taken from the environment as a consequence of our actions, the other more centred on our capabilities of internally representing the outer world.

From the first perspective, perceptuomotor behaviour when passing under obstacles was previously investigated in a task in which observers walked toward and passed under a horizontal barrier set at different height in front of them

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(Steffanucci & Geuss, 2010; Van der Meer, 1997; Wagman & Malek, 2008). In this natural situation, it has been demonstrated that estimating the possibility of passing under high obstacles could rely on the perceptual information provided by the environment itself—that is to say, an affordance, based on a ratio issued from common properties of the subject and the environment (Gibson, 1979; Warren 1984; Warren & Whang 1987). Within the theoretical framework of affordances, Van der Meer (1997) identified a body-scaled critical height leading to a ducking response, specifically when the barrier elevation is on the amount of 1.04 times the actor's body height for an adult walking at normal speed. A similar body-scaled strategy was also observed without motion, in subjects reporting from a stationary viewpoint the critical height at which they perceived the barrier as "passable" without bending the head (Marcilly & Luyat, 2008; Steffanucci & Geuss, 2010; Wagman & Malek, 2008). In these cases of full vision, the information about passability that is naturally present in the environment is directly perceptible from the structured visual surrounding and does not require any spatial representation. One candidate is the vertical visual direction of motion of the obstacle: "Up" means "passable", "down" means "nonpassable".

From the other perspective, however, under particular conditions, such as in impoverished visual environment, or when displacements toward the obstacle are not directly an option, estimating the possibility of passing under high obstacles may rely on internalized spatial representations that could be crucial for avoiding collision (McIntyre, Zago, Berthoz, & Lacquaniti, 2001). Particularly, these representations should be defined with respect to specific spatial directions related from the body or gravitational external cues learned through our daily experience. Among them, vertical and horizontal directions represent crucial references that require to be reconstructed, when not directly accessible, in order to anticipate the consequence of actions. For instance, programming a movement for the interception of falling objects was found to require a representation of the direction and dynamics of gravity, even in its absence (Le Séac'h, Senot, & McIntyre, 2010). In the matter of the study reported here, questioning the ability to pass under high obstacles in the absence of real motion requires one to figure out a horizontal self-motion (relative to the earth ground). In this context, the effectiveness of the predicted action depends on the ability to represent an accurate horizontal displacement on the basis of available spatially related sensory inputs. Some seminal works have demonstrated that the horizontal direction, when referred to the eyes, is only judged −2° lower than the physical reference in darkness (Howard, 1986; MacDougall, 1903). However, recent studies suggested that several environmental factors, such as postural and visual cues, could significantly influence the horizon estimation.

Regarding the effect of postural context, Bringoux, Tamura, Faldon, Gresty, and Bronstein (2004), showed that, in complete darkness, body orientation linearly influenced the subjective horizon in a range from 20° forward to 30° backward body tilts. A forward tilt induced a proportional underestimation of horizon height, relative to the physical reference. A comparable linear relationship was subsequently observed when judging objects' elevation and the possibility of passing under them, suggesting that the two estimations shared common processes, intimately linked to the perceived horizontal direction (Bringoux, Robic, Gauthier, & Vercher, 2008). The origin of this body tilt effect observed in darkness upon judgements of passability was recently investigated, demonstrating that several body parts could jointly intervene in this phenomenon (Bourrelly, Bringoux, & Vercher, 2009; Bourrelly, Vercher, & Bringoux, 2011). For instance, we previously highlighted the influence of postural configurations, by manipulating whole-body tilt, trunk tilt alone, and head tilt alone (Bourrelly et al., 2011). Specifically, when compared to the influence of whole-body orientation, the subjective passability was found to be mainly dependent on the orientation of the head (0.77 cm.deg^{-1}) and trunk (0.27 cm.deg^{-1}) but not on legs orientation. Overall, these studies addressed the question of how multiple spatial references (i.e., body-related or gravity-related) are combined to build a composite reference frame for spatial orientation.

It is also well known that the internally represented horizontal direction is influenced by the static and dynamic visual context. For instance, the perceived horizontal direction has been found to be noticeably deviated towards the pitch orientation of a static tilted visual frame (Matin & Li, 1992; Stoper & Cohen, 1989). From a dynamical point of view, other studies demonstrated the influence of the direction of a translational visual motion upon horizontal direction judgements. For instance, Wu, He, and Ooi (2005) showed that a dynamic visual scene simulating a linear forward motion of the observer could shift the internalized horizontal direction toward the optic flow orientation.

The way postural and visual factors may interact for spatial representation remains nevertheless to be further investigated. Recently, Bourrelly, Vercher, and Bringoux (2010) investigated whether the combination of body tilt and visual cues could impact the perceived direction of a visually induced self-motion. In that case, the direction of the illusory motion, although indicated by visual cues (namely by the focus of expansion of a translational optic flow) has been found to be linearly influenced by body orientation. On the other hand, it has also been reported that vision can fully capture the perception of self-orientation in unusual conflicting situations, such as in the famous "inverted room paradigm" formally investigated by Howard and Templeton (1966) and Jenkin, Dyde, Jenkin, Howard, and Harris (2003).

The question arises as to whether visual cues—namely, those issued from a radial optic flow inducing a forward–horizontal self-motion—may help reduce or even cancel the formerly observed body tilt influence on the subjective passability under obstacles in darkness (Bourrelly et al., 2011; Bringoux et al., 2008). Specifically, if such visual cues provide relevant information congruent with the task requirement (i.e., estimating a horizontal direction), one could expect a reduced influence of body orientation upon subjective passability. We then tested and compared the ability of passing under obstacles at different body orientations under two visual conditions (without visual surroundings vs. with horizontal optic flow). Besides, findings from this task will help us better understand the interaction between the different systems of coordinates involved in the internal representation of spatial directions.

EXPERIMENTAL STUDY

Method

Subjects

Twenty-four subjects with normal or corrected-to-normal vision (by lens correction) gave their informed consent to participate in the study, in compliance with the ethical committee regulating human experimentation in France. Twelve subjects (5 males, 7 females; mean age 26.6 ± 2.0 years) were tested with no visual surroundings, and 12 other subjects (8 males, 4 females; mean age 29.3 ± 7.8 years) were tested with horizontal optic flow. None of them presented a previous history of vestibular and neurological symptoms. All were naive as to the hypothesis under study.

Apparatus

For each visual condition, subjects were seated on a padded tilting chair allowing body rotations in pitch. They were restrained by means of a shoulder harness with their head strapped and secured on a headrest fixed on the chair. The head was positioned, so that the naso-occipital axis was orthogonal to the direction of gravity when the chair was vertically oriented. The chair was adjusted in height so that the subject's transocular axis coincided with the axis of rotation of the chair. In this way, eye level was kept at the same height with respect to the floor reference (1.34 m) regardless of the tilt magnitude. Subjects were placed in front of a screen at a distance of 2.28 m. The visual angle of sight was 81° (horizontal) × 48° (vertical) when binocularly viewed by observers wearing elliptic customized goggles. This ensured that the squared edges of the screen were masked.

A PC Dell Precision 380 computer (Processor: Intel Core i7 950; graphic card: PNY GeForce

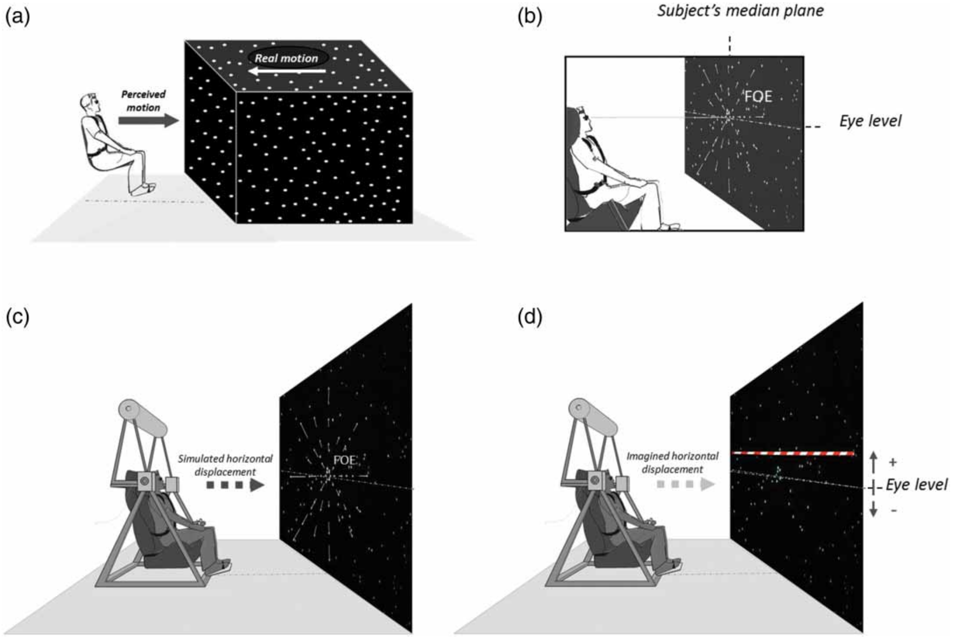

Figure 1. *(a) Illustration of the optic flow display presented in a 3D-visual environment. The visual stimulus consisted in an optic flow field as viewed by an observer translating forward into a 3D cloud of stationary dots. (b) Relative to the stationary observer, the projected stimulus consisted in a cluster of 400 circular dots which radially expanded toward him. The optic flow field was designed to simulate a horizontal displacement. This was obtained by projecting the focus of expansion (FOE), at subjects' eye level, along their median plane. (c) The optic flow was projected for 2 s. (d) At* $t = 2$ *s, the optic flow stopped and the visual scene was kept static while a horizontal car park barrier was projected at different heights onto the screen. Subjects had to respond about their possibility of passing under the bar imagining a horizontal displacement.*

GTX 580 1536 MB) generated the visual stimulus via our in-house ICE software. A video-projector (refresh rate set to 85 frames/s) projected the visual stimulus onto the screen. In the control condition, the stimulus consisted in a horizontal bar (2 m long, 5 cm wide), looking like a parking barrier, projected onto the screen at different heights relative to the subjects' eye level. No visual surroundings were provided in this condition. By contrast, in the horizontal optic flow condition, the visual stimulus was set to simulate an optic flow field viewed by an observer translating forward into a 3D cloud of 400 stationary dots (diameter = 5 mm without local expansion), moved at a constant speed of 66 m s^{-1} [see Bourrelly et al., 2010, for more details; Figure 1(a)]. Relative to the stationary observer, the projected stimulus consisted in a cluster of circular dots, which radially expanded toward him [Figure 1(b) and (c)]. The central focus of expansion of the moving cloud of dots was kept in line with the subjects' eye level, along their median plane [Figure 1(b)]. In this way, the observer experienced a feeling of self-motion in a forward horizontal direction across the visual scene [Figure 1(c)]. The total number of dots was always kept constant on the screen, so that new dots appeared at randomly determined positions in the screen when others went out. When the optic flow stopped, a similar horizontal car park bar was projected onto the screen at different heights relative to the subjects' eye level [Figure 1(d)].

For each condition, subjects were required to estimate whether they could pass under the bar, imagining a forward horizontal displacement. Subjects held in both hands digital response push buttons for judgement settings. Responses were recorded by using the ADwin-Gold system (Keithley©) piloted via our in-house Docometer software. Throughout the experiment, subjects were placed in darkness without any other external visual cue than the visual scene projected onto the screen.

Procedure

Nine angles of body tilt (0°; −5°, −10°, −15°, −20° forward; and +5°, +10°, +15°, +20° backward relative to gravity) were manipulated for each visual condition. For each body orientation, 18 bar elevations (0; +2.5, +5, +7.5, +10, +12.5, +15, +17.5, +20, +25 cm upward elevations; and −2.5, −5, −7.5, −10, −12.5, −15, −17.5, −20 cm downward elevations from eye level; i.e., respectively, 0, ±1.2°, ±2.4°, ±3.5°, ±4.7°, ±5.9°, ±7°, ±8.2°, ±9.6°, and +11.6° elevations from eye level) were randomly presented to the subjects. Before the lights were turned off, subjects were required to attentively consider the distance that separated them from the screen. A first presentation of the car park bar was given to the subjects in order to help them to evaluate its width and its distance of projection (kept constant across the trials).Subjects were asked to answer the following question: "Do you think you could pass under the bar, in the present body orientation, imagining a forward horizontal displacement of your body?".

Subjects were first positioned at the desired body angle relative to gravity in complete darkness. The chair was rotated at constant velocity during 11 s, with a period of initial acceleration and final deceleration of 2 s ($0.4°\cdot s^{-1}$ and $0.2°\cdot s^{-2}$ for ±5° tilt, $0.8°\cdot s^{-1}$ and $0.4°\cdot s^{-2}$ for ±10° tilt, $1.2°\cdot s^{-1}$ and $0.6°\cdot s^{-2}$ for ±15° tilt, $1.6°\cdot s^{-1}$ and $0.8°\cdot s^{-2}$ for ±20° tilt). This was followed by 15 s of rest. This specific duration was chosen as a compromise between the weakest vestibular resting discharge allowing consideration of postrotational effects as negligible (Benson, 1990; Goldberg & Fernandez, 1977) and limited somatosensory adaptation due to the subsequent period of static tilt (Higashiyama & Koga, 1998).

Stationary subjects were then asked to open their eyes and to observe the visual scene that was projected in front of them. In the control condition, subjects were instructed to gaze at the horizontal bar, which appeared on the screen for 4 s. Then, the bar was switched off, and subjects were asked to respond about the possibility of passing under the bar, via a forced-choice judgement by means of two hand-held buttons. In the horizontal optic flow condition, subjects were asked to observe the projected optic flow for 2 s. During this phase, in which all participants reported having experienced a clear feeling of forward self-motion, subjects were required to orient their gaze in the direction toward which they felt they were translating. Then, the visual scene was frozen, and the horizontal bar appeared on the screen for 0.3 s while the subjects were required to gaze at the bar (the delay of saccadic eye movements being 200 ms + 85 ms of decision process, one can easily consider that less than 300 ms was sufficient for the subjects to orient their gaze toward the bar; Robinson, 1973). The optic flow was stopped before the bar appeared in order to avoid the observers referring to purely visual allocentric coding—namely, judging passability by a direct comparison between central focus of expansion and bar elevation. Then, the visual scene disappeared, and subjects were asked to respond about the possibility of passing under the bar, using the same forced-choice judgement. Judgement settings were recorded via the ADwin-Pro system (Keithley©) piloted via our in-house software (Docometre). None of the subjects reported any difficulty in following the task requirements. At the end of the sequence, the chair was brought back to the vertical, and the room lights were turned on for 5 s before a new sequence was launched. For a given body orientation, each visual stimulus was repeated three times in a pseudorandomized order. This order was strictly counterbalanced for half of the subjects. Finally, the total number of judgements was 486 (3 × 18 × 9) for a total session duration of 60 min per visual condition. The instructions were frequently repeated to keep subjects alert and concentrating on the task throughout the experiment. During the experiment, subjects were not informed about the motion direction simulated by optic flow or about the number and height of bar elevations.

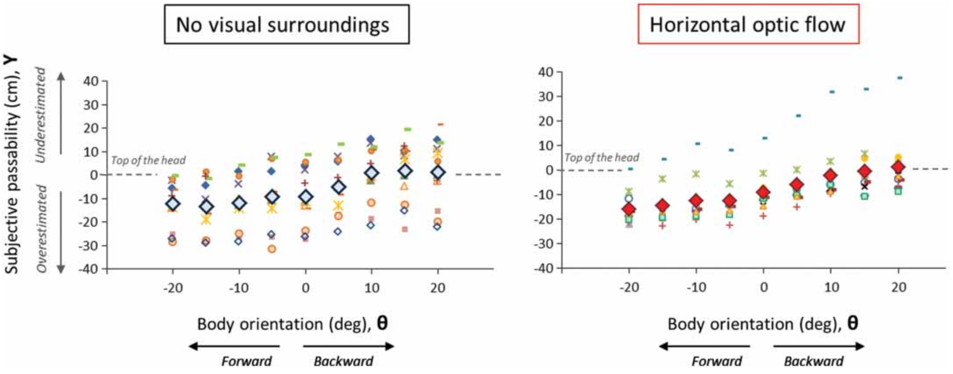

Figure 2. *Individual subjective passability and mean subjective passability (◆) relative to the top of the head obtained for different body orientations, in both visual conditions, with no visual surroundings and with horizontal optic flow. The figure shows comparable individual profiles although individual differences in the offsets.*

Data processing

For each visual condition, judgement settings were first converted into binary values. For each bar elevation, a score of 1 was attributed when subjects thought they could pass under the bar, and a score of 0 was attributed when subjects responded they could not pass under the bar. A subsequent "probit" model, using a nonlinear regression analysis for dichotomic variables, was achieved on the binary responses obtained for each body orientation in order to determine for each bar height the probability p that subjects estimated they could pass under the bar. This permitted us to mathematically determine an indirect variable—that is, the subjective passability, corresponding to the minimal subjective height (in cm) relative to eye level at which subjects estimated they could pass under the bar ($p = 50\%$). The slope of the tangent at the inflection point of the probit curve gave an indication about the discrimination sensitivity of the so-called subjective passability relative to the chosen increments; the sharper the slope, the higher the discrimination sensitivity. An analysis of variance (ANOVA) with repeated measures was performed on the slopes of the probit function to ensure there was no difference in the discrimination sensitivity whatever the experimental condition. Judgements of "subjective passability", initially referred to eye level for convenience, were subsequently reported to the top of the head, defined as the highest physical point of the head from the horizontal floor of the room measured for each subject in each body orientation. Hence, data were expressed in term of vertical deviation (or error, in cm) relative to the top of the head (that is, the true level of passability). Positive values corresponded to an overestimation of the possibility of passing under obstacles relative to the top of the head, and negative values corresponded to an underestimation of the possibility of passing under obstacles (Figure 2).

Preliminary analyses were conducted on the variance distribution (i.e., Levene's test assessing variance homogeneity for both groups of subjects as well as direct comparison of intrasubject variances between groups and body orientations). As no difference was found on this parameter, we were allowed to subsequently perform mean comparisons of the subjective passability observed in all the experimental situations.

To that aim, a 2 (visual condition: with no visual surroundings and with horizontal optic flow) × 9 (body orientation: 0°; −5°, −10°, −15°, −20° forward; and +5°, +10°, +15°, +20° backward relative to gravity) ANOVA with repeated measures on the last factor was conducted on the subjective passability calculated for each subject. A linear regression analysis was then applied to the data to characterize the type of influence exerted by body orientation for each visual condition. Finally, differences between visual conditions were also tested by comparing the

Table 1. *The main body orientation effect*

	Body orientation								
Body orientation	*−20°*	*−15°*	*−10°*	*−5°*	*0°*	*5°*	*10°*	*15°*	*20°*
−20°	—	*ns*	*ns*	*	***	***	***	***	***
−15°		—	*ns*	*	***	***	***	***	***
−10°			—	*ns*	*	***	***	***	***
−5°				—	*ns*	***	***	***	***
0°					—	**	***	***	***
5°						—	***	***	***
10°							—	*ns*	*ns*
15°								—	*ns*
20°									—

Note: Summary table of the Newman–Keuls pairwise comparisons for the mean estimates of subjective passability.
$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$. *ns* = no significant difference.

slopes of the regression lines obtained for each subject in each condition (t-test for independent samples).

Results

Probit analysis

A nonlinear regression analysis (probit function) was performed on the binary values to determine the subjective passability for each subject in each experimental condition (see "Method"). To assess the discrimination sensibility of the probit processing, a one-way ANOVA with repeated measures was performed on the slopes calculated at the inflection point of the probit function curve for each body orientation. Results showed there was no significant difference in the discrimination sensitivity of the subjective passability, whatever the body orientation in the control condition, $F(8, 88) = 1.14$; $p = .34$, as well as in the horizontal optic flow condition, $F(8, 88) = 1.18$; $p = .32$.

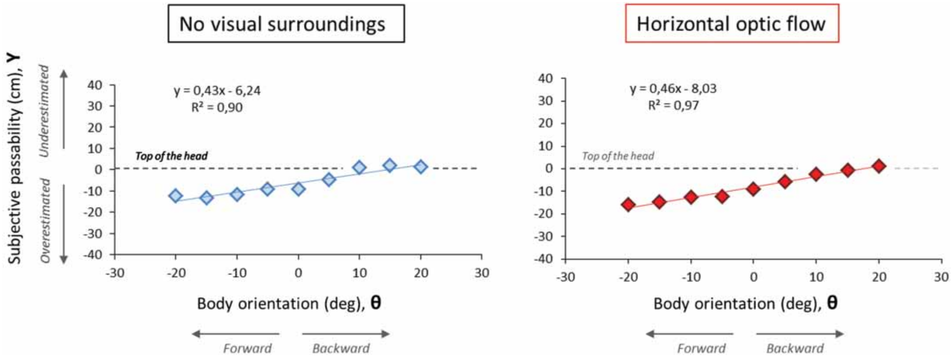

Figure 3. *Linear regression applied to the mean estimates of the subjective passability under obstacles relative to the angle of tilt with no visual surrounding, and with horizontal optic flow. The more the subjects were tilted forward (up to −20-deg), the lower the thresholds, that is, the more the subjects overestimated the obstacle elevation and their capacity of passing under. The equation of the regression line shows an influence of body orientation about 43% and 46%, respectively, on the subjective estimates. The coefficients −6.24 and −8.03 show a general lowering of the subjective passability relative to the top of the head, that is the true level of passability, at 0° of pitch body orientation. Overall, negative values indicated that the possibility of passing under the bar was overestimated. R^2 provides a measure of how well the recorded data are likely to be predicted by the linear statistical model, ($^{***} = p < .001$). Note that the effect of body tilt upon subjective passability is fully comparable in both visual conditions (43% and 46%).*

Table 2. *Results of the linear regression analysis between the mean subjective "passability" and the angle of tilt*

Experimental conditions	*Equation of the regression lines*	R^2	p
No visual surroundings	$y = 0.43\theta - 6.24$	.90	<.001
Horizontal optic flow	$y = 0.46\theta - 8.03$	.97	<.001

Note: Mean subjective "passability" in cm. Angle of tilt in degrees.

Mean comparisons of subjective passability

The 2 (visual condition) × 9 (body orientation) ANOVA conducted on the mean estimates of subjective passability revealed a significant effect of body orientation, $F(8, 178) = 62.03$, $p < .001$, $1 - \beta = 1$ (Figure 2). By contrast, no difference was found between the two visual conditions, $F(1, 22) = 0.20$, $p = .66$; $1 - \beta = .07$, and no significant interaction was found between the visual condition and body orientation, $F(8, 176) = 0.78$, $p < .62$, $1 - \beta = .36$. This means that the subjective passability in complete darkness did not differ from estimates obtained with horizontal optic flow. In other words, the main effect of body orientation upon judgements was not affected by the visual condition. Post hoc analyses (Newman–Keuls test) are reported in Table 1.

Linear regression analysis

A linear regression analysis was applied to the individual estimates of subjective passability in order to characterize the influence of body orientation upon the judgements (Figure 3). Results highlighted a significant linear effect of body tilt on the subjective passability in both visual conditions [$F(1, 106) = 47.22$, $p < .001$, $1 - \beta = .99$ with no visual surroundings, and $F(1, 106) = 23.12$, $p < .001$, $1 - \beta = .99$ with horizontal optic flow]. Specifically, the more the subjects were tilted forward, the more they underestimated the possibility of passing under a given obstacle. The equations of the regression lines calculated on the mean subjective estimates are summarized in Table 2.

The equations of the regression lines were about $y = a\theta + b$, where "y" corresponds to the subjective passability, "a" to the weight of the body orientation influence in cm.deg^{-1}, "θ" to the body orientation angle, and "b" to the offset of the regression line, here characterizing the general lowering of the subjective estimates relative to the top of the head—that is, the true level of passability. Results showed a comparable linear influence of body orientation whatever the visual condition (0.43 cm.deg^{-1} and 0.46 cm.deg^{-1}, with no visual surroundings and with horizontal optic flow, respectively) as well as comparable negative offsets in both judgements (−6.24 and −8.03, respectively).

In order to compare the linear influences between the two visual conditions, a t-test for independent samples was conducted on the slope coefficients derived from the individual regression lines obtained for each participant in each visual condition. Results did not reveal any significant differences between visual conditions ($t = 0.37$; $p = .71$).

Discussion

The present study investigated whether orientational visual cues from optic flow may help to reduce the influence of body tilt previously observed in darkness on estimating the passability under a barrier when imagining a forward horizontal displacement (Bourrelly et al., 2009, 2011; Bringoux et al., 2008). The underlying issues were to better understand how spatial references could interact for the perception of space.

The main finding of this study was that the subjective passability was significantly affected by the angle of body tilt, even when the horizontal direction of displacement was clearly specified by optic flow. The relative influence of visual and postural cues on this spatial task are first discussed, before considering the way in which the different available spatial cues may interact and lead to a unified perception of space.

Visual versus postural information for estimating the passability under obstacles

As previously observed by Bourrelly et al. (2009), our results showed that the mean subjective passability is overall lower than the physical minimal height required to achieve the task (−6.24 cm and −8.03 cm with no visual surroundings and with horizontal optic flow, respectively). These results highlighted a global overestimation of the possibility of passing under obstacles (i.e., typically, subjects estimated they were able to pass under obstacles that were actually located below the top of their head; Bourrelly et al., 2009; Bringoux et al., 2008). This phenomenon may be related to the 30-deg backward orientation of the saccular and utricular maculae relative to the head (Rosenhall, 1972). Indeed, as proposed in particular by Bortolami, Pierobon, DiZio, and Lackner (2006), this tilt may cause a bias (zero shift and backward–forward asymmetry) in the vestibular signal, when the head is positioned in a zero-tilt posture (we used the naso-occipital axis as a reference for horizontality). As a consequence, obstacles whose elevation is referred to the subjective visual horizon will be considered higher than they actually are, since the head is perceived as more tilted than it actually is.

The core result of the present study is that the substantial effect of body tilt on estimating the possibility of passing under high obstacles was not attenuated by directional cues issued from optic flow. We still found indeed a proportional influence of body orientation on the judgements in a ±20deg range. Specifically, the more the body was oriented downward, the more the possibility of passing under high obstacles was overestimated. Conversely, this overestimation was reduced when the body was oriented backward. Most importantly, the effect of body tilt upon subjective passability is comparable for a similar task but performed in complete darkness (46% vs. 43%, respectively). Then, it is obvious from the present data that the subjective passability was attracted toward a body-related direction despite the fact that the horizontal direction of self-motion was visually specified by optic flow.

As a whole, these findings support a greater influence of postural cues (e.g., idiotropic, Mittelstaedt, 1992) relative to visual cues than has usually been reported for other common spatial judgement tasks. Indeed, most of the previous studies manipulating postural and/or visual context when asking for the subjective visual or postural vertical (Barnett-Cowan & Harris, 2008; Howard & Childerson, 1994) or the visual perceived eye level (Li, Dallal, & Matin, 2001) emphasized the prominent role of vision upon tilt. Several hypotheses may be advanced to explain this apparent discrepancy, mostly related to the nature of visual information. Considering the present results, it could be suggested that the structure of the projected optic flow is not rich enough to accurately specify self-motion direction while the body is tilted. However, the unambiguous feeling of self-motion reported here by the subjects is a strong support for considering the visual flow as relevant to generate vection. One may also hypothesize that additional information about external space through more natural and meaningful visual scenes could increase the influence of vision upon judgements (Bringoux et al., 2009). For instance, adding a fixed 3D frame surrounding the dynamic visual scene could enhance the anchoring role of visual cues and, incidentally, diminish the body tilt attraction found in the present experiment. Still, to our knowledge, this study is the first to report such a remaining and still consistent effect of postural orientation in a spatial task where visuospatial cues are otherwise available.

Weighting spatial references into a "composite" reference frame?

If, as noticed above, postural orientation has been found to strongly influence the subjective passability, one has also to consider the non-negligible role of visual and/or gravity-related cues in judgement making. Indeed, perceptual responses were not 100% dependent upon postural orientation (as shown by the regression line coefficient), and the remaining influence of gravitational or/and visual cues raises the issue of how this information is combined to yield a unified perception of space.

We assume here that available sensory cues in the present task convey spatial information about salient directions of space, called references

(Howard, 1982). Among them, we consider egocentric references (i.e., body-related axes such as the head-referenced eye level or the *z*-longitudinal body axis), allocentric references (i.e., salient directions from the surroundings such as the perspective lines of a room or given by the orientation of the support surface), and geocentric references (i.e., anchoring earth-based directions, such as the direction of gravity and the physical horizon). In usual situations, these spatial references naturally matched, some of them being issued from different sensory inputs (e.g., gravity sensing by vestibular and somatosensory cues), whereas others were sometimes conveyed by single sensory inputs (e.g., up–down direction of the surroundings mediated by visual cues only). In this context, estimating the spatial location of an object, for instance the height of an obstacle, can be done by using any of the available references. However, when these references are noncongruent (i.e., spatial conflicting situation), the question arises as to how these spatial cues are processed and integrated by the central nervous system (CNS).

Here, we propose to extend the recent views explaining multisensory integration process (i.e., probabilistic approaches based on Bayesian models; Ernst & Banks, 2002; Vingerhoets, De Vrijer, Van Gisbergen, & Medendorp, 2009) at the level of spatial references. According to this, we hypothesize that the CNS may attribute different weights to the available spatial references, not only depending on their reliability (see the Appendix supporting a limited predictive power of a simple model based on signals reliability), but also on previous spatial experience and expectations in order to build a coherent perceptual space. Specifically, during the integration process, if the CNS may likely take into account the signal-to-noise ratio giving access to a spatial reference (sensory reliability), it may also assimilate priors affecting the way the reference is a priori regarded (sensory relevance).

In this framework, our data clearly support the idea of a substantial weight attributed to some egocentric references when the reliability/relevance of allocentric and geocentric references is low. Specifically, it is obvious in our task that the visually defined direction of self-motion, which specified an allocentric reference of horizontality, might not be very salient since it had to be extracted from optic flow. Furthermore, the gravity-related cues giving access to the geocentric reference of horizontality (through vestibular and somatosensory inputs) have been found rather imprecise (when considering nonrefreshed vestibular graviceptive inputs; Bringoux et al., 2004) or subject to adaptation (because of the progressive decay of the somatosensory information coding static touch and pressure; Higashiyama & Koga, 1998). On the other hand, as it is rather usual to experience forward motion along a sagittal head axis (Pozzo, Papaxanthis, Stapley, & Berthoz, 1998), head-referenced eye level may be naturally considered as an egocentric reference for horizontality (Stoper & Cohen, 1989) and may be substantially weighted by the CNS receiving otherwise ambiguous spatial information. If head-referenced eye level is a good candidate to become here a key reference for horizontal estimation of self-motion used for judgements of passability, its weight seems to remain unchanged whatever the body tilt (in the range of the tested angles). Indeed, the linear regression analysis attested to a similar and constant influence of the egocentric reference across various body orientations. We suggest here that the weight of this constant influence can be directly obtained from the regression line coefficient (i.e., 0.46 cm.deg^{-1} for the horizontal optic flow condition).

Following our main interpretation, and assuming that an internal representation of space is required to perform the task when facing conflicting and/or impoverished sensory environments, we hypothesize that a unique "composite" reference frame could emerge from the weighted combination of the available spatial references (Bringoux et al., 2008; Gueguen, Vuillerme, & Isableu, 2012; Luyat, Mobarek, Leconte, & Gentaz, 2005). This view is somehow different from the more classical ones supporting that several reference frames could be specifically elaborated at a representational level (Batista, 2002; Brotchie, Andersen, Snyder, & Goodman, 1995; Ghafouri, Archambault, Adamovich, & Feldman, 2002; Snyder, Grieve, Brotchie, & Andersen, 1998). Indeed, if some previous works have suggested that spatial reference frames may be identified as preexistent neurophysiological structures, exclusive from one to others (Galati et al., 2000; Snyder et al., 1998), some recent studies argue for less distinctive loci of spatial representations, often overlapped and differently activated depending on the task constraints (Committeri et al., 2004; Lopez, Lacour, & Borel, 2005). Hence, composite representations may arise from the combination between several spatial references. Further research is needed to explore the way a subjective reference frame may emerge, adapt, and transfer across different spatial tasks. Computational approaches could be a powerful tool for predicting perceptual consequences associated to the combination of redundant or concurrent spatial inputs. A preliminary step to initiate such an approach is presented in the Appendix.

Conclusion

Overall, this study strongly supports the hypothesis of a substantial egocentric influence on subjective passability as a powerful phenomenon resistant to the presentation of horizontal cues in the visual scene. These findings could be particularly relevant in the context of aeronautics where pilots, oriented 30° backward (Roumes & Grau, 2003) may have to judge earth-based directions of space under poor visual conditions (under fog or darkness). This study may also be of value for further research on multisensory implication in space perception. For example, it could be particularly interesting to question the contribution of specific sensory cues in the reweighting processes affecting the combination between available spatial references. In this vein, the changes observed in the weight of a specific spatial reference over time could be highly informative to better understand how these spatial cues dynamically interact (Bringoux et al., 2009; Scotto Di Cesare, Bringoux, Bourdin, Sarlegna, & Mestre, 2011).

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APPENDIX

A computational model based on maximum-likelihood estimation

A complementary support to discuss our results lies in the conceptual framework of computational models (Bayesian model; Tagliabue & McIntyre, 2011). Maximum-likelihood estimation (MLE) is indeed a method for estimating the parameters of a statistical model. When applied to a data set, MLE provides estimates for the model's parameters based on signal reliability. The latter, which is defined by the inverse of the response variability associated to a given input, may be considered as the weight attributed to this input. In the present section, we developed a complementary analysis relying on Bayesian rules for testing how subjective passability, when combined visual and body-related cues are available, could be predicted from respective unimodal conditions.

Some recent studies considered single visual stimulation without tilt as the "unimodal" visual condition for testing MLE model on spatial estimates (e.g., Gueguen et al., 2012; Vingerhoets et al., 2009). We adopted the same assumption for studying the integration of visual and body-related cues for judgements of subjective passability. Specifically, we selected the data from two subjects who both ran the three following experiments.

The first experiment corresponded to the now-reported control condition where passability was judged at different body tilts without visual surroundings (body-related cues only: *B*).

The second experiment manipulated the optic flow orientation without body tilt; subjects were asked to judge the orientation of the visually induced self-motion relative to the physical horizon (Bourrelly et al., 2010) (visual cues only: *V*).

The third experiment manipulated both body-related cues (body tilt) and visual cues (horizontal optic flow) as reported in the present study (body-related cues and visual cues: *BV*).

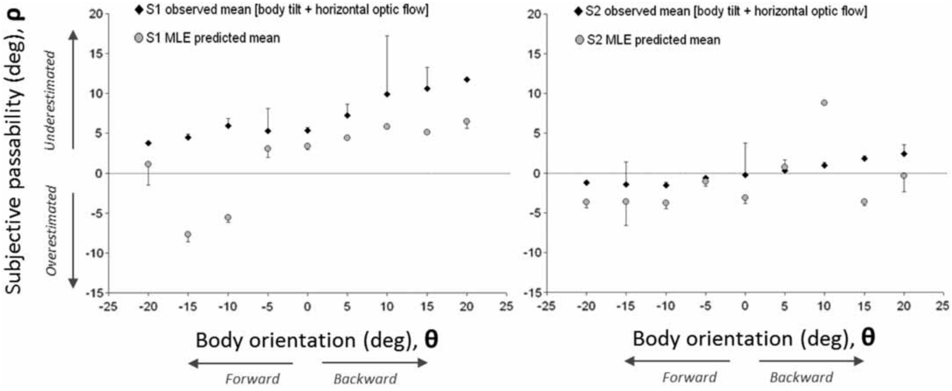

Figure A1. *Comparison between observed data and model predictions (Maximum Likelihood Estimations based on the combination of single visual and body-related cues) on judgements of subjective passability relative to the angle of tilt for 2 subjects. Substantial differences were clearly apparent between observed and predicted means for these participants.*

We then computed the within-subject reliability of each single condition (B, V, and BV) for each angle of tilt. The following equation reflects the computation of the body-related weight w_B associated to its reliability according to the measured variance σ^2 observed in B and V.

$$w_B = \frac{\sigma_V^2}{\sigma_B^2 + \sigma_V^2}$$

Mean data recorded in both B and V conditions were weighted relative to their reliability to predict data in the combined condition following the equation above:

$$x_{BV} = w_B x_B + w_V x_V$$

x_{BV} corresponds to the predicted data for the combined condition (i.e., subjective passability at a given angle of body tilt with horizontal optic flow), x_B and x_V to the mean spatial estimates (i.e., subjective passability or central focus of expansion location) relative to the physical horizon in the respective "unimodal" conditions B and V, and w_B and w_V to their associated reliability. According to MLE, the within-subject variance in the combined condition would depend on the within-subject variance in the unimodal conditions and should be lower. Theoretical within-subject variance predicted for BV should be as follows:

$$\sigma_{BV}^2 = \frac{\sigma_B^2 \sigma_V^2}{\sigma_B^2 + \sigma_V^2}$$

The results of the model for both subjects are illustrated in Figure A1.

As reflected by Figure A1 the predictive power of the present MLE analysis run on two subjects is rather poor for these specific cases. Several interpretations may account for this observation.

First of all, one could argue that the spatial tasks themselves were different between V and B or BV conditions. Indeed, while subjects were asked to judge the direction of the perceived motion induced by optic flow in the V condition, they were asked to judge the capability of passing under an obstacle in the B and BV conditions. Nevertheless, it is worth mentioning that both tasks were geocentric—that is, both types of judgements were referred to the physical horizon and, therefore, might be based on the same underlying processes (as it was already demonstrated for judgements of the gravity-referenced eye level and subjective passability (Bringoux et al., 2008).

Second, one of the major problems when applying this model to spatial perception is that one cannot strictly consider a purely unimodal condition arising from the visual stimulation, since body-related cues can never be suppressed (except for a somatosensory-deafferented patient, who would be also labyrinthine defective!). In other words, the assumption of unimodality in the "single" V condition may be criticized as body-related cues cannot be excluded from the stimulation. As a consequence, the presence of body orientation cues in the V condition could bias the reliability of visual cues in the model and consequently yield substantial differences with the observed data.

Finally, other existing models for spatial multisensory integration might have been at work in the present case, such as "winner-takes-all" models (e.g., Bonneh, Cooperman, & Sagi, 2001) where a particular sensory cue may "overwrite" all the others. For instance, in line with the last type of model, based on sensory capture phenomenon, it has been shown that the perceived distance of self-motion when both visual and body-related cues were present was perceptually closer to that perceived during physical motion only. Of course, we should remain cautious on these findings and the former interpretations as only two subjects could have been tested from our database. At the same time, only three repetitions per angle/condition were available for intrasubject variance computation. All in one, further investigations remain to be done for improving the predictive power of sensory integration models for spatial orientation.

Localisation spatiale égocentrée

Pointage continu : Modification graduelle du vecteur gravito-inertiel et conflit entre informations visuelles et gravito-inertielles

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RESEARCH ARTICLE

Spatial localization investigated by continuous pointing during visual and gravitoinertial changes

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Abstract In order to accurately localize an object, human observers must integrate multiple sensory cues related to the environment and/or to the body. Such multisensory integration must be repeated over time, so that spatial localization is constantly updated according to environmental changes. In the present experimental study, we examined the multisensory integration processes underlying spatial updating by investigating how gradual modifications of gravitoinertial cues (i.e., somatosensory and vestibular cues) and visual cues affect target localization skills. These were assessed by using a continuous pointing task toward a body-fixed visual target. The "single" rotation of the gravitoinertial vector (produced by off-axis centrifugation) resulted in downward pointing errors, which likely were related to a combination of oculogravic and somatogravic illusions. The "single" downward pitch rotation of the visual background produced an elevation of the arm relative to the visual target, suggesting that the rotation of the visual background caused an illusory target elevation (induced-motion phenomenon). Strikingly, the errors observed during the "combined" rotation of the visual background and of the gravitoinertial vector appeared as a linear combination of the errors independently observed during "single" rotations. In other words, the centrifugation effect on target localization was reduced by the visual background rotation. The observed linear combination indicates that the weights of visual and gravitoinertial cues were similar and remained constant throughout the stimulation.

Keywords Target localization · Multisensory integration · Continuous pointing · Visual cues · Vestibular cues · Somatosensory cues

Introduction

The spatial localization of an object relies on the integration of multiple sensory cues available to the observer. In daily life, the environment and the observer are rarely static. In this context, localizing an object requires a continuous updating of its position based on motion cues about the body and the environment. Such updating mainly relies on sensory cues such as vestibular and somatosensory cues, here referred to as gravitoinertial (**Gi**) cues, and visual cues. In the present study, we examined the multisensory integration processes underlying spatial updating by investigating how environmental changes (i.e., experimental manipulations of both visual and **Gi** cues) affect target localization, as assessed through a continuous pointing task.

In changing visual surroundings, the invariant properties of gravity constitute a relevant reference for spatial localization (Howard 1982; McIntyre et al. 1998; Mittelstaedt 1983; Pozzo et al. 1998). However, it is well known that a modification of the **Gi** environment (e.g., in weightlessness or during linear acceleration) impairs object localization (for a review, Lackner and DiZio 2004). Specifically, during a forward linear acceleration such as that produced by off-axis centrifugation, a false sensation of object elevation usually happens (i.e., the oculogravic illusion, Clark and Graybiel 1951). This perceptual illusion has been

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mostly explained as a consequence of the lowering of the visual horizon, considered as a main reference for the judgment of objects' height (Cohen et al. 2001; Graybiel 1952). At the same time, when the observer has to reach the perceived object during centrifugation, he/she is submitted to an illusory perception of body tilt (i.e., the somatogravic illusion, Graybiel 1952), which may lead to compensatory arm responses. In addition, a perceptual drift of the arm position relative to the body could influence pointing movements toward the perceived object during centrifugation (Bourdin et al. 2006). Hence, multiple and complex factors appear to be at work while pointing toward a visual target in a modified **Gi** environment.

Some studies investigated whether adding visual cues could attenuate the behavioral consequences of **Gi** modifications upon spatial localization. Such attenuation was found by adding visual information relative to the physical horizon or by using optic flow to induce an antero-posterior displacement (Eriksson et al. 2008; Lessard et al. 2000; Tokumaru et al. 1998). Although de Graaf et al. (1998) have already tested the effectiveness of rotating the visual scene in order to reduce the somatogravic illusion, the effect of moving visual cues on target localization during centrifugation has never been investigated, to our knowledge. This may, however, constitute a promising way of investigation since it is well established that, in a non-modified **Gi** environment, moving the visual background strongly influences target localization (i.e., induced-motion illusion, Duncker 1929; Post et al. 2008). Specifically, when a static visual target is presented, a moving visual background usually produces an illusory perception of target motion, in a direction opposite to the background motion, while the visual background is perceived static.

The purpose of the present study was to investigate how continuous and synchronized visual and **Gi** changes affect the spatial localization of a body-fixed visual target. To that aim, the visual background and/or the **Gi** vector were gradually rotated during a continuous pointing task. We assumed that a continuous pointing task, already used by Siegle et al. (2009) and Bresciani et al. (2002), allows the continuous inference of the target localization process. Besides, this task allows a better understanding of multisensory integration processes involved in spatial localization. Based on recent suggestions that sustained weights are attributed to the different sensory modalities available to the observer (Barnett-Cowan and Harris 2008; Bourrelly et al. 2010; Bringoux et al. 2008), we hypothesized that despite gradual modifications of visual and **Gi** stimuli, the weight attributed to visual and **Gi** cues would be preserved when both stimuli are simultaneously presented. With respect to how visual and **Gi** cues would be combined, several studies have shown that various sensory cues are integrated in a manner consistent with a weighted linear combination of the responses obtained with individual cues (for a review, Angelaki et al. 2009). We thus hypothesized that the pointing errors observed during the combined manipulation of visual and **Gi** cues would correspond to the linear combination of the visual influence (i.e., target elevation due to the "induced-motion" illusion) and the **Gi** influence (i.e., mainly issued from the coupled somatogravic and oculogravic illusions).

Methods

Participants

Seventeen right-handed subjects (9 men and 8 women; mean age ± SD: 25.2 ± 4.0 years) participated in this experiment. They reported having normal or corrected-to-normal vision and no neurological or sensorimotor disorders. All gave informed consent prior to the study, in accordance with the local ethics committee and the 1964 Declaration of Helsinki.

Apparatus

As illustrated in Fig. 1, subjects sat on a bucket seat fixed to a rotating platform. They were positioned off-axis, facing the platform center, with their inner ear radially positioned 1.90 m away from the rotation axis. A four-point safety belt was used to prevent subjects' trunk displacement. Clockwise centrifugation was servo-controlled to fit a pattern of angular velocity increasing linearly from 0° to $120^\circ\ \mathrm{s}^{-1}$ in 30 s (Fig. 2). During the platform rotation, centrifugal force ($\vec{c}$) was added to gravitational force ($\vec{g}$), producing a non-linear rotation of the **Gi** vector.[1]

A 3D head-mounted display (HMD, 3D Cybermind hi-Res900®, Cybermind Interactive Nederland, The Netherlands; resolution: 800 × 600 pixels; field of view: 31.2° diagonal for each eye) was used to display a stereoscopic visual background. The HMD was fixed to the adjustable headrest used to prevent head motion. Customized software was used to create a visual background composed of an octagonal 3D prismatic structure that reinforced horizontal and vertical reference lines (Fig. 1). A pink virtual target of 1 cm in diameter was projected at the center of the visual background and was always static relative to the observer. Nevertheless, subjects were not informed that the target was static and positioned at the center of the visual screen. The visual background and target appeared at 1.5 and .8 m from eye position, respectively. It should be noted that the HMD device prevented subjects from having visual

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[1] $\mathrm{Gi\_angle} = a\tan\left(\frac{\vec{c}}{\vec{g}}\right)$

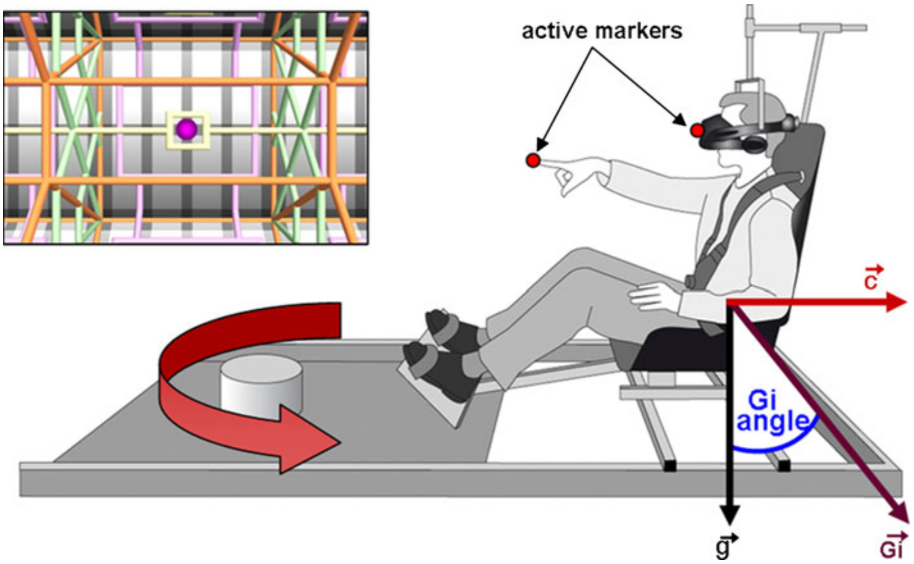

Fig. 1 Experimental setup. Subjects wore a head-mounted display showing a central body-fixed target and, for most conditions, a structured background as illustrated in the *upper-left panel*. The platform could rotate and thus modify the **Gi** angle relative to the vertical. *Dots* on the hand and head represent active markers for data acquisition. **c** Centrifugal force, **G** gravitational force, **Gi** gravitoinertial force

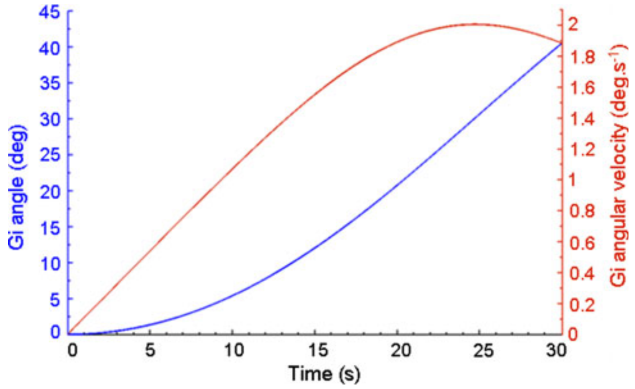

Fig. 2 **Gi** angle (*higher curve*) and angular velocity (*lower curve*) modifications during the centrifugal platform rotation from 0 to 120° s^{-1} in 30 s

feedback about the experimental setup and about their current arm location.

Infrared active markers were placed on the right index fingertip and at the cyclopean eye location on the HMD. These locations were sampled at 200 Hz using an optical motion tracking system (Codamotion Cx1®, Charnwood Dynamics Ltd, Leicestershire, UK; accuracy: .05 mm). A real-time acquisition system (ADwin-Pro®, Jäger, Lorsch, Germany) driven by customized software was used to control visual background and **Gi** vector rotations and to collect data.

Procedure

Throughout the experimental trials, subjects were required to maintain their gaze on the virtual target and to point as accurately as possible toward the virtual target with their right index finger, arm outstretched. All participants were rotated once before the beginning of the experiment, in order to familiarize them with centrifugation effects.

During the experiment, we manipulated the **Gi** and/or the visual background pitch rotation in 5 experimental conditions (Fig. 3). The **GI** condition involved a centrifugation (causing **Gi** vector rotation) without visual background. The **GI–Vis**$^{\mathbf{F}}$ condition replicated the **GI** condition with an additional structured **Vis**ual background, which was **F**ixed relative to the observer and presented throughout the centrifugation. The **Vis**$^{\mathbf{R}}$ condition involved a **R**otation of the **Vis**ual background without centrifugation. **GI**, **GI–Vis**$^{\mathbf{F}}$ and **Vis**$^{\mathbf{R}}$ conditions were the so-called single conditions. Kinematics of the visual background rotation was the same as those of the **Gi** vector rotation (Fig. 2), and the rotation was performed in the same pitch downward direction. The **GI–Vis**$^{\mathbf{R}}$ condition involved both **Gi** vector and **Vis**ual background **R**otations. In this so-called combined condition, the rotations of the visual background and **Gi** vector were synchronized.

Before each trial, subjects had to place their right index finger at the starting position, indicated with a standardized tactile mark on the right leg. A trial began with the appearance of the visual target accompanied by the static visual background, except in the **GI** condition. A concomitant auditory signal prompted the participant to point toward the target and to keep the index finger on its perceived location until the end of the trial. Seven seconds after the auditory signal, the visual background and/or the **Gi** vector could be rotated with an increasing velocity during 30 s (Fig. 2). A second auditory signal and the suppression of visual cues (i.e., the HMD screen became black) indicated the end of the trial, prompting subjects to bring their arm back on the tactile mark. In the conditions including centrifugation, a deceleration phase began,

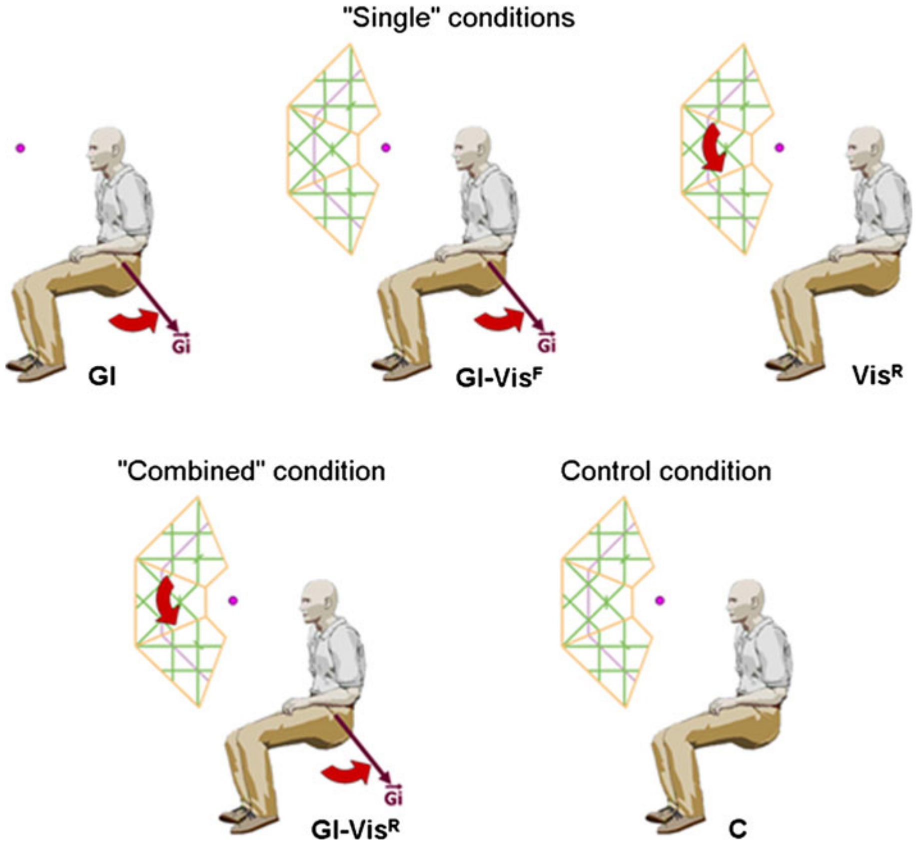

Fig. 3 Experimental conditions. **GI** **Gi** vector rotation without visual background. **GI–Vis^{F}** **Gi** vector rotation with fixed visual background. **Vis^{R}** visual background rotation without **Gi** vector rotation. **GI–Vis^{R}** **Gi** vector and visual background rotation. **C** fixed visual background without **Gi** vector rotation. *Arrows* represent the rotation of the visual background and the **Gi** vector. The target, presented at eye level, always remained fixed relative to the observer

following a profile inverse to the acceleration phase. A 30-s period of rest was finally allowed before the next trial started. This resting period allowed for the suppression of post-rotational effects due to semi-circular canal stimulation (Benson 1990), and limited possible fatigue or motion sickness.

All 17 subjects performed 4 trials in each of the 4 aforementioned conditions. The experimental session thus consisted of 16 trials presented in a pseudo-random, counterbalanced order. Following these 16 trials, a control trial of an equivalent duration was presented and involved a fixed visual background without centrifugation (Fig. 3). This **C** control condition was used as a baseline for comparison analyses. The complete experimental session lasted approximately 1 h.

Data processing

Data were first low pass, Butterworth-filtered (cut-off frequency: 10 Hz; order: 2). Angular errors of continuous pointing in the sagittal plane were analyzed from the beginning of the trial to the end of the visual background and/or **Gi** vector rotation (i.e., $t = 30$ s; see Fig. 2). For each trial, the markers on the cyclopean eye and the right index indicated the angle between the pointing finger and eye level. Pointing errors were determined by referring the current pointing angle to the initial angle reached prior to any rotation (i.e., $t = 0$ s).

Statistical comparisons were made on the means and standard deviations of pointing errors for all experimental conditions. To that aim, we used analyses of variance (ANOVAs) with repeated measures and post hoc tests (Newman–Keuls) or *t* tests for dependant samples. The effect size ($\eta^2 p$) and the power ($1 - \beta$) of each test were provided.

Multiple linear regression analyses were performed on the mean pointing errors (i.e., the between-subjects mean) and individual pointing errors (i.e., the within-subject mean of the 4 trials per condition) observed in the **GI–Vis^{R}** condition. Based on the least squares method, these analyses were achieved to find a model that could better predict the data obtained in the "combined" condition with the "single" conditions as predictors. The coefficient of determination (R^2) was used to determine the quality of fit of the multiple linear regressions on the mean pointing errors in the **GI–Vis^{R}** condition. The predictive power of the models was estimated by the calculation of the root mean square error (RMSE) on individual pointing errors. RMSE evaluates the differences between predicted and observed pointing errors, lower values of RMSE indicating a better fit. The level of significance was .05 for all analyses.

Results

Final pointing errors

For each participant, the rotation of the **Gi** vector or of the visual background affected final pointing accuracy (assessed at $t = 30$ s). Figures 4 and 5 show that even though the target always remained stationary, the rotation of the visual background (**Vis**$^{\mathbf{R}}$ condition) yielded an upward shift of the pointing response (**Vis**$^{\mathbf{R}}$ mean $= +1.9°$), whereas the rotation of **Gi** vector (**GI** and **GI–Vis**$^{\mathbf{F}}$ conditions) yielded errors in the opposite, downward direction (**GI** mean $=$ $-2.4°$; **GI–Vis**$^{\mathbf{F}}$ mean $= -2.0°$). Strikingly, when the **Gi** vector and the visual background were synchronously rotated, pointing accuracy was not substantially affected (**GI–Vis**$^{\mathbf{R}}$ mean $= +.1°$) compared with the control condition (**C** mean $= -.4°$).

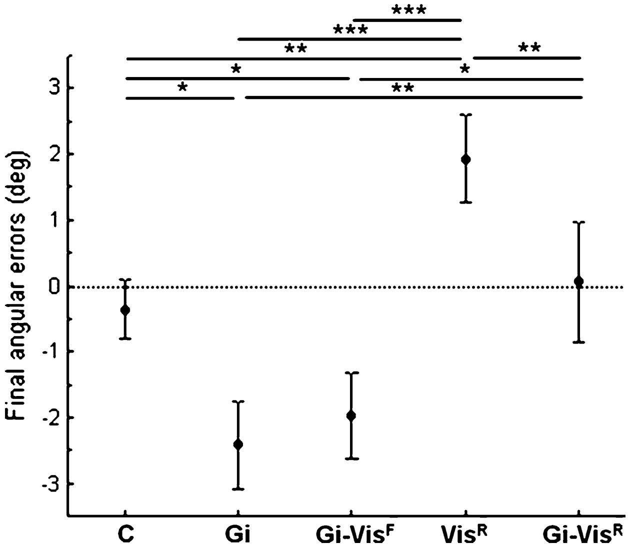

Fig. 4 Mean final pointing *errors* as a function of experimental conditions. Negative pointing *errors* correspond to downward pointing. *Error bars* represent standard errors. $^*P < .05$; $^{**}P < .01$; $^{***}P < .001$

A 5-condition repeated-measures ANOVA on final pointing errors revealed a significant effect of the main factor $[F_{(4,64)} = 11.98$, $P < .001$, $\eta^2 p = .43$, $(1 - \beta) = 1.00]$. As illustrated in Fig. 4, post hoc analyses showed that final pointing errors observed when a “single” stimulus was manipulated (either visual or **Gi** cues) significantly differed from the final pointing errors in the **C** control condition. On the other hand, final pointing errors in the “combined” condition did not statistically differ from those in the **C** condition (**C** vs. **GI–Vis**$^{\mathbf{R}}$, $P = .55$). The ANOVA performed on the within-subject standard deviation of the final pointing errors in **GI**, **GI–Vis**$^{\mathbf{F}}$, **Vis**$^{\mathbf{R}}$ and **GI–Vis**$^{\mathbf{R}}$ conditions did not reveal any significant difference $[F_{(3,48)} = 1.82$, $P = .16$, $\eta^2 p = .10$, $(1 - \beta) = .44]$.

Further analysis indicated that our data were not substantially affected by fatigue or learning effects. Indeed, final pointing errors were negligible in the last, control condition trial (mean $= -.4°$). Moreover, a 4-condition × 4-trial position ANOVA confirmed that there was no significant trial position effect on final pointing errors $[F_{(3,30)} = .25$, $P = .86$, $\eta^2 p = .03$, $(1 - \beta) = .09]$ and no significant interaction $[F_{(9,90)} = 1.01$, $P = .44$, $\eta^2 p = .09$, $(1 - \beta) = .47]$.

Time course of pointing errors

Figure 5 shows that in **GI**, **GI–Vis**$^{\mathbf{F}}$ and **Vis**$^{\mathbf{R}}$ conditions, pointing errors gradually increased after stimulation onset (i.e., $t = 0$ s). Relative to the **C** condition, pointing errors

Fig. 5 Mean pointing *errors* as a function of time. Negative pointing *errors* correspond to downward pointing. *Thick lines* illustrate significant differences between a given condition and the **C** control condition ($P < .05$). *Areas* represent positive standard errors (note that the standard error for the **C** condition is not represented because trial number differed from the other experimental conditions). The *dotted line* corresponds to the data predicted by the multiple linear regression on the mean pointing errors (see “Time course of pointing errors”)

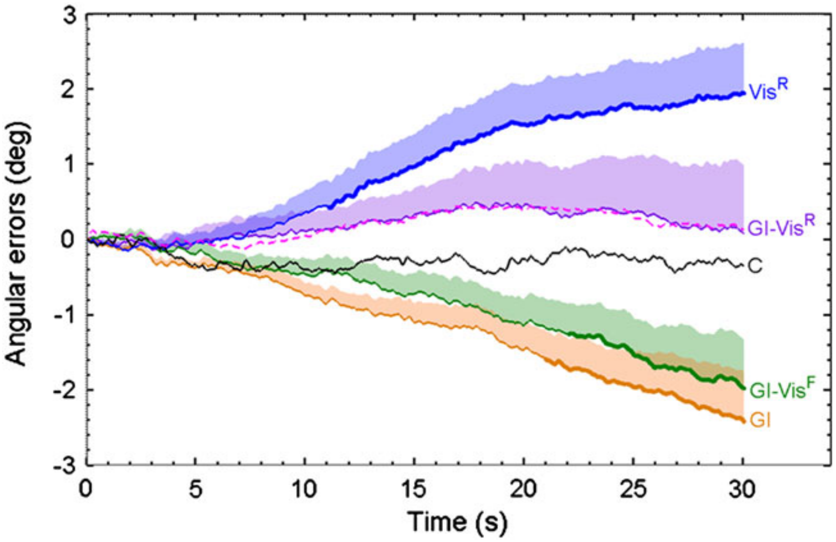

Table 1 Latency (in s) of the first significance in mean pointing errors between conditions

	C	**GI**	**GI–Vis^{F}**	**Vis^{R}**	**GI–Vis^{R}**
C	–	21.0	22.0	11.1	ns
GI		–	ns	9.0	10.1
GI–Vis^{F}			–	11.1	13.7
Vis^{R}				–	20.0
GI–Vis^{R}					–

Latencies are given relative to the stimulus onset, i.e., rotation of **Gi** vector and/or visual background ($t = 0$ s). ns indicates that no statistical difference was found. Similar latencies were obtained when data were normalized with respect to the control condition (i.e., by subtracting, for each subject, the pointing errors in the control condition from the mean pointing errors in a given condition)

first appeared in the **Vis^{R}** condition and then in **GI** and **GI–Vis^{F}** conditions (Table 1). Pointing errors remained negligible throughout the trial in both **C** and **GI–Vis^{R}** conditions. To investigate more precisely how the experimental manipulations dynamically affected pointing accuracy over time, a 5-condition ANOVA was carried out on pointing errors every 5 ms throughout the trial. When the ANOVA revealed a significant main effect (starting 8.6 s after trial onset [$F_{(4,64)} = 2.53$, $P = .049$, $\eta^2 p = .14$, $(1 - \beta) = .68$] to the end of the trial), post hoc analyses were performed. This method (e.g., Sarlegna et al. 2003) was used to obtain the latency of the first significant difference between two given conditions, even though sensory integration likely started before the statistical analysis reached significance. This analysis confirmed that, relative to the **C** condition, pointing errors first differed in the **Vis^{R}** condition (Table 1). Errors then differed between **C** and **GI** or **GI–Vis^{F}** conditions. Across the trials, no significant difference was found between the pointing errors in the two "single" conditions including **Gi** vector rotation (**GI** vs. **GI–Vis^{F}**, $P > .05$) or between that in **GI–Vis^{R}** and **C** conditions. Comparisons were then made between the pointing errors in the trial achieved in the **C** condition and that in the different trials of each other condition to verify the consistency of response latencies. These were similar across trials for the **GI** condition (mean = 21.9 ± 1.8 s), **GI–Vis^{F}** condition (mean = 19.3 ± .5 s) and **GI–Vis^{R}** condition (no trial latency could be extracted since no significant differences were found). However, latencies in the **Vis^{R}** condition appeared more variable (mean = 12.8 ± 7.3 s), even though it had no effect upon the final pointing errors, as attested by the non-significant trial position and trial position × condition effects (see "Final pointing errors").

To further investigate the pointing errors observed in the **GI–Vis^{R}** condition relative to those observed in the "single" conditions (constituting the "combined" condition), we first tested the hypothesis of a simple additive effect (i.e., **GI–Vis^{R}** = **Vis^{R}** + **GI–Vis^{F}**). A paired t test was conducted every 5 ms between the pointing errors observed in the **GI–Vis^{R}** condition and the sum of the pointing errors observed in the "single" **Vis^{R}** and **GI–Vis^{F}** conditions. No statistical difference was observed throughout the trial ($P > .05$, as illustrated in Fig. 5). In addition, no significant difference was found between the pointing errors in the **GI–Vis^{R}** condition and the sum of the pointing errors in **Vis^{R}** and **GI** conditions. The R^2, used to evaluate the quality of the model **GI–Vis^{R}** = **Vis^{R}** + **GI–Vis^{F}**, was .36 ($P < .001$).

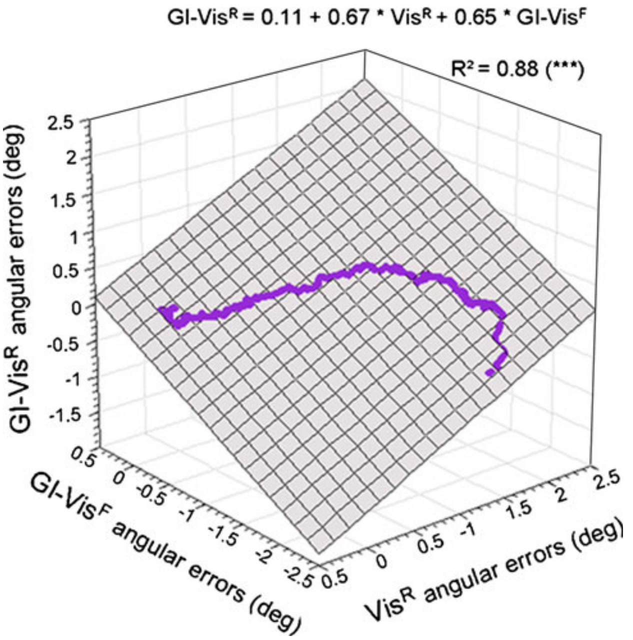

Fig. 6 Multiple linear regression on between-subject mean fitted to the **GI–Vis^{R}** mean pointing errors (*line*) as a function of the mean pointing *errors* observed in the single conditions **Vis^{R}**. The multiple regression *plane* is represented by the *hatched area* following the equation given above the *graph*. ***$P < .001$

We tested how better a multiple linear regression would explain pointing errors in the **GI–Vis^{R}** condition. First, we investigated the origin of the pointing errors obtained in the "combined" condition by performing multiple linear regressions on individual pointing errors (mean of the 4 trials for each subject) and averaging each equation parameter (ordinates to the origin and **Vis^{R}** and **GI–Vis^{F}** weights). The average equation (**GI–Vis^{R}** = −.22 + .05 × **Vis^{R}** + .72 × **GI–Vis^{F}**) did not explain a large part of variance when applied on the mean pointing errors ($R^2 = .39$, $P < .001$). Second, we assessed the quality of fit of a multiple linear regression on the mean pointing errors in the **GI–Vis**$^{\mathbf{R}}$ condition based on the mean pointing errors observed in the "single" conditions. Figure 6 presents the multiple regression plane that best explained **GI–Vis**$^{\mathbf{R}}$ mean pointing errors (plane equation: **GI–Vis**$^{\mathbf{R}}$ = .11 + .67 × **Vis**$^{\mathbf{R}}$ + .65 × **GI–Vis**$^{\mathbf{F}}$, $R^2 = .88$, $P < .001$). The similar equation parameters .67 and .65 suggest that the weights of visual cues and **Gi** cues were similar in the "combined" condition.[2] In addition, these weights seemed to be constant across the trial as attested by the close planar relationship between the predictors and the data observed in the **GI–Vis**$^{\mathbf{R}}$ condition ($R^2 = .88$). Figure 5 also illustrates the quality of the fit by plotting the observed data in the **GI–Vis**$^{\mathbf{R}}$ condition and the data predicted by the multiple linear regression. In order to estimate the predictive power of these models, the RMSE was calculated for each subject. We found that the predictive power of the model of multiple linear regression on the mean pointing errors was significantly higher than the model of averaged parameters based on multiple linear regressions on individual pointing errors (mean RMSE = 1.19 ± .90 and 1.74 ± 1.62, respectively; $t_{(16)} = 2.70$; $P < .05$).

Discussion

The aim of the present study was to determine the multisensory integration processes underlying spatial localization during "combined" changes of visual and **Gi** cues. To do so, we investigated how, during **Gi** vector rotation, a visual background rotation influenced the localization of a body-fixed target, as inferred from a continuous pointing task. Our results showed that the "single" rotation of the **Gi** vector or the visual background specifically affects the pointing accuracy, since downward and upward errors were observed, respectively. More interestingly, the synchronous rotation of the visual background and the **Gi** vector yielded a cancelation of the pointing errors, which were similar to that of the control condition. In terms of multisensory integration processing, our data suggest a linear combination of **Gi** and visual cues whose weights remained constant across the range of the tested stimulation.

Before dealing with the combined influences of **Gi** and visual cues, we will first discuss the specific effect of the modified **Gi** environment upon target localization, assessed by continuous pointing. Target localization impairments during centrifugation have been largely explained by the oculogravic illusion (Carriot et al. 2005; Graybiel 1952), which leads, for instance, to a false sensation of target elevation during a forward linear acceleration. In parallel during the same stimulation, the observer is submitted to an illusory sensation of backward body tilt (i.e., the somatogravic illusion; Benson 1990; Graybiel 1952). Since it is widely assumed that both illusions are intimately linked, one could expect that in our task, the illusory target elevation (i.e., oculogravic illusion) concomitantly occurred with an illusory elevation of the arm in space as a consequence of the illusory backward body tilt (somatogravic illusion). If both illusions simultaneously appeared with the same magnitude, the observer would not have to modify his/her arm position relative to the target, as both would be sensed elevated to the same extent. However, our data do not support this hypothesis since the arm moved downward in the **Gi** condition. One possibility is that, in the present study, the somatogravic illusion was stronger than the oculogravic illusion and that compensatory arm responses resulted in downward pointing errors. Dissociation between oculogravic and somatogravic illusions would be consistent with recent findings of Carriot et al. (2006). Indeed, these authors investigated the effect of centrifugation upon the subjective visual horizon (considered as a reference for target localization and reflecting the magnitude of the oculogravic illusion) and the subjective proprioceptive horizon (reflecting the magnitude of the somatogravic illusion). Carriot et al. (2006) observed that the subjective proprioceptive horizon and the subjective visual horizon were differently affected when facing the rotation axis. This is in line with our aforementioned interpretation as it suggests that the somatogravic illusion and the oculogravic illusion differed in magnitude.

The centrifugation resulted in pointing errors that arose at a similar latency in **GI** and **GI–Vis**$^{\mathbf{F}}$ conditions (~21 s relative to the control condition). Incidentally, this latency is close to the time constant of the semi-circular canals (i.e., 20 s; Howard 1982). The latency that we found may reflect the slow build-up of the oculogravic and somatogravic illusions (Curthoys 1996). This latency may also reflect the time at which the somatogravic condition differed from the oculogravic condition.

Adding a fixed visual background (**GI–Vis**$^{\mathbf{F}}$ vs. **GI**) did not significantly reduce the effect of centrifugation upon continuous pointing toward a body-fixed target. This might appear surprising because in a non-modified **Gi** environment, adding a static visual landmark or a structured visual background to a dark environment improves the localization of targets in space (Lemay et al. 2004; Magne and Coello 2002). However, Eriksson et al. (2008) pointed out that spatial localization should not be improved during centrifugation if the visual background is not related to the

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[2] These values should not be viewed as relative weights of **Gi** and visual cues whose sum would necessarily correspond to 100% in the multisensory integration process.

external Earth-fixed reference frame but instead is related to the body. Based on this idea and given that we used a head-mounted display (the visual background was thus anchored to the head), the somatogravic and oculogravic illusions may not have been affected in our study. Indeed, in our study, adding a visual background during centrifugation does not appear to help the observer to have a more precise idea of his body configuration and target location in space and thus to improve continuous pointing accuracy.

When the visual background was rotated without any **Gi** modifications (**Vis^R** condition), we found a progressive elevation of continuous pointing which could be interpreted as a consequence of an illusory target elevation. This induced-motion phenomenon has already been described at length in the literature for localization judgments and discrete pointing movements (Bridgeman et al. 1981; Post et al. 2008). Post and Lott (1990) also suggested that the strength of induced motion is mostly related to the visual background velocity. Our results seem consistent with this idea since pointing errors gradually increased with the visual background velocity.

Strikingly, when the visual background was rotated while the **Gi** vector was simultaneously rotated (**GI–Vis^R** condition), the effects of the centrifugation were cancelled since pointing errors did not significantly differ, across the trial, from that observed in the control condition. In order to improve spatial localization skills during a linear acceleration, researchers have tried to define how the different sensory modalities participate in these illusions. In this vein, studies have demonstrated that the absence of vestibular cues does not suppress the somatogravic illusion (Clément et al. 2001), thus highlighting the importance of somatosensory cues. Studies have already tried to minimize such illusion in modified **Gi** environments by manipulating somatosensory cues (with pressure and vibration cues reinforcing the gravity direction; Rupert 2000; van Erp and van Veen 2006). However, given the importance of visual cues for spatial orientation and localization (Howard 1982), studies mostly aimed at minimizing these illusions by adding visual cues. Adding a congruent optic flow (i.e., visual cues that are coherent with the produced acceleration) has been shown to improve spatial localization skills (Eriksson et al. 2008; see also Lessard et al. 2000). Here, we found a salient way to cancel centrifugation effects on spatial localization by adding non-congruent visual cues (i.e., visual background rotation), which basically biased target localization in the opposite direction of the effects produced by a modified **Gi** environment. Conversely, one could view our findings as reflecting the cancelation of the illusory consequences of the visual background rotation (induced motion) by centrifugation.

The present study suggests that the "combined" rotation of the visual background and the **Gi** vector corresponds to the linear combination of the "single" rotations. Indeed, the multiple linear regression on the mean pointing errors shows that the proportion of explained variance by a linear equation was $R^2 = .88$. This indicates that the weights of **Gi** and visual cues remained constant across the stimulation. The present study may thus bring further insight into the way sensory inputs are integrated for spatial localization during concomitant changes in visual background and **Gi** cues. According to Howard (1997), sensory weighting processes are based on cue dominance, dissociation or cue reweighting. Here, the possibility of sensory dominance, even visual dominance, might be dismissed because the weights of **Gi** and visual cues were found to be similar. In fact, there is no consensus in the literature with respect to the dominant sensory modality since visual dominance (Gibson 1950), vestibular dominance (Mittelstaedt 1999) or somatosensory dominance (Mergner and Rosemeier 1998) has been proposed. In addition, it is commonly observed that spatial localization skills are influenced by several sensory modalities (Barnett-Cowan and Harris 2008; Bringoux et al. 2004; Cohen et al. 2001; Rossetti et al. 1995). In this vein, recent data evoked a reweighting process that characterized the relative influence of each cues, depending on the time period (Bringoux et al. 2009), the stimulus intensity (Oie et al. 2002) or the cue reliability (Angelaki et al. 2009; Ernst and Banks 2002). For instance, Angelaki et al. (2011) reported that the integration of visual and vestibular cues relied on sensory weighting processes where each weight is inversely proportional to the cue variability. It thus would have been reasonable to expect a modulation of the weight attributed to the different sensory cues over time, when both stimuli were provided. This is not what we observed since our findings support the idea of a constant weighting of both visual and **Gi** cues, despite the progressive change in stimulation intensities. Several studies have already suggested that constant weights are attributed to the sensory modalities available to the observer (Barnett-Cowan and Harris 2008; Bourrelly et al. 2010; Bringoux et al. 2008). Our study not only suggests that a constant weighting of visual and **Gi** cues takes place when both stimuli are combined but also suggests that these weights remain constant across the range of stimulation manipulated. Further experiments need to be carried out to examine whether these weights remain constant during more complex or desynchronized stimulations.

Conclusion

Our study showed that continuous pointing toward a body-fixed target is modified by a gradual change in visual or **Gi** cues. The more visual background or the **Gi** vector was rotated, the larger the pointing errors were. During the "combined" changes of **Gi** and visual cues, the centrifugation effects on continuous pointing were cancelled by the visual background rotation. The "combined" rotation of visual background and **Gi** vector thus appeared to affect target localization as predicted by a linear combination of both "single" stimulations over time. The evolution of continuous pointing errors across the different conditions suggests that the respective weights attributed to the visual and **Gi** cues were kept constant across the range of the tested stimulations. Here, we suggest that visual cues can be used to reduce illusions caused by **Gi** changes and which cause most cases of spatial disorientation (Benson 1990). Hence, these data may be of value for the ergonomic design of assistive devices in aeronautics.

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Pointage discret : Influence de l'inclinaison progressive du corps en tangage et conflit entre informations visuelles et posturales

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Combined Influence of Visual Scene and Body Tilt on Arm Pointing Movements: Gravity Matters!

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Abstract

Performing accurate actions such as goal-directed arm movements requires taking into account visual and body orientation cues to localize the target in space and produce appropriate reaching motor commands. We experimentally tilted the body and/or the visual scene to investigate how visual and body orientation cues are combined for the control of unseen arm movements. Subjects were asked to point toward a visual target using an upward movement during slow body and/or visual scene tilts. When the scene was tilted, final pointing errors varied as a function of the direction of the scene tilt (forward or backward). Actual forward body tilt resulted in systematic target undershoots, suggesting that the brain may have overcompensated for the biomechanical movement facilitation arising from body tilt. Combined body and visual scene tilts also affected final pointing errors according to the orientation of the visual scene. The data were further analysed using either a body-centered or a gravity-centered reference frame to encode visual scene orientation with simple additive models (i.e., 'combined' tilts equal to the sum of 'single' tilts). We found that the body-centered model could account only for some of the data regarding kinematic parameters and final errors. In contrast, the gravity-centered modeling in which the body and visual scene orientations were referred to vertical could explain all of these data. Therefore, our findings suggest that the brain uses gravity, thanks to its invariant properties, as a reference for the combination of visual and non-visual cues.

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Introduction

The brain continuously receives a flow of spatial information from several sensory channels about the ever-changing states of the environment and the body. Producing an appropriate behaviour such as goal-directed arm movements involves continuous adjustments in response to, for instance, active or passive body displacements. Indeed, when pointing toward an object while being tilted, the Central Nervous System (CNS) has to take into account the directional shift of gravitational force which is no longer aligned with the longitudinal body axis. In addition to force-field characteristics, visual cues due to body or object displacement are also integrated. This is illustrated by the fact that a tilt of the visual scene influences the perceived orientation of the self or of an object to be reached [1,2]. Here we investigated the influence of body and/or visual scene tilts on arm pointing movements to better understand the processes underlying body and target localization as well as motor planning and control. This study specifically focused on the combination of spatial cues at the basis of sensorimotor control during combined body and visual scene tilts.

Tilting the visual scene has been found to influence many spatial orientation tasks such as the judgment of visual straight ahead or longitudinal head axis [3,4]. In addition to these perceptual judgments, motor consequences of visual scene tilts have also been reported on arm pointing movements [1,2,5: unpublished]. For instance, Welch and Post [1] showed that the final accuracy of reaching movements was altered as a function of the direction of the visual scene tilt in pitch. These authors argued that final errors were mainly due to the inability to accurately localize the physical eye level. Subjective eye level has indeed been shown to be linearly influenced by the pitch tilt of the visual scene [4,6,7]. Since target position in elevation, even referred to a body-fixed reference, has been found to be partly coded relative to eye level [8,9], perceived target location would be consequently impaired when the visual scene is tilted. These previous studies [1,2,5] exclusively focused on the effects of visual scene pitch tilt on final accuracy and not on motor organization. However, a detailed kinematic analysis is required to finely understand sensorimotor control processes.

Contrasting with visual scene tilt, tilting the body in roll or in pitch has biomechanical consequences as the gravitational vector is no longer aligned with the longitudinal body axis. The CNS must then update the gravity-related constraints applied to the body, and particularly to the arm, for maintaining the accuracy of goal-directed movements. However, the few studies dealing with the influence of pitch body tilt on arm pointing movements presented contradictory results [2,10,11]. While Smetanin and Popov [11] found target overshoots associated to upward pointing movements during prone or supine body orientation, other studies did not show any significant influence of fast (12 deg.s^{-1}, [2]) or slow pitch body tilt (0.05 deg.s^{-1}, [10]) on final pointing accuracy. Analyzing arm movement kinematics may help further understand these seemingly contradictory results. For instance, Le Seac'h and McIntyre [12] reported that the timing and shape of arm pointing movement varied relative to body orientation in the roll dimension (i.e., vertical posture vs. reclined on the left side) which may account for changes in final position. Here, we analysed movement kinematics to determine how well subjects predicted the consequences of gravity on the arm and whether they adjusted their movement during its execution.

The core issue of the present study concerned the way spatial cues relative to visual scene and body orientation are combined for the planning and control of a goal-directed arm movement. It is well established that combined body and visual scene tilts influence the judgement of body orientation [13–15]. However, while some studies revealed that judgement errors during combined body and scene tilts mainly corresponded to visual errors [16,17], other studies showed that errors during combined head and visual scene tilts appeared as an additive combination of the errors observed during each single tilt [18]. To our knowledge, only Fouque et al. [2] investigated the influence of combined body and visual scene tilts in pitch on sensorimotor control. These authors showed that the accuracy of pointing movements toward a visual target presented at eye level could be impaired when coupling body and scene tilts arising from fast rotations. Final errors were similar to those observed during visual scene tilt alone as body tilt alone did not seem to affect movement endpoint. In this work [2], the fact that body tilt had no significant influence on final accuracy may be due to the correct compensation of gravity action on the body [19–22], which may have been facilitated by the fast (i.e., $v = 12$ deg.s^{-1}), easily detectable rotation pattern. It is unclear, however, what may happen in the case of tilts below semi-circular canals thresholds [23,24] which may complexify the compensation of gravity constraints on the body.

Here, we tested the influence of very slow (i.e., 0.05 deg.s^{-1}) body and/or visual tilts on the final accuracy of arm pointing movements which reflects motor planning and online control mechanisms [25,26] and we also analysed early kinematic parameters which mostly reflect motor planning [27,28]. Combined conditions were manipulated so that the direction of body and visual scene tilts remained unchanged or was shifted. This gave us the opportunity to study the combination process of spatial cues underlying the control of arm pointing movements. Specifically, we tested whether the subjects' motor behavior better corresponds to an egocentric (i.e., body-centered) or external (i.e., gravity-centered) encoding of sensory information.

Methods

Participants

Fifteen right-handed subjects (9 men and 6 women; mean age ± SD: 23±3 years) were recruited from the students and staff of Aix-Marseille University to participate in this experiment. Right hand preference was assessed with the 10-item version of the Edinburgh handedness inventory [29], and all subjects had a laterality quotient greater than 50. Subjects reported having normal or corrected-to-normal vision and no neurological or sensorimotor disorders. Stereoscopic vision was checked using the Randot Stereotest® with all individual scores greater than 70 s of arc. All participants gave written informed consent prior to the study, in accordance with the 1964 Declaration of Helsinki and the written consent of a local institutional review board (IRB) from the Institute of Movement Sciences which specifically approved this study.

Apparatus

Subjects were seated on a tilting chair, firmly maintained by a six-point seatbelt (Fig. 1a). The chair could be tilted in the pitch dimension by rotating around an axis positioned under the seat (Fig. 1c). The chair was rotated by lengthening/shortening an electric jack (Phoenix Mecano, thrust: 3 kN, clearance: 0.6 m, precision 0.12 mm) attached to the back of the seat. The tilt angular profile was servo-assisted using an inclinometer fixed to the chair (AccuStar, resolution: 0.1 deg; range: ±60 deg). The tilt velocity was set at 0.05 deg.s^{-1} following an acceleration phase at 0.005 deg.s^{-2}. An adjustable drainpipe was used to support the arm weight in the starting position to prevent arm fatigue. During the experimental trials, earphones provided white noise to mask any auditory cues (e.g., from the rotating chair or the computers).

A 3D head-mounted display (HMD, 3D Cybermind hi-Res900, Cybermind Interactive Nederland, The Netherlands; resolution: 800×600 pixels; field of view: 31.2 deg diagonal for each eye) was fixed horizontally onto a headrest attached to the seat. This headrest was adjustable in elevation to the subject size. The HMD was used to display a stereoscopic visual background. The visual scene was composed of a 3D grid that reinforced horizontal and vertical reference lines positioned at different depth levels (overall scene depth: 3.15 m, see Figure 1b and c). The front of the scene was positioned at 1.5 m from eye position. The scene could rotate in the pitch dimension, around an axis of rotation positioned at 2.65 m from eye position (i.e., 1.15 m further from the visual scene front) in the middle of the screen in the vertical plane (Fig. 1b). Because rotating the scene around the chair axis of rotation might induce several additional illusions due to vertical translational optic flow (e.g., target induced motion, [30] and vection, [31]),

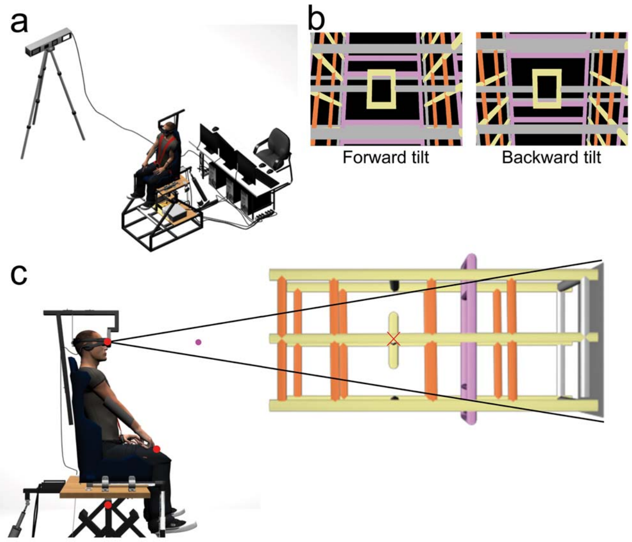

Figure 1. Experimental setup. a) Global view of the apparatus including the tilting chair, the HMD, the motion tracking system and the cluster of computers. **b**) Side view of the tilting chair. The sketch represents a subject in the initial standard position with the right arm outstretched in a drainpipe. Red dots represent the markers tracked with the motion capture system. They were positioned on the index fingertip, at eye level, and on the chair axis of rotation. The HMD displayed a visual target (pink dot) located straight ahead and a structured visual background as illustrated in front of the subject. The red cross, which was not displayed to subjects, corresponds to the center of scene rotation. **c**) Screen captures of the visual scene actually viewed by subjects' right eye when tilted 18 deg forward (left panel) and backward (right panel).

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which could induce opposite effects on arm pointing movements, we rotated the background around the centre of the screen to minimize the occurrence of such illusions. This specific rotation is sufficient to induce errors in judgement relative to the environment or to the body as simple tilted planes did [32,33]. A pink virtual target (diameter: 1 cm) was projected at the centre of this visual background, in the frontal plane and was always fixed relative to the observer, even during visual and/or body tilts; i.e., the target was positioned at Head-Referenced Eye Level (HREL: transversal plane of the head passing through the eyes; [34]). The target was presented at 0.8 m from the eye position. The HMD device prevented subjects from having visual feedback about the experimental setup and about their current arm location.

An optical motion tracking system (Codamotion cx1 and MiniHub, Charnwood Dynamics Ltd, Leicestershire, UK), was placed at 2.5 m laterally from the chair and 1.9 m vertically from the ground. Infrared active markers were placed on the right index fingertip and at eye level on the HMD to compute angular pointing errors. Markers' position data were sampled at 200 Hz. A real-time acquisition system (ADwin-Pro, Jäger, Lorsch, Germany) running at 10 kHz was driven by a customized software (Docometre) to synchronously control kinematic data collection as well as visual background and/or chair tilts.

Procedure

During the experiment, subjects sat on the rotating chair and were prompted to point toward the visual target. For each condition, the chair and the visual background were initially set at 0 deg (i.e., at vertical). At the beginning of each pointing trial, subjects put their extended arm in the drainpipe and positioned their right index finger at the starting position, indicated by a standardised tactile landmark (a 2 cm^2 piece of Velcro) on their right thigh. A double auditory signal announced the onset of a pointing block. Three seconds later, the visual target appeared with an auditory signal prompting the subjects to point toward the target. Subjects were asked to reach the target, which remained visible during 1 s, in a single-joint shoulder movement (arm outstretched) and to maintain final arm position until target disappearance. The task instructions were given as follows: 'Once the target appears, reach the target with the arm outstretched, as fast and as accurately as possible. Target appearance is associated to an auditory tone. You have to reach the target before its disappearance. When the target is extinguished, bring your outstretched arm back to the standard position'. This standard position corresponded to the arm in the drainpipe and the index finger on the tactile landmark. A new target appeared 3 s after the previous target disappeared. This sequence was repeated 6 times and constituted a pointing block.

The sequence of events for each experimental condition is illustrated in Figure 2. Pointing blocks were performed at 0, 6, 12 and 18 deg during continuous body and/or visual tilts from 0 to 19 deg. The rotating chair was not stopped during the pointing blocks to avoid any effect of acceleration and deceleration phases. Since the same spatiotemporal profiles were used for visual and body tilts, the tilt of the visual scene was not stopped during pointing blocks. As a consequence, a pointing block was designed to start 0.5 deg before the intended angle of body and/or visual tilts and to end 0.5 deg after. For example, to assess the effect of a 6 deg body or visual scene tilt, arm pointing movements were performed each 0.2 deg from 5.5 deg to 6.5 deg of tilt.

Subjects were also required to verbally indicate whether they felt tilted when prompted by an auditory tone differing from that used in the pointing task. This perceptual task was repeated every 2 deg, from 1 deg to 19 deg of body and/or visual scene tilts. Results related to this concurrent task will be presented in details elsewhere.

Once the body and/or the visual scene were tilted by 19 deg, the visual scene disappeared. If the body was actually tilted, the chair was tilted back to 0 deg with a pseudo-random profile in which we varied the magnitude and duration of the acceleration and deceleration phases. Between conditions, the HMD was removed and a period of rest in full ambient light during at least 1 min was consistently provided before the next condition started. This resting period was used to suppress post-rotational effects due to semi-circular canal stimulation [23,24] and to limit possible fatigue. The subsequent body and/or visual scene tilts condition began only when subjects did not feel tilted anymore.

The experimental conditions consisted in tilts of the body and/or the visual scene in the pitch dimension with forward tilts (body and/or visual scene) and backward tilt (visual scene only) up to 19 deg using the same velocity profile. We chose to perform only forward body tilt as we expected that this direction would yield larger consequences on arm pointing movement. Indeed, the results of Fouque et al. [2] showed no significant errors for fast backward body tilt while a trend could be observed for forward body tilt. Figure 2 illustrates the 5 experimental conditions tested in the present study: $\mathbf{S_{fwd}}$: forward visual scene tilt (top of the visual scene away from the observer) without body tilt; $\mathbf{S_{bwd}}$: backward visual scene tilt (top toward the observer) without body tilt; $\mathbf{B_{fwd}S}$: forward body tilt with a visual **s**cene kept parallel relative to the subject; $\mathbf{B_{fwd}S_{fwd}}$: forward body tilt and forward visual scene tilt; $\mathbf{B_{fwd}S_{bwd}}$: forward body tilt with backward visual scene tilt. These experimental conditions and their associated names were defined in a body-centered reference frame (i.e., visual scene referred to the observer, Fig. 2).

All 15 subjects performed 3 repetitions in each of the 5 aforementioned conditions, which were presented in a pseudo-random, counterbalanced order. A training session without body and/or visual scene tilts was provided before data collection actually started to familiarize subjects with both perceptual and motor tasks. The whole experimental session lasted about 2 hours.

Data processing

Position data from the markers on the right index fingertip, the HMD and the rotation axis of the rotating chair were low-pass filtered with a dual-pass, no-lag Butterworth filter (cut-off frequency: 10 Hz; order: 2). This allowed us to compute the angular pointing position in the sagittal plane relative to the eye elevation (i.e., HREL) for the entire movement, which took into account instantaneous chair orientation. Arm movement onset and offset were defined when angular velocity in the sagittal plane respectively reached above and dropped below 5% of peak velocity [10,19,21,27,35,36]. Final position (i.e., movement endpoint) was calculated from the angle between the index and HREL (i.e., target location). Selected kinematic parameters were peak acceleration (PA), time-to-peak acceleration relative to movement duration (rTPA), reaction time (RT) and movement duration (MD).

The main purpose of the subsequent analyses was to test the effect of tilt in the different experimental conditions. Prior to this issue, we investigated any potential order effect of the 6 successive arm pointing movements composing a pointing block. To that aim, we conducted 5 condition ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$, $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$, $\mathbf{B_{fwd}S_{bwd}}$)×4 angle (0, 6, 12, 18 deg)×6 pointing succession (number 1 to number 6) repeated-measures ANOVAs on the mean of the 3 repetitions for all kinematic parameters. These analyses did not reveal any significant effect of pointing succession upon the interaction condition x angle of tilt, and statistical

Figure 2. Experimental conditions and procedure. Body and/or visual scene tilts are depicted for angles at which pointing movements were requested (i.e., 6, 12 and 18 deg) for each experimental condition ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$, $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{bwd}}$, $\mathbf{B_{fwd}S_{fwd}}$). Pink lines correspond to the visual scene orientations and dotted lines to the longitudinal body orientations. We mentioned the angle of visual scene orientation relative to the longitudinal body orientation (i.e., in a body-centered reference frame) as 'S/b' and relative to vertical as 'S/v' (i.e., in a gravity-centered reference frame). Associated single and combined conditions relative to the body-centered (i.e., body) and gravity-centered (i.e., g) reference frame are provided under each experimental condition. The lower panel of the figure illustrates the sequence of events including the different pointing blocks required during a trial (i.e., from 0 to 18 deg of body and/or visual scene tilt relative to the observer).
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comparisons were conducted on the mean (i.e., average of the 6 pointing movements ×3 repetitions) for all experimental conditions and angles of tilt, using 5 condition ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$, $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$, $\mathbf{B_{fwd}S_{bwd}}$) ×4 angle of tilt (0, 6, 12, 18 deg) repeated-measures ANOVAs. As we wanted to focus on the general effect of tilt, planned comparisons were systematically performed to contrast the control situation at 0 deg vs. all the tilted situations (6 deg, 12 deg and 18 deg).

Modeling. First, we considered 'single' vs. 'combined' conditions when coding visual scene orientation in a body-centered reference frame (see Figure 2). Using these spatial coordinates, $\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$, and $\mathbf{B_{fwd}S}$ corresponded to single conditions (i.e., single rotation of the body or the visual scene relative to the observer), and $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$ to combined conditions (i.e., combined rotations of the body and the visual scene relative to the observer). We thus examined whether kinematic parameters observed in these combined conditions could correspond to the additive combination (i.e., unweighted sum) of the data observed in the corresponding single conditions. To that aim, we rebased data relative to final position, PA, rTPA, RT and MD so that this unweighted sum model could be applicable. Hence, for a given data type, the mean of a given parameter obtained at 0 deg was subtracted from the means obtained for tilted orientations. Data predicted by this model were computed by simply adding the mean values (average of the 6 pointing movements x 3 repetitions) issued from each single condition associated to both combined condition for each kinematic parameter (final position, PA, rTPA, RT and MD). Hence, for each subject, $\mathbf{B_{fwd}S_{fwd}}$ predicted data corresponded to the unweighted algebraic sum of $\mathbf{B_{fwd}S}$ and $\mathbf{S_{fwd}}$ data, and $\mathbf{B_{fwd}S_{bwd}}$ predicted data corresponded to the unweighted algebraic sum of $\mathbf{B_{fwd}S}$ and $\mathbf{S_{bwd}}$ data. We then tested whether this unweighted sum model could predict the combined conditions for a given kinematic parameter using 2 data type (observed data from a combined condition vs. predicted data from body-centered modeling) x 3 angle of tilt (6, 12, 18 deg) repeated-measures ANOVAs for each combined condition ($\mathbf{B_{fwd}S_{bwd}}$, $\mathbf{B_{fwd}S_{bwd}}$). Note that 0 deg was excluded from the analyses because the mean of both data types at this angle was always set at 0 for all parameters. In order to compare observed and predicted data, we focused our interest on the comparison between data types as well as from the interaction data type x angle of tilt.

Alternatively, we considered 'single' vs. 'combined' conditions when coding visual scene and body orientation in a gravity-centered reference frame (see Figure 2). Using these spatial coordinates, $\mathbf{S_{fwd}}$, and $\mathbf{B_{fwd}S_{bwd}}$ were defined as single conditions (i.e., single rotation of the body or the visual scene relative to vertical), and $\mathbf{B_{fwd}S}$ and $\mathbf{B_{fwd}S_{fwd}}$ as combined conditions (i.e., combined rotations of the body and the visual scene relative to vertical). With this gravity-centered modeling, predicted data $\mathbf{B_{fwd}S}$ corresponded to the algebraic sum of $\mathbf{B_{fwd}S_{bwd}}$ and $\mathbf{S_{fwd}}$ data, and $\mathbf{B_{fwd}S_{fwd}}$ predicted data corresponded to the algebraic sum: $\mathbf{B_{fwd}S_{bwd}}+2\times\mathbf{S_{fwd}}$. As previously, data predicted by this model were computed for each rebased kinematic parameter (final position, PA, rTPA, RT and MD). We also tested whether this gravity-centered model could predict these new combined conditions for a given variable using a 2 data type (observed data from a combined condition vs. predicted data from gravity-centered modeling) ×3 angle of tilt (6, 12, 18 deg) repeated-measures ANOVAs.

Overall, post-hoc tests (Newman-Keuls) were performed when necessary and the level of significance was set at .05 for all statistical analyses.

Results

Prior analyses were conducted to test any potential effect of the 6 successive pointing movements within each pointing block that could interact with the factors manipulated in the study. The analyses, detailed in the *Appendix*, revealed that even though an effect of pointing succession or an interaction between this factor and the angle of tilt appeared for several parameters; i) it cannot be considered as a consequence of the experimental design itself (i.e., continuous rotation); ii) it did not influence the interaction condition x angle of tilt for any given variable, this interaction representing the core interest of the study. Therefore, for the sake of clarity, we averaged in the subsequent analyses the values obtained from 6 pointing movements ×3 repetitions, hence yielding a mean individual observation for a given condition at a given tilt. The first part of the result section reports behavioural data while the second section is dedicated to modeling.

Final pointing accuracy

The analysis of final accuracy revealed an effect of condition ($F_{(4,56)} = 4.4$; $p<.01$), angle of tilt ($F_{(3,42)} = 6.7$; $p<.001$) as well as an interaction condition x angle of tilt ($F_{(12,168)} = 7.2$; $p<.001$). It should be noted that none of the post-hoc results revealed a difference between conditions at 0 deg, indicating that the baseline was similar in all experimental conditions. The subsequent description focused on comparisons between angles of tilt (i.e., 0, 6, 12 and 18 deg) for a given condition, and notably on positions relative to the baseline of 0 deg (i.e., final errors).

Overall, the angle of tilt influenced final pointing accuracy for each of the single conditions ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$ and $\mathbf{B_{fwd}S}$, Fig. 3a). Positive positions relative to baseline (overshoots) were found in $\mathbf{S_{fwd}}$ and negative positions relative to baseline (undershoots) in $\mathbf{S_{bwd}}$ with errors increasing from 0 to 12 deg and remaining stable between 12 and 18 deg. Body tilt without scene tilt ($\mathbf{B_{fwd}S}$) induced negative errors with approximately the same magnitude at 6, 12 deg and 18 deg (difference of −1.3±1.5 deg., −1.1±1.7 deg and −1.4±1.7 deg relative to the baseline, respectively; no statistical difference between angles of tilt). Combined body tilt with scene tilted forward ($\mathbf{B_{fwd}S_{fwd}}$) or scene tilted backward ($\mathbf{B_{fwd}S_{bwd}}$) both yielded negative errors relative to baseline (Fig. 3b). However, while errors in $\mathbf{B_{fwd}S_{fwd}}$ differed from baseline only at 18 deg (−1.7±1.8 deg of difference; $p<.01$), errors in $\mathbf{B_{fwd}S_{bwd}}$ differed from baseline at each angle of tilt (−2.1±1.2 deg at 6 deg, −2.7±1.3 deg at 12 deg and −3.9±1.3 deg at 18 deg of difference; $p<.001$ for all comparisons). In addition, it should be noted that final position in $\mathbf{B_{fwd}S_{fwd}}$ differed from that in $\mathbf{S_{fwd}}$ at 12 and 18 deg ($p<.01$ and $p<.001$, respectively). By contrast, at 18 deg, positions in $\mathbf{B_{fwd}S_{bwd}}$ differed from positions in both $\mathbf{B_{fwd}S}$ ($p<.001$) and $\mathbf{S_{bwd}}$ ($p<.01$).

In order to focus on the overall effect of tilt upon conditions, whatever its magnitude, we performed planned comparisons between 0 deg vs. tilted situations (i.e., 6, 12 and 18 deg) for each condition. Planned comparisons showed statistical differences between errors in 0 deg and tilted situations for $\mathbf{S_{bwd}}$ ($p<.05$), $\mathbf{B_{fwd}S}$ ($p<.05$), $\mathbf{B_{fwd}S_{bwd}}$ ($p<.001$) but not for $\mathbf{S_{fwd}}$ ($p = .07$) and $\mathbf{B_{fwd}S_{fwd}}$ ($p = .28$). This analysis thus confirmed the effect of tilt on the final pointing errors in $\mathbf{S_{bwd}}$, $\mathbf{B_{fwd}S}$ and $\mathbf{B_{fwd}S_{bwd}}$ conditions regardless of the tilt magnitude.

Movement kinematics (PA, rTPA, RT and MD)

We analysed peak acceleration (PA) to assess whether, in parallel to final accuracy, an early modification of movement pattern also appeared as a function of angle of tilt and condition. The 5 condition ×4 angle of tilt repeated-measures ANOVA revealed a significant effect of condition ($F_{(4,56)} = 2.7$; $p<.05$), angle of tilt ($F_{(3,42)} = 7.7$; $p<.001$) as well as a significant interaction condition x angle of tilt ($F_{(12,168)} = 3.2$; $p<.001$). Figure 4, which depicts the results of planned comparisons for PA as a function of condition and orientation (0 deg vs. tilted), shows that PA was smaller when the body was actually tilted, whatever the scene orientation, as compared to 0 deg body orientation (mean difference of 180±46 deg.s^{-2}, $p<.01$;

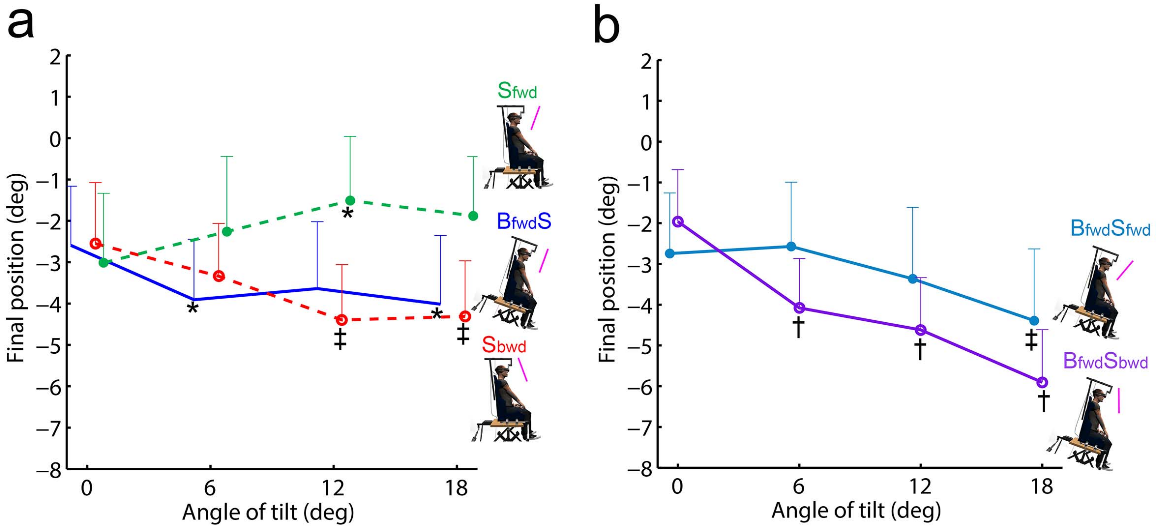

Figure 3. Final pointing position as a function of conditions and angles of tilt. a) Single conditions ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$ and $\mathbf{B_{fwd}S}$) relative to the angle of tilt. b) Combined conditions ($\mathbf{B_{fwd}S_{bwd}}$ and $\mathbf{B_{fwd}S_{fwd}}$) relative to the angle of tilt. Symbol positioned below a given value of a specific angle and condition represents a statistical difference with 0 deg in this specific condition (*: $p<.05$; ‡: $p<.01$; †: $p<.001$). Note that final positions are also statistically different for $\mathbf{B_{fwd}S_{bwd}}$ between 6 deg vs. 12 deg or 18 deg ($p<.001$ and $p<.01$, respectively) and for $\mathbf{B_{fwd}S_{fwd}}$ between 6 deg vs. 18 deg ($p<.01$). Conditions are illustrated on the right side of each figure with pink lines representing the scene orientation (N.B., scene depth distance was not at scale). Vertical bars denote positive standard errors.
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150±48 m.s^{-2}, $p<.01$ and 182±45 deg.s^{-2}, $p<.01$; in $\mathbf{B_{fwd}S}$, $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$ conditions, respectively). In the $\mathbf{S_{bwd}}$ condition in which final undershoots were observed, a smaller PA was also found when tilted as compared to the 0 deg body orientation (mean difference: 92±42 deg.s^{-2}, $p<.05$).

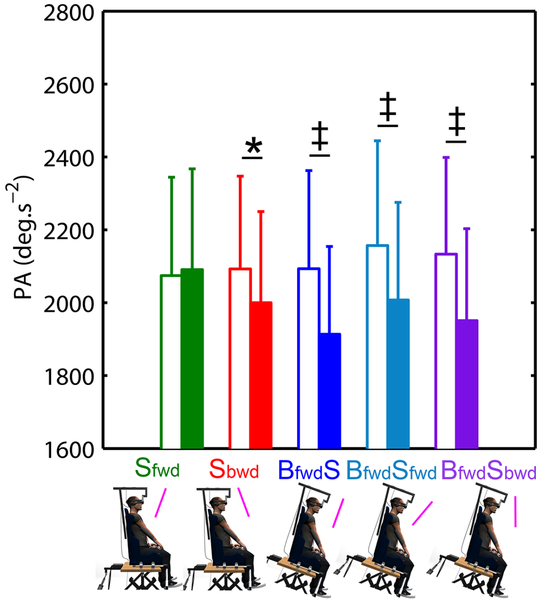

Figure 4. Peak acceleration (PA) as a function of condition and body and/or visual scene orientation (0 deg: white bars; tilted: coloured bars). Differences in planned comparisons between tilted vs. 0 deg orientations are represented for a given condition. Vertical bars denote positive standard errors. *: $p<.05$; ‡: $p<.01$; †: $p<.001$.
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Figure 5a shows that some common spatiotemporal features of the movement were observed when the body and/or the scene was tilted as compared to 0 deg orientation. This was confirmed by the presence of a main effect of the angle of tilt for rTPA ($F_{(3,42)} = 5.8$; $p<.01$), RT ($F_{(3,42)} = 10.1$; $p<.001$) and MD ($F_{(3,42)} = 5.3$; $p<.01$) revealed by 5 condition ×4 angle of tilt repeated-measures ANOVAs. In addition, there was neither main effect of condition (rTPA: $F_{(4,56)} = 0.3$; $p = .85$; RT: $F_{(4,56)} = 0.5$; $p = .74$, MD: $F_{(4,56)} = 2.4$; $p = .06$) nor interaction condition x angle of tilt (rTPA: $F_{(12,168)} = 1.3$; $p = .20$; RT: $F_{(12,168)} = 0.9$; $p = .51$, MD: $F_{(12,168)} = 1.3$; $p = .24$) for these parameters. Planned comparisons, thus based on the set of all experimental conditions, revealed a shorter time-to-peak acceleration relative to MD (rTPA) in tilted situations as compared to 0 deg (8.6±0.7%MD vs. 9.3±0.8%MD; Fig. 5b). Second, RT in tilted situations was higher as compared to 0 deg (417±12 ms vs. 403±10 ms; Fig. 5c). Third, MD was longer in tilted situations as compared to 0 deg (492±28 ms vs. 483±28 ms; Fig. 5d).

In summary, both common (rTPA, RT and MD) and condition-specific (PA) changes were found on arm kinematics when the body and/or the scene was tilted as compared to vertical orientation.

Body-centered modeling

We first examined whether the previous variables (final position, PA, rTPA, RT, MD) observed in the combined conditions defined in a body-centered reference frame (i.e., $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$) could be predicted by the unweighted sum of associated single conditions ($\mathbf{S_{fwd}}$, $\mathbf{S_{bwd}}$ and $\mathbf{B_{fwd}S}$).

We first compared observed and predicted data regarding final pointing errors in $\mathbf{B_{fwd}S_{fwd}}$ on the one hand and in $\mathbf{B_{fwd}S_{bwd}}$ on the other hand. In $\mathbf{B_{fwd}S_{fwd}}$, the repeated-measures ANOVA revealed no main effect of data type ($F_{(1,14)} = 0.1$; $p = .72$) nor angle of tilt ($F_{(2,28)} = 2.2$; $p = .13$) but showed an interaction data type x angle of tilt ($F_{(2,28)} = 3.4$; $p<.01$). At 6 and 12 deg, the data

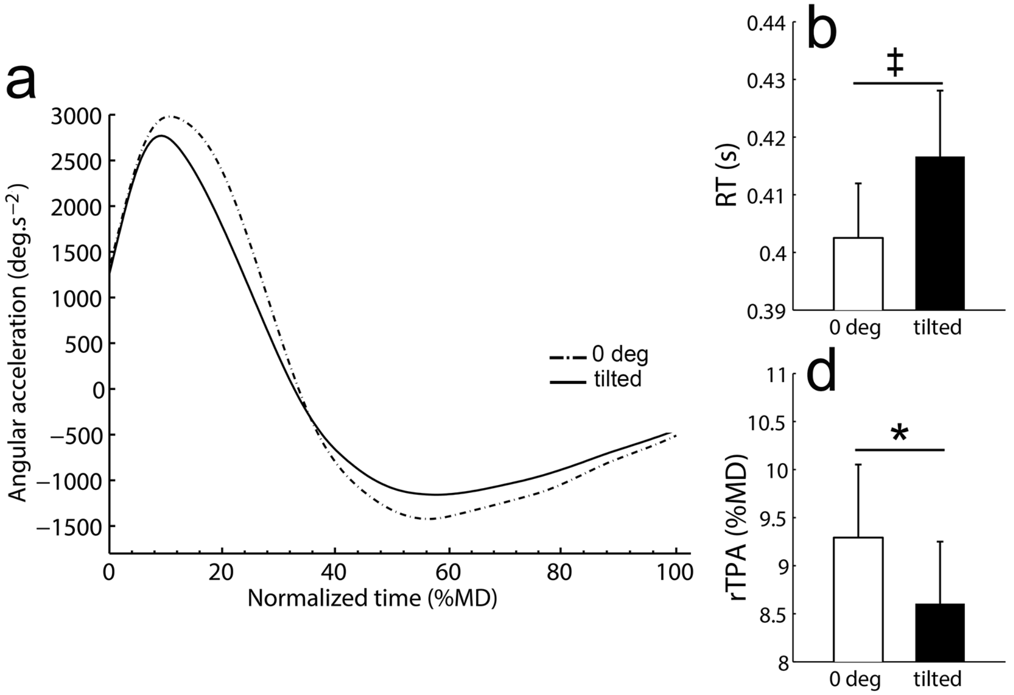

Figure 5. Movement pattern relative to orientation (0 deg vs. tilted). a) Typical normalized acceleration profile relative to MD as a function of orientation (mean of all conditions). Differences in planned comparisons between tilted vs. 0 deg orientations were provided on the right panel for rTPA (**b**), RT (**c**), and MD (**d**). Vertical bars denote positive standard errors. *: $p<.05$; ‡: $p<.01$; †: $p<.001$.
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observed in $\mathbf{B_{fwd}S_{fwd}}$ did not differ from the data predicted by this unweighted sum model (Fig. 6a). At 18 deg however, the predicted data statistically differed from the observed data ($p<.05$).

In $\mathbf{B_{fwd}S_{bwd}}$, the repeated-measures ANOVA revealed a main effect of the angle of tilt ($F_{(2,28)} = 5.1$; $p<.05$). However, the analysis did not reveal any significant effect of data type ($F_{(1,14)} = 0.0$; $p = .92$) nor interaction data type x angle of tilt ($F_{(2,28)} = 1.4$; $p = .24$), indicating that data predicted by this unweighted sum did not differ from the observed data at all angles.

We used similar analyses on PA, rTPA, RT and MD to determine whether the observed data in combined conditions

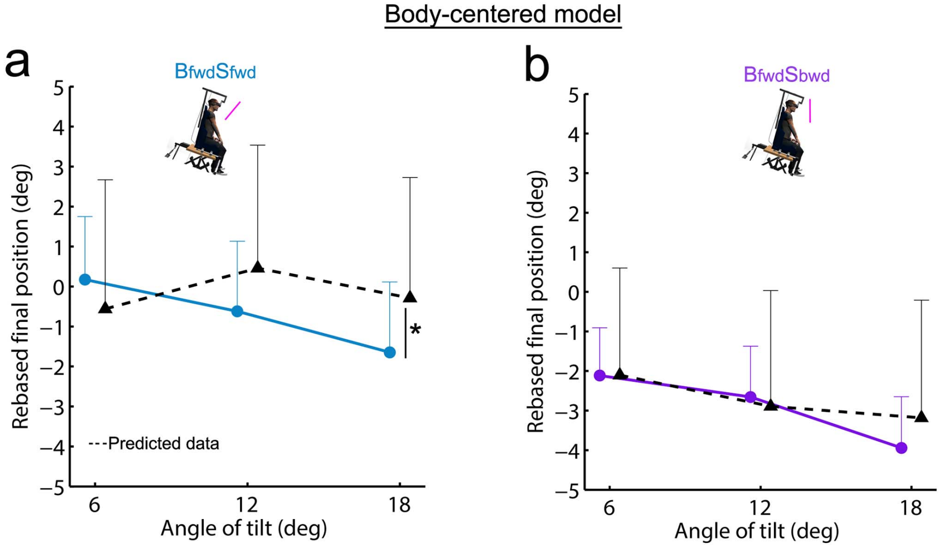

Figure 6. Final pointing position observed in combined conditions (solid lines) and associated predicted data (black dotted line) by the body-centered model. a) Combined condition $\mathbf{B_{fwd}S_{fwd}}$ and predicted data by the unweighted sum. **b**) Combined condition $\mathbf{B_{fwd}S_{bwd}}$ and predicted data by this unweighted sum. Vertical bars denote positive standard errors. *: $p<.05$; ‡: $p<.01$; †: $p<.001$.
doi:10.1371/journal.pone.0099866.g006

could be determined by this body-centered unweighted sum model.

Regarding PA, the repeated-measures ANOVA performed for $\mathbf{B_{fwd}S_{fwd}}$ revealed no significant effect of the angle of tilt ($F_{(2,28)} = 0.4$; $p = .70$) nor data type ($F_{(1,14)} = 0.0$; $p = .96$). Even if we found an interaction data type x angle of tilt ($F_{(2,28)} = 4.8$; $p < .05$), post-hoc tests revealed that data predicted by this unweighted sum model did not statistically differ from the observed data (at 6 deg: $p = .35$; at 12 deg: $p = .27$; at 18 deg: $p = .22$; Fig. 7a). For $\mathbf{B_{fwd}S_{bwd}}$, repeated-measures ANOVA also showed no effect of angle of tilt ($F_{(2,28)} = 0.8$; $p = .48$) nor data type ($F_{(1,14)} = 0.1$; $p = .73$). The interaction data type x angle of tilt ($F_{(2,28)} = 4.0$; $p < .05$) indicated that the predicted data differed from the observed data at 12 deg ($p < .05$; Fig. 7b). However, as observed data showed that PA was similar for most of the experimental conditions (see Figure 4), the results regarding PA modeling should be taken with caution.

Regarding rTPA, the repeated-measures ANOVA performed for $\mathbf{B_{fwd}S_{fwd}}$ showed a main effect of data type ($F_{(1,14)} = 16.3$; $p < .01$) but no effect of angle of tilt ($F_{(2,28)} = 1.2$; $p = .30$) nor interaction data type x angle of tilt ($F_{(2,28)} = 0.1$; $p = .88$). Overall, the predicted data thus differed from observed data (Fig. 7c). The analysis for $\mathbf{B_{fwd}S_{bwd}}$ revealed no main effect of data type ($F_{(1,14)} = 2.5$; $p = .13$), angle of tilt ($F_{(2,28)} = 2.2$; $p = .13$) nor interaction data type x angle of tilt ($F_{(2,28)} = 1.1$; $p = .36$; Fig. 7d).

Regarding RT, data predicted by this unweighted sum model did not differ from observed data for both $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$ conditions (Fig. 7e and Fig. 7f) as attested by repeated-measures ANOVAs. No main effect of data type was found ($\mathbf{B_{fwd}S_{fwd}}$: $F_{(1,14)} = 0.7$; $p = .41$; $\mathbf{B_{fwd}S_{bwd}}$: $F_{(1,14)} = 0.3$; $p = .61$) nor interaction data type x angle of tilt ($\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 0.3$; $p = .75$; $\mathbf{B_{fwd}S_{bwd}}$: $F_{(2,28)} = 0.5$; $p = .62$). The analyses revealed an effect of angle of tilt for $\mathbf{B_{fwd}S_{fwd}}$ ($F_{(2,28)} = 5.3$; $p < .05$) but not for $\mathbf{B_{fwd}S_{bwd}}$ ($F_{(2,28)} = 1.0$; $p = .36$).

With respect to MD (Fig. 7g and 7h), repeated-measures ANOVAs neither revealed any main effect of data type ($\mathbf{B_{fwd}S_{fwd}}$: $F_{(1,14)} = 0.0$; $p = .92$; $\mathbf{B_{fwd}S_{bwd}}$: $F_{(1,14)} = 0.1$; $p = .80$), angle of tilt ($\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 0.9$; $p = .40$; $\mathbf{B_{fwd}S_{bwd}}$: $F_{(2,28)} = 0.9$; $p = .40$), nor interaction data type x angle of tilt ($\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 0.6$; $p = .56$; $\mathbf{B_{fwd}S_{bwd}}$: $F_{(2,28)} = 1.4$; $p = .26$).

Overall, considering this model in a body-centered reference frame, no clear conclusion could be drawn regarding the combination of visual and body orientation cues when looking at PA, rTPA, RT and MD. Regarding final accuracy, the model could account for the data in $\mathbf{B_{fwd}S_{fwd}}$ condition but failed to account for the data at each angle of tilt in $\mathbf{B_{fwd}S_{bwd}}$ condition. It is worth noticing, however, that the orientation of the visual scene relative to gravitational vertical differed in these combined conditions defined in a body-centered reference frame (i.e., in $\mathbf{B_{fwd}S_{bwd}}$ the scene is aligned with gravity whereas in $\mathbf{B_{fwd}S_{fwd}}$ the scene is tilted relative to gravity; see Figure 2). We then tested whether a similar model could be even more relevant only by reconsidering 'single' and 'combined' conditions in a gravity-centered reference frame.

Gravity-centered modeling

We first compared observed and predicted data regarding final pointing positions for then new considered combined condition $\mathbf{B_{fwd}S}$ on the one hand and $\mathbf{B_{fwd}S_{fwd}}$ on the other hand (Fig. 8). The repeated-measures ANOVA revealed a main effect of angle of tilt ($\mathbf{B_{fwd}S}$: $F_{(2,28)} = 3.6$; $p < .05$; $\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 3.4$; $p < .05$) but no effect of data type ($\mathbf{B_{fwd}S}$: $F_{(1,14)} = 0.2$; $p = .70$; $\mathbf{B_{fwd}S_{fwd}}$: $F_{(1,14)} = 0.0$; $p = .98$) nor interaction data type x angle of tilt ($\mathbf{B_{fwd}S}$: $F_{(2,28)} = 2.0$; $p = .16$; $\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 1.1$; $p = .36$). Overall, these analyses indicated that final positions predicted by this gravity-centered model did not differ from observed data, whatever the angle of tilt.

We used similar analyses on PA, rTPA, RT and MD to determine whether the observed data in $\mathbf{B_{fwd}S}$ and $\mathbf{B_{fwd}S_{fwd}}$ combined conditions would fit with the data issued from the gravity-centered modeling (Fig. 9).

Overall, we found no main effect of angle of tilt for PA ($\mathbf{B_{fwd}S}$: $F_{(2,28)} = 0.9$; $p = .42$; $\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 1.3$; $p = .29$), rTPA ($\mathbf{B_{fwd}S}$: $F_{(2,28)} = 0.9$; $p = .41$; $\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 0.0$; $p = .97$), RT ($\mathbf{B_{fwd}S}$: $F_{(2,28)} = 2.0$; $p = .16$) and MD ($\mathbf{B_{fwd}S}$: $F_{(2,28)} = 2.9$; $p = .07$; $\mathbf{B_{fwd}S_{fwd}}$: $F_{(2,28)} = 0.8$; $p = .48$). A main effect of angle of tilt only appeared for RT in $\mathbf{B_{fwd}S_{fwd}}$ ($F_{(2,28)} = 11.4$; $p < .001$). In addition, no main effect of data type was observed in the combined conditions $\mathbf{B_{fwd}S}$ (PA: $F_{(1,14)} = 0.0$; $p = .96$; rTPA: $F_{(1,14)} = 0.0$; $p = .89$; RT: $F_{(1,14)} = 1.5$; $p = .25$; MD: $F_{(1,14)} = 0.5$; $p = .48$) and $\mathbf{B_{fwd}S_{fwd}}$ (PA: $F_{(1,14)} = 0.0$; $p = 1.0$; rTPA: $F_{(1,14)} = 3.1$; $p = .10$; RT: $F_{(1,14)} = 1.1$; $p = .30$; MD: $F_{(1,14)} = 0.2$; $p = .67$). Finally, no interaction data type x angle of tilt appeared for $\mathbf{B_{fwd}S}$ (PA: $F_{(2,28)} = 1.1$; $p = .34$; rTPA: $F_{(2,28)} = 1.1$; $p = .35$; RT: $F_{(2,28)} = 2.9$; $p = .07$; MD: $F_{(2,28)} = 0.2$; $p = .84$) or $\mathbf{B_{fwd}S_{fwd}}$ (PA: $F_{(2,28)} = 1.9$; $p = .17$ rTPA: $F_{(2,28)} = 0.8$; $p = .46$; RT: $F_{(2,28)} = 0.9$; $p = .42$; MD: $F_{(2,28)} = 0.8$; $p = .45$). In summary, the kinematic variables predicted by the gravity-centered model fitted with the observed data for both combined conditions $\mathbf{B_{fwd}S}$ and $\mathbf{B_{fwd}S_{fwd}}$.

Discussion

This experiment was designed to investigate whether slow pitch tilts of the body and/or the visual scene influence the organization of arm pointing movements toward a visual target. Overall, body and/or visual scene tilts both induced final errors as compared to non-tilted situations. Tilting the visual scene alone yielded final pointing errors depending on the direction of the visual scene. Tilting the body forward with a scene kept parallel relative to the observer yielded undershoots (negative errors) with respect to the non-tilted situations. The effect of actual body tilt on movement execution could be observed early (i.e., at peak acceleration), thus reflecting changes in motor planning, and appeared to be independent of the scene orientation. When defined in a body-centered reference frame, combined conditions including body and visual scene tilts also induced final errors, which were differently related to the final errors observed in the corresponding single body or scene tilt conditions. The final errors issued from forward body tilt associated to backward scene tilt corresponded to the additive combination (i.e., unweighted sum) of the final errors in the related single stimulations. In contrast, the final errors observed with forward body tilt associated to forward scene tilt appeared close to those observed during single body tilt. Data modeling based on a gravity-centered reference frame appears to offer a unifying explanation for the whole data since predicted final errors never differed from observed ones. These points will be further discussed in the following sections.

Scene tilt affected perceived target location and sensed gravity orientation

Final errors appeared to vary as a function of the direction of visual scene tilt, with overshoots for forward visual scene tilt and undershoots for backward visual scene tilt. This result may be interpreted as an altered estimation of target location caused by the scene tilt rather than by self- or target-motion perception when considering the characteristics of the visual stimulation (i.e., slow pitch tilt with reduced visual motion). Indeed, several authors suggested that small central field of view and low velocity rotation

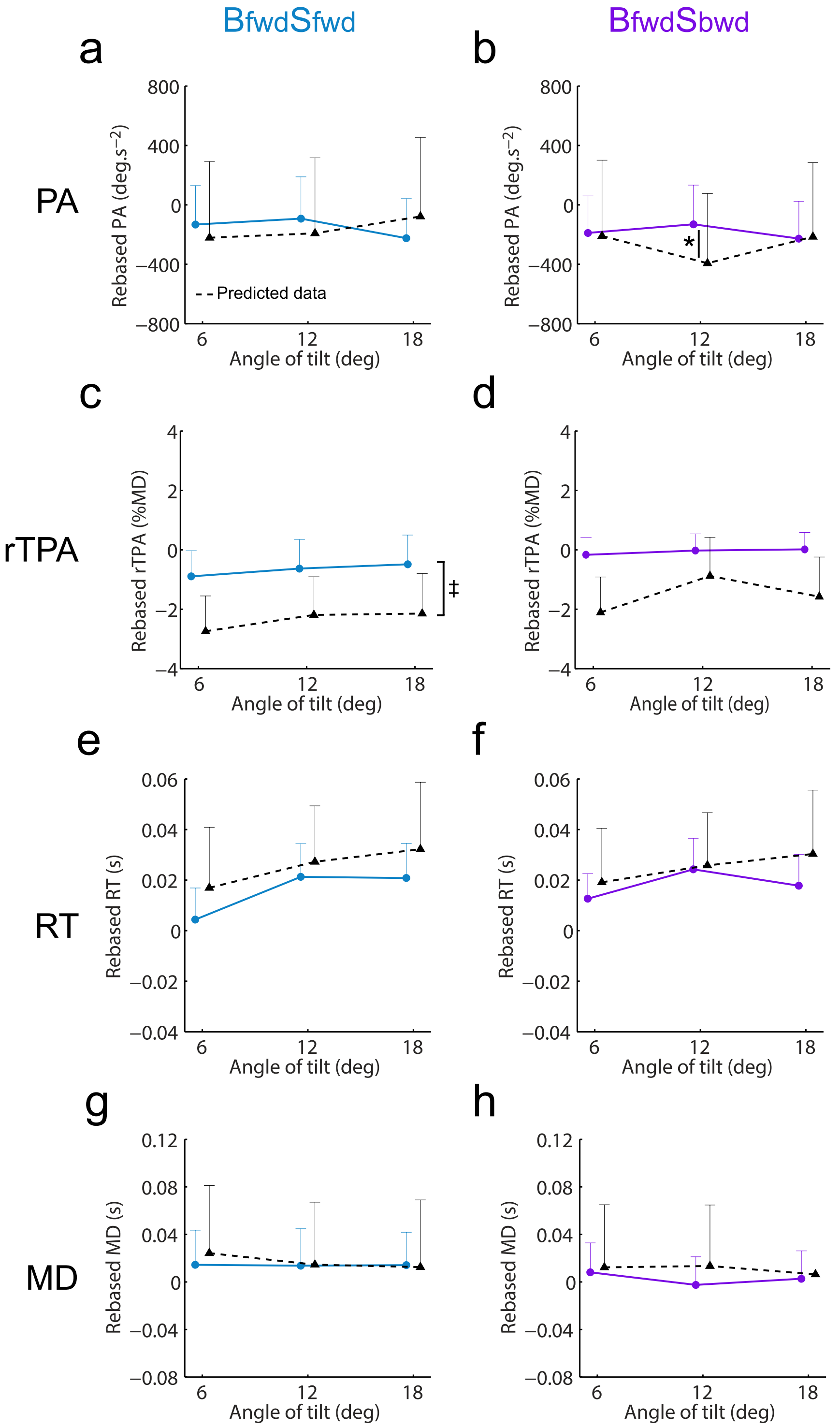

Figure 7. Kinematic parameters observed in combined conditions (solid lines) and associated predicted data (black dotted line) by the body-centered model. Observed and predicted data for PA (**a,b**), rTPA (**c,d**), RT (**e,f**) and MD (**g,h**) were provided for both combined conditions (left panel: $\mathbf{B_{fwd}S_{fwd}}$; right panel $\mathbf{B_{fwd}S_{bwd}}$). Vertical bars denote positive standard errors. The lines between conditions depict differences at a given angle and the bracket depicts an overall difference between conditions (i.e., effect of data type without interaction data type x angle of tilt). *: $p<.05$; ‡: $p<.01$; †: $p<.001$.
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do not induce vection [31,37]. In line with our interpretation, a pitch-tilted scene has been found to bias the perceived target elevation [4,38,39]. Matin and Fox [4] indeed showed that when the perceived eye level is lowered by a downward (i.e., top forward) room tilt, objects located at physical eye level appear to be higher. Conversely, when the perceived eye level is elevated by an upward (i.e., top backward) room tilt, objects located at physical eye level appear lower. As a consequence, goal-directed move-

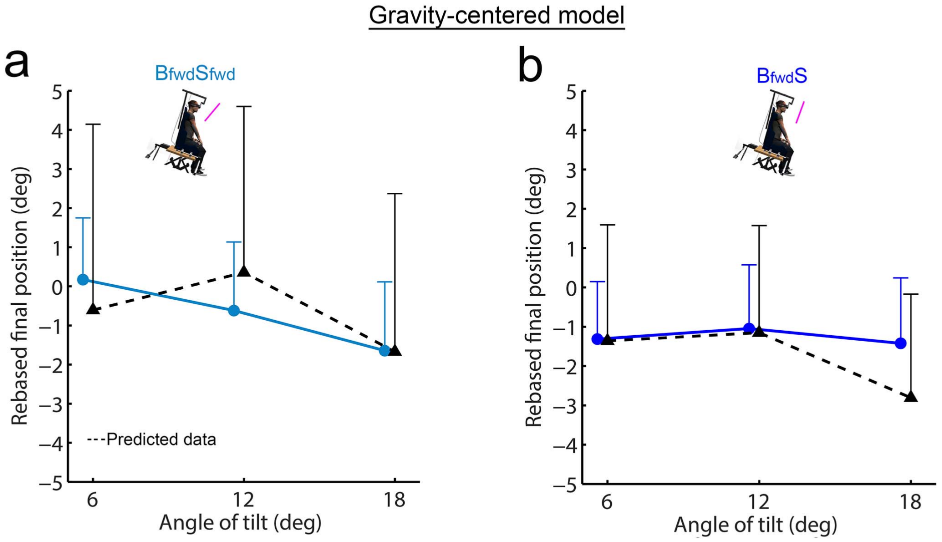

Figure 8. Final pointing position observed in the conditions $B_{fwd}S$ and $B_{fwd}S_{fwd}$ (solid lines) and associated predicted data (black dotted line) by the gravity-centered model. a) Combined condition $B_{fwd}S_{fwd}$ and predicted data by this model. **b**) Combined condition $B_{fwd}S$ and predicted data by this model. Vertical bars denote positive standard errors.
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ments performed here without body tilt would be altered in the direction of the misperceived target location, i.e., overshoots for forward tilts inducing subjective target elevation and undershoots for backward tilts inducing subjective target lowering. The increase in final errors between 6 and 12 deg, for both visual scene rotations, are consistent with Ballinger unpublished study [5] in which absolute final errors were of 1.6 and 2.2 deg relative to baseline for 7.5 and 15 deg of room pitch tilt, respectively. In addition, the relative higher effect of the backward visual scene rotation as compared to the forward visual scene rotation (i.e., significant pointing error only at 12 deg compared to 12 deg and 18 deg, respectively) is in line with Welch and Post results [1] which showed higher effect of backward as compared to forward 20 deg pitch tilt of a room (≈2.3 deg vs. ≈1.2 deg relative to baseline, respectively).

In addition to the previous interpretation, we suggest that the estimation of gravity orientation relative to the body may have been altered and thus, may have affected arm pointing kinematics but might involve reduced final errors [1]. In a visual changing environment, target position coding relative to an external reference such as gravity would seem an efficient strategy due to its invariant properties [40–43]. In addition, Welch and Post [1] previously suggested that the target was not purely coded relative to an egocentric reference frame (i.e., coding relative to the body) as, in their study, pointing errors were lower than perceptual errors associated to eye level estimation (corresponding to a pure egocentric target localization). Here, we found that some kinematic changes associated to visual scene tilts were expressed in a similar way during actual forward body tilt (i.e., non-significant effects of condition and condition x angle). This supported a, at least partial, external target coding implying here that the target location to an altered estimate of gravity orientation, as suggested by Welch and Post [1]. Specifically, movement patterns were found to be more 'cautious' when the scene and/or the body were tilted alone, compared to non-tilted situations (longer reaction time, longer movement duration and shorter time-to-peak acceleration relative to movement duration). These findings are in line with those of Gaveau and Papaxanthis [35] who found that slower upward arm pointing movements (i.e., longer movement duration) exhibited a decreased duration of the first movement phase. (i.e., shorter time-to-peak acceleration relative to movement duration) compared to faster movements. Here, we observed a comparable change in motor organization when subjects faced body and/or scene tilts in which arm movement duration was longer. Specifically, the duration of the last movement phase was increased when subjects and/or visual scene were no longer aligned with gravity, which might allow for a greater online control during movement execution. According to several authors [27,44,45], this result suggests that subjects would encounter difficulties in integrating the direction of gravity relative to the body in the motor command during a complex visuopostural situation (i.e., when visual and/or body orientation was no longer aligned with gravitational vertical). This complex visuopostural situation could also be linked to the fact that none of our experimental conditions induced fully coherent multisensory stimulation as the visual scene was not rotated around the same axis as the body. Such difficulties in integrating the direction of gravity relative to the body has also been suggested by Welch and Post [1] but this hypothesis was not at that time fully supported by specific kinematic observations.

Specific changes in movement kinematics due to actual body tilt

We found that forward body tilt associated to a scene kept parallel relative to the observer induced modifications of the motor plan, as reflected by the analysis of peak acceleration, and produced final undershoots with respect to the non-tilted baseline. Noticeably, body tilt induced final pointing errors whose magnitude was comparable to that observed with scene tilt. Therefore, one may expect that such pointing modifications could be linked to a similar process based on the combination of cues related to the visual scene and/or the body orientation relative to the vertical. Geometrically speaking, tilting the body did not require updating the egocentric location of a target that was

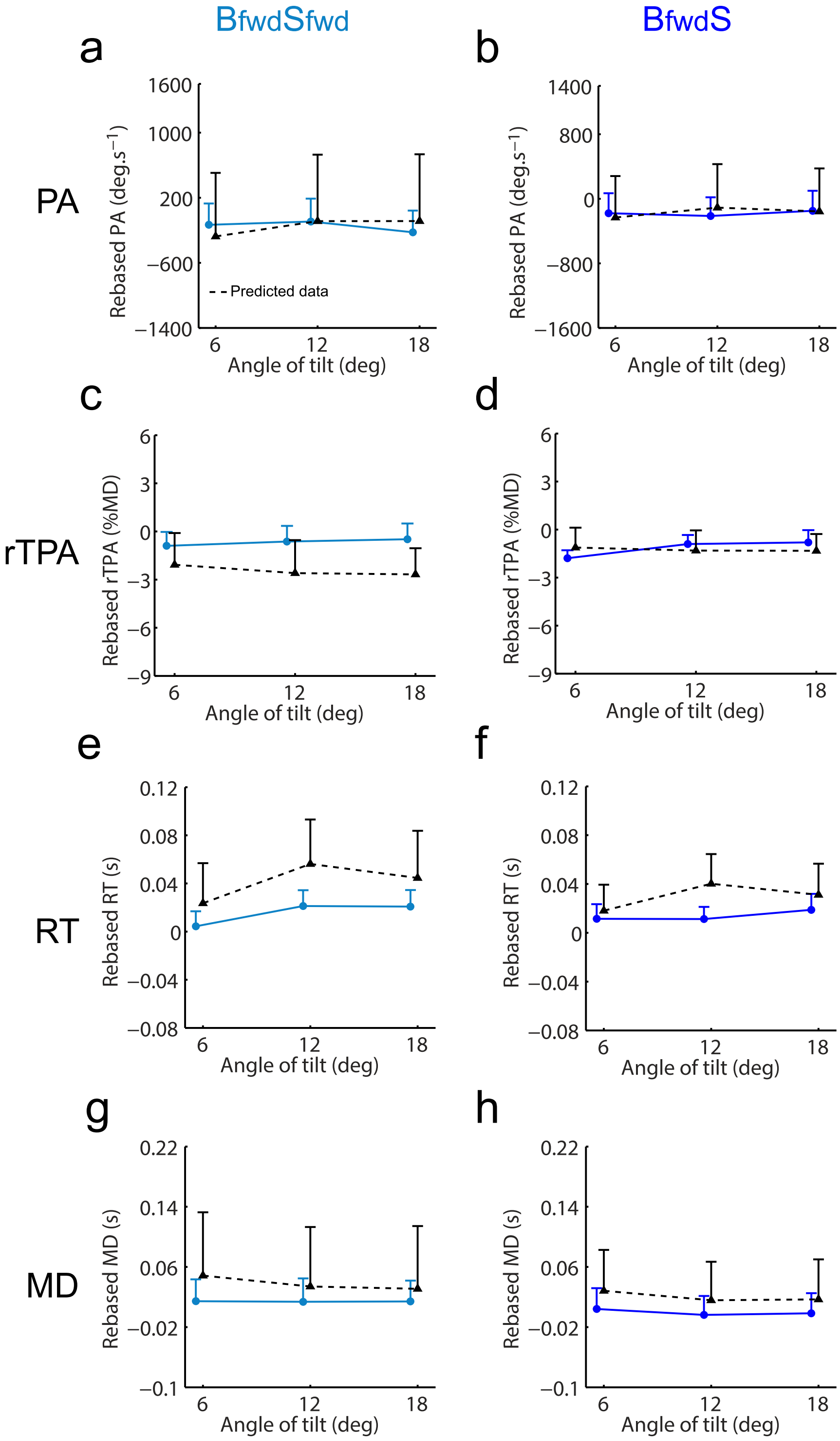

Figure 9. Kinematic parameters observed in conditions $B_{fwd}S$ and $B_{fwd}S_{fwd}$ (solid lines) and associated predicted data (black dotted line) by the gravity-centered model. Observed and predicted data for PA (**a,b**), rTPA (**c,d**), RT (**e,f**) and MD (**g,h**) were provided for both conditions (left panel: **$B_{fwd}S_{fwd}$**; right panel: **$B_{fwd}S$**). Vertical bars denote positive standard errors. The lines between conditions depict differences at a given angle. *: $p<.05$.

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always presented at Head-Referenced Eye level. However, when an observer has to point toward the intended target, he has to take into account the changes of gravity constraints acting on the body and, particularly, on the arm (i.e., gravity-centered coding is required). We suggest that modifications of arm pointing movements during forward body tilt may not be the consequence of target localization errors, as previous results showed that roll body tilt does not induce changes in the accuracy of horizontal

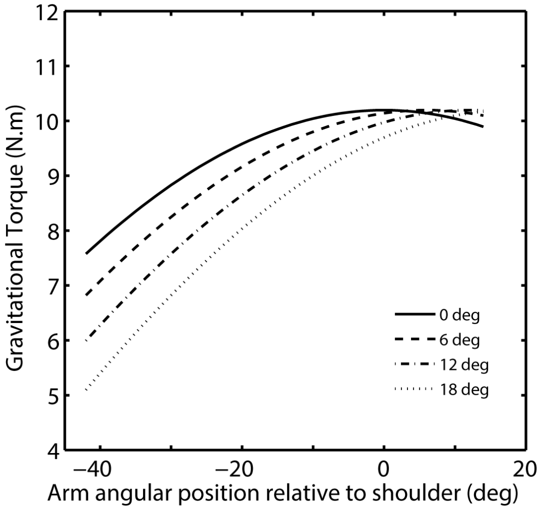

Figure 10. Theoretical gravitational torque at the centre of mass of the arm for each body tilt (0 to 18 deg) as a function of arm angular position relative to the shoulder horizon. Torque was provided from the arm starting position (mean arm position relative to the shoulder = -42 deg) to the final required arm position at eye level (mean arm position relative to the shoulder = 14 deg). Values correspond to an average subject of 70 kg with a 0.35 m upperarm, a 0.30 m forearm, a 0.20 m hand and eye-shoulder distance of 0.21 m.
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target localization [46]. Rather, we argue for an inadequate sensorimotor implementation of the estimated gravitational influence in arm motor planning and control, namely an overestimation of the biomechanical facilitatory influence of gravity upon arm elevation on arm pointing movement. Indeed, when subjects are tilted forward, gravity facilitates the arm shoulder elevation as the gravitational torque to overcome is, on average, smaller (see Figure 10). As a consequence, the required force to rotate the arm toward the target located at HREL was lower, particularly at movement onset. Had subjects not take into account the change of gravity direction relative to their arm prior to or during movement execution and executed the same arm motor command when tilted as when non-tilted, they would have overshot the target (positive errors relative to the baseline). On the contrary, our data showed that body tilt induced final undershoots (negative errors relative to the baseline). This result is rather consistent with previous studies reporting small -however non significant- undershoots during forward body tilt without visual scene [2,10]. For instance, Bourdin et al. [10] reported final pointing errors of −1.04, −0.39 and −0.98 deg for body tilt at 2, 4 and 8 deg, respectively.

We suggest that final pointing errors observed during slow body tilt may not be considered as simple biomechanical consequences of body tilt. In line with this claim, several studies support the idea of a prior integration of predicted gravitational effects on arm motor command [19–21,35,36,47–49]. Here we also found that arm movement control was modified at an early stage since body tilt, whatever the scene orientation, induced an early modification of movement pattern with a lower PA compared to when the body was not tilted. Given that gravitational torque applied on the arm when tilted would increase the PA, our findings support the idea of a predictive control of the arm movement taking into account the consequences of gravity on the arm [22]. This hypothesis is based on studies that have already showed that early movement features (e.g., PA, rTPA) reflect motor planning [19,27,28]. However, this predictive control may not be fully adapted as, at movement endpoint, we still found final undershoots when the body was tilted forward. Final undershoots associated to lower PA have been also found in microgravity [49,50], also suggesting a prior overcompensation for the biomechanical consequences of weightlessness on the arm. Overcompensation might be the optimal solution when subjects encounter difficulty integrating gravity, as undershooting can be viewed as functional since movement length, energy and time are all minimized.

Combination of errors induced by visual scene and body tilt

Overall, we found final undershoots for both combined conditions regardless of the scene tilt direction. Considering our conditions in a body-centered reference frame, we found that when the body was tilted forward and the scene was tilted backward, final pointing errors appeared as an additive combination (i.e., unweighted sum) of the errors observed for single body and scene tilt alone. On the other hand, when both the body and the scene were tilted forward, final pointing errors could not be fully accounted for by this model. We suggest that this difference of combination could be linked to the absolute orientation of the visual scene relative to gravitational vertical. We extended the latter hypothesis by considering that the control of arm movement could have been performed by encoding the body and visual cues in a gravity-centered reference frame. This hypothesis is supported by the absence of difference between all predicted and observed data (final error and kinematic parameters) when conditions are defined relative to gravity.

The link between final errors and gravity can be discussed first when considering experimental conditions in a body-centered reference frame. Indeed, final errors differed between combined conditions $\mathbf{B_{fwd}S_{fwd}}$ and $\mathbf{B_{fwd}S_{bwd}}$ as a function of the direction of rotation of the visual scene relative to the observer. Nonetheless in these conditions, the visual scene orientation also differed relative to gravitational vertical. While the combined condition including forward body and scene tilts induced an increased deviation of the scene orientation relative to gravity (see Figure 2), the combination of forward body tilt and backward scene tilt kept the visual scene always parallel to gravitational vertical. Previous studies already showed a substantial influence of 'visual gravity' in spatial orientation tasks and sensorimotor tasks [12,27]. Specifically, Sciutti et al. [27] recently showed that visual vertical feedback influenced the planning of horizontal pointing movements whereas horizontal visual feedback did not affect the planning of vertical pointing movements. According to Le Seac'h & McIntyre [12], motor commands need to anticipate gravity consequences on motor execution, and gravitational vertical is taken into account through multiple sensory cues, notably visual. Gravitational vertical may have a particular status compared to the other directions [51]. Indeed, several studies suggested that it would be integrated as an internal model [20,22]. In one condition of the present experiment, the fact that the visual scene remained oriented at gravitational vertical could increase its relevance. Conversely, when the visual scene was no longer aligned with gravity, the weight of its associated spatial cues might have substantially decreased in favour of body-related cues. However, dominance of body-related cues when the visual scene is not aligned with gravity, does not automatically mean that the weight of visual cues is decreased when other body-related cues are available. Indeed, we observed an influence of single visual scene rotation while static body orientation cues remained available. Therefore, combination of spatial cues might also depend on the nature of body-related cues: static (i.e., unchanged body orientation) versus dynamic (i.e., actual –even slow– body rotation). Overall, we argue that the absolute orientation of the scene appears determinant in the combination process.

While absolute vertical may play a major role in the control of pointing movements considering a body-centered reference frame, one may further hypothesize that the absolute vertical could constitute the reference for encoding visual and non-visual orientation cues. In such a gravity-centered reference frame, the condition including forward body tilt and backward visual scene tilt relative to the observer can be considered a single condition because it provides a stable visual reference in space. In parallel, the combined conditions in this gravity-centered reference frame included a perturbation of the visual scene orientation relative to gravity as well as body orientation (i.e., $\mathbf{B_{fwd}S}$ and $\mathbf{B_{fwd}S_{fwd}}$ conditions). Our results indicate that a linear combination of data in the single conditions can account for the data in both of these combined conditions, when we consider final errors as well as all tested kinematic variables. Overall these results support the idea that gravity is an invariant reference for the planning and control of pointing movement. Gravity-centered coding would here enable a more reliable reference frame than body-centered coding, mainly because both the visual and body orientation were modified in our experiment. This hypothesis is supported by the study of Burns and Blohm [45] showing that the encoding of pointing movement characteristics relies more on external references than egocentric ones when the head is tilted. Gravity-centered coding hence would provide a stable reference frame for movement control [43,52], an idea consistent with the report that in the absence of gravity, goal-directed movements become inaccurate (for review see [53]). Recently, Tagliabue et al. [44] added that there is no prior given to the egocentric reference frame when performing a sensorimotor task. With the principles of the Maximum Likelihood Estimation [54], these authors [44] demonstrated that the CNS tends to maximise the weight of spatial coordinates that minimize the output variability. In the present experiment, one might expect that body-related and visual cues relative to gravity led to less variable arm movements, a hypothesis which needs to be tested in further experiments.

Conclusion

We showed that pointing toward a target during slow body and visual scene tilt provides a way to investigate combination rules of spatial cues involved in sensorimotor control. Our results suggest that the gravity plays a crucial role for the planning and control of arm pointing movements. The CNS may use gravity, thanks to its invariant properties, as a reference for the combination of visual and non-visual cues. The selected form of combination process expressed in the control of arm pointing movements may then arise from the spatial context mediated by the available cues.

Appendix

The influence of pointing succession was investigated through 5 condition×4 angle of tilt×6 pointing succession ANOVAs performed on final position, PA, rTPA, RT and MD. First, a main effect of pointing succession was found for PA, RT and MD (see Table S1).

Second, the analyses revealed that the interaction angle of tilt x pointing succession was significant for final position, PA, RT and MD (Table S1). Overall, as presented in Figure S1, the evolution across pointing succession did not follow a clear pattern. Indeed, the analysis of final position, RT and MD did not show a global increase or decrease across pointing for tilted compared to non-tilted situations. These results suggested that the continuous rotation, used in our protocol, was not the cause of the pointing succession effect. We rather suggest that the pointing succession effect, due to the repetitions of pointing movements, differed in tilted and non-tilted conditions because of differences in visuo-postural constraints. For PA and MD, the interaction angle of tilt x pointing succession mainly suggested that the first pointing movement (P1) differed from the subsequent ones, since from P2 to P6 the pattern of pointing was similar for each angle of tilt (Fig. S1b and S1d). When comparing P1 to the other pointing movements, MD tended to be longer and PA smaller when tilted, probably reflecting the exposure to a new perturbation (see also section *Kinematic parameters*). The presence of a novel perturbation (i.e., visual and/or body rotation) could also explain why the RT was reduced across trials at a slower rate in tilted conditions as compared to 0 deg (see Figure S1c). Finally, the results showed that contrary to non-tilted situations, the tilted situations did not induce a high modulation of the final positions across the successive pointing movements (see Figure S1a). We argued that the regulation of final position over the successive pointing movements at 0 deg was no longer possible when the situation was perturbed (i.e., visual and/or body rotation).

Most importantly, the interaction condition x pointing succession and the interaction condition x angle of tilt x pointing succession were not significant for all variables (Table S1). These results indicate that the described statistical effects did not affect the interaction between the angle of tilt and condition, which remains the primary interest of the study.

Finally, an interaction condition x angle of tilt was found for final position and PA. For final position, post-hoc results revealed that in the condition $\mathbf{B_{fwd}S_{bwd}}$, 0 deg differed from 6, 12 and 18 deg ($p<.001$ for all comparisons), and in the condition $\mathbf{S_{bwd}}$, 0 deg differed from 12 and 18 deg ($p<.01$ and $p<.05$, respectively). Planned comparisons showed statistical differences in final position between 0 deg and tilted situations for $\mathbf{S_{bwd}}$ ($p<.05$), $\mathbf{B_{fwd}S}$ ($p<.05$), $\mathbf{B_{fwd}S_{bwd}}$ ($p<.001$) but not for $\mathbf{S_{fwd}}$ ($p=.13$) and $\mathbf{B_{fwd}S_{fwd}}$ ($p=.42$). Planned comparisons showed statistical differences in PA between 0 deg and tilted situations for $\mathbf{S_{bwd}}$ ($p<.05$), $\mathbf{B_{fwd}S}$ ($p<.01$), $\mathbf{B_{fwd}S_{fwd}}$ ($p<.01$) and $\mathbf{B_{fwd}S_{bwd}}$ but not for $\mathbf{S_{fwd}}$ ($p=.75$). Overall, these latter results were similar to those presented in the main manuscript (See sections *Final Accuracy* and *Movement kinematics*) were we averaged the values obtained from 6 pointing movements x 3 repetitions.

Supporting Information

Figure S1 Interaction pointing succession x angle of tilt for final position (a), PA (b), RT (c) and MD (d). Vertical bars denote positive standard errors. Statistical differences between pointing movements for a given angle of tilt are provided in Table S2.
(EPS)

Table S1 Statistical results of the 5 condition x 4 angle of tilt x 6 pointing succession ANOVAs performed on final position, PA, rTPA, RT and MD. Significant effects are presented in bold. *: p<.05; ‡: p<.01; †: p<.001.
(EPS)

Table S2 Post-hoc results of the significant angle of tilt x pointing succession interactions which were revealed on final position, PA, rTPA, RT and MD. This table provides statistical differences between pointing movements for a

given angle of tilt. n.s: non-significant, *: $p<.05$; ‡: $p<.01$; †: $p<.001$.
(EPS)

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Author Contributions

Conceived and designed the experiments: CS FS CB DM LB. Performed the experiments: CS. Analyzed the data: CS. Contributed reagents/materials/analysis tools: CS. Wrote the paper: CS FS CB DM LB.

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Microgravité et restitution d’un moment pseudo-gravitaire à l’épaule

Bringoux, L., Blouin, J., Coyle, T., Ruget, H., & Mouchnino, L. (2012). Effect of gravity-like torque on goal-directed arm movements in microgravity. Journal of Neurophysiology, 107, 2541-2548.

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Effect of gravity-like torque on goal-directed arm movements in microgravity

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[1]*Institut des Sciences du Mouvement "Etienne-Jules Marey," CNRS and Aix-Marseille Université and* [2]*Laboratoire de Neurosciences Cognitives-CNRS and Aix-Marseille Université, Marseille; and* [3]*Institut de Médecine et de Physiologie Spatiales/Clinique Spatiale, MEDES-IMPS-BP 74404, Toulouse, France*

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Bringoux L, Blouin J, Coyle T, Ruget H, Mouchnino L. Effect of gravity-like torque on goal-directed arm movements in microgravity. *J Neurophysiol* 107: 2541–2548, 2012. First published February 1, 2012; doi:10.1152/jn.00364.2011.—Gravitational force level is well-known to influence arm motor control. Specifically, hyper- or microgravity environments drastically change pointing accuracy and kinematics, particularly during initial exposure. These modifications are thought to partly reflect impairment in arm position sense. Here we investigated whether applying normogravitational constraints at joint level during microgravity episodes of parabolic flights could restore movement accuracy equivalent to that observed on Earth. Subjects with eyes closed performed arm reaching movements toward predefined sagittal angular positions in four environment conditions: normogravity, hypergravity, microgravity, and microgravity with elastic bands attached to the arm to mimic gravity-like torque at the shoulder joint. We found that subjects overshot and undershot the target orientations in hypergravity and microgravity, respectively, relative to a normogravity baseline. Strikingly, adding gravity-like torque prior to and during movements performed in microgravity allowed subjects to be as accurate as in normogravity. In the former condition, arm movement kinematics, as notably illustrated by the relative time to peak velocity, were also unchanged relative to normogravity, whereas significant modifications were found in hyper- and microgravity. Overall, these results suggest that arm motor planning and control are tuned with respect to gravitational information issued from joint torque, which presumably enhances arm position sense and activates internal models optimally adapted to the gravitoinertial environment.

weightlessness; motor control; arm kinematics; movement accuracy; position sense

PRODUCING ADAPTED MOTOR COMMANDS in a novel environment necessitates taking into account the moving limb characteristics and environmental dynamics within the motor planning (Davidson et al. 2005; Guillaud et al. 2011; Papaxanthis et al. 2005; Shadmehr and Moussavi 2000). However, these prerequisites are not always fulfilled, since movements performed in new force fields appear inaccurate during initial exposure, in terms of trajectory and final position. For instance, studies conducted in weightless environments have reported decreased accuracy of goal-directed arm movements performed without visual feedback compared with what is usually observed on Earth (Bock et al. 1992; Carriot et al. 2004; Fisk et al. 1993; Watt 1997; Whiteside 1961).

This decrease in performance has been mostly explained by the alteration of limb position sense in modified gravitational environments (Bock 1992; Lackner and DiZio 1992; Roll et al. 1993, 1998). Spaceflight experiments, including limb matching tasks under muscle vibration (Lackner and DiZio 1992) and perceptual estimates of limb location (Young et al. 1993) have indeed suggested that proprioception is not as effective in weightlessness as in normogravity. The origin of this proprioceptive impairment is still a matter of debate. Some studies suggested that it could result from the absence of gravity-based vestibular inputs, leading to a decreased vestibulospinal influence on muscle spindle sensitivity (Lackner and DiZio 1992, 2000). Here, the misperceived limb configuration prior to movement execution would render the motor command ill-adapted to the new gravitational environment. However, studying manual catching of falling balls by astronauts, McIntyre et al. (2001) found that slower interceptive behaviors observed in microgravity cannot be fully explained by reduced muscle tone, at least when visual feedback is available to control movements.

There is also some evidence that muscle spindle firing modifications during active contraction against a load strongly influence position sense on Earth (Allen et al. 2008; Ansems et al. 2006; Proske 2006). In addition, following Weber's intuition that "our muscles always perceive space as affected by gravity" (Weber 1922), several researchers have explored subjects' ability to match the position of their forearms submitted to differential loads in normogravity. They found that when the matching limb is differentially loaded, the error in the reference angle produced is related to the imposed external torque (Bock 1994; Worringham and Stelmach 1985). Gooey et al. (2000), also using a forearm matching task, gave further support to this hypothesis by showing that a forearm made weightless is perceived as more flexed than it actually is.

Here, we tested whether reestablishing gravity-like torque (with an elastic system) during goal-directed arm movements in microgravity can compensate for the perturbing effect of weightlessness on movement accuracy. Furthermore, as the absence of gravity is also known to alter the spatiotemporal structure of the movement (Papaxanthis et al. 2005), we also examined whether gravity-like arm loading can restore movement kinematics. Specifically, we hypothesized that providing gravity-like arm loading in microgravity would allow subjects to produce movements with similar accuracy and a spatiotemporal organization as in normogravity.

MATERIALS AND METHODS

Participants. Eight right-handed human volunteers (3 women and 5 men, mean age = 31 yr) participated in the experiment. Three had no prior microgravity experience, whereas the remaining five had participated in at least two previous parabolic flight campaigns. All subjects gave signed informed consent in compliance with the Hel-

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sinki Convention. The experiment was approved by the flight testing center of the French Army (CEV) and a local Ethics Committee.

Apparatus and experimental setup. The experiment was conducted in the A-300 ZEROg aircraft chartered by the French Centre National d'Etudes Spatiales (CNES) for parabolic flight studies during parabolic flight campaign #59. During the experiment, the plane is flown such that the resultant gravitoinertial force, when present, is normal to the aircraft floor. A parabolic maneuver is composed of three distinct phases: 20 s of hypergravity (1.8 g, pull-up phase) followed by 22 s of microgravity (0 g) before a second period of 20 s of hypergravity (1.8 g, pull-out phase). The aircraft ran a sequence of 30 parabolas per flight organized in 6 groups of 5 parabolas separated by 5- to 8-min periods of level flight. The experiment was completed in two consecutive days.

Subjects were tested on board prior to each flight in normogravity (1g condition; Fig. 1*A*). In this condition, they were lying prone (face down) on a padded table (2 m long × 0.9 m wide × 0.9 m high), with their right arm free to move off the side of the table. The right forearm was kept extended with a light rigid gutter fixed along the elbow joint. The prone orientation was adopted to match the pseudogravitational constraints induced in the 0gE condition detailed below. In this orientation, the gravity facilitated the arm movement in the shoulder's sagittal plane from 0° (i.e., arm actively oriented toward the feet along the trunk axis) to 90° (i.e., arm normal to the trunk) and acted against the movement from 90° to 180° (i.e., arm oriented toward the head-up direction). In other words, the gravitational torque at the shoulder was positive until 90° and then became negative beyond 90°.

When tested during parabolic flights, subjects were tightly restrained supine on the cabin floor with straps and pads (Fig. 1, *B–D*). Their right upper limb, maintained extended as in the 1g condition, was the only body segment free to move. In the microgravity condition (0g; Fig. 1*B*) no external force was exerted on the reaching arm, irrespective of its orientation (i.e., no gravitational torque at the shoulder). In the hypergravity condition (1.8g; Fig. 1*D*), always presented during the first phase of the parabola (i.e., pull-up), an external force acted against the arm movement from 0° to 90° (i.e., negative hypergravitational torque) but facilitated the movement from 90° to 180° (i.e., positive hypergravitational torque). Hence, the 1.8g condition cannot be simply considered as an "enhanced" 1g condition relative to 0g, but rather as a condition in which the gravitational constraints are also reversed with respect to 1g.

During selected microgravity episodes, hereafter referred to as the 0gE condition, two pairs of elastic bands were attached to each side of the right arm's gutter at the elbow level and fixed to a sturdy metallic frame behind and in front of the subject's shoulder (Fig. 1*C*). The combined strain of these elastic bands varied according to the arm orientation. The elastic configuration was determined so as to mimic the gravitational influence of the 1g condition at the shoulder level, where subjects produced arm movements in a prone position. Specifically for each subject, a neutral position (i.e., balanced strain) was reached when the arm was oriented 90°. The combined strain facilitated the arm movement from 0° to 90° (positive pseudogravitational torque) and acted against the movement from 90° to 180° (negative pseudogravitational torque). A mathematical simulation (detailed in APPENDIX) was performed to enable the selection of suitable elastics and to compare the shoulder torque evolution in both the 1g and 0gE conditions for all targeted angles. The variation of the shoulder torque across the different angular positions in this 0gE condition closely matched that observed in the 1g condition. This could only be achieved by using different body orientations relative to the cabin floor in the 1g and 0gE conditions (i.e., prone and supine orientations, respectively).

Reflecting markers were positioned at anatomical landmarks of the right upper limb (acromion, lateral epicondyle of humerus, styloid process of ulna). These markers were used for arm kinematic recordings by means of an optoelectronic system (E.L.I.T.E.) operating at a sampling frequency of 100 Hz. The corresponding local accuracy in the three-dimensional marker reconstruction was ~1 mm.

Procedure. In each experimental condition (i.e., 1g, 1.8g, 0g, and 0gE), subjects moved their outstretched right arm toward different sagittal orientations. All movements were performed with the eyes closed to prevent any visually based corrections. Each movement started with the arm directed toward the feet along the trunk axis (0°). This initial position, which required the arm to be actively maintained in the 1g, 0gE, and 1.8g conditions, was controlled and validated by the experimenter prior to each trial. Three egocentric orientations were defined as angular targets (i.e., spatial goals) relative to this initial arm position: 45° (i.e., midangular position between the arm down along the trunk axis and the arm normal to the trunk), 90° (i.e., the arm normal to the trunk), and 135° (i.e., midangular position between the arm normal to the trunk and the arm up along the trunk axis). Visual examples of these orientations

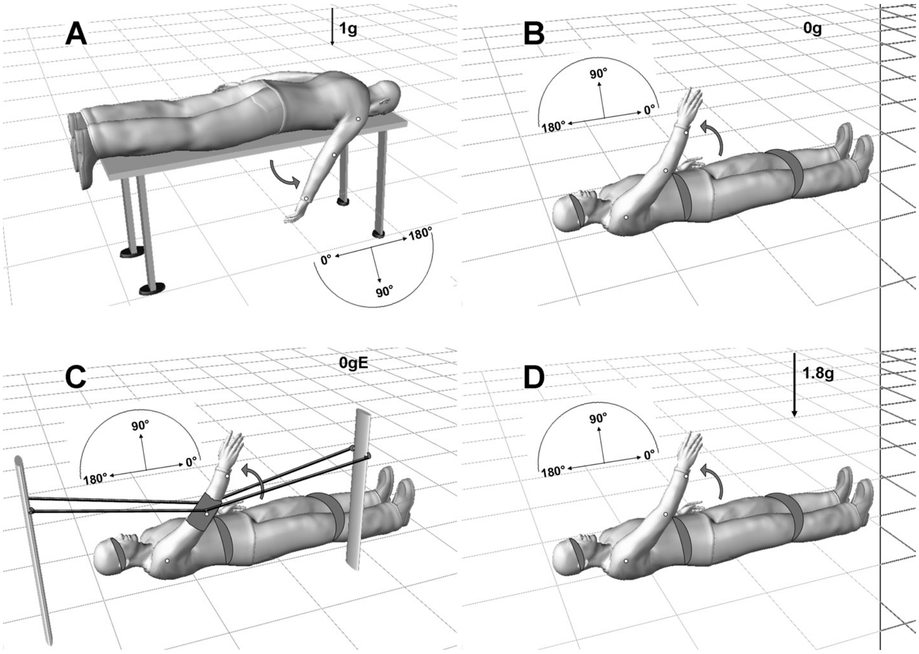

Fig. 1. Illustration of the experimental setup in the 4 environment conditions. *A*: in the 1g condition, subjects performed arm movements facilitated by gravity from 0° to 90° (angle referred to the arm starting position along the body) and hindered by gravity beyond 90°. *B*: in the 0g condition, there was no gravitational force acting on the vestibular system or on the arm. *C*: in the 0gE condition, although gravity was no longer present at the vestibular level, elastic bands mimicked the gravitational constraints on the arm exerted in 1g. *D*: in the 1.8g condition, the hypergravitational field hindered arm movements from 0° to 90° and facilitated them beyond 90°.

were given by the experimenter prior to the flights. To provide quick instructions regarding the targeted angles, we used the labels "down," "ahead," and "up" for the 45°, 90° and 135° orientations, respectively. During the experiment, these labels were subsequently announced by the experimenter in a pseudorandom order, prior to each trial. The goal of the subjects was to reach "as accurately as possible" toward these angular positions with the eyes closed.

Four subjects were tested per flight (2 flights were dedicated to this experiment in the campaign). During each flight, the first pair of subjects were tested from *parabola 1* to *parabola 14* and the last pair were tested from *parabola 16* to *parabola 29*. Of the first pair, only one subject was equipped with elastic bands from *parabola 1* to *parabola 7*. During the 5-min pause between *parabola 7* and *parabola 8*, the elastic bands were removed and attached to the other subject. During the 8-min pause between *parabola 15* and *parabola 16*, a new pair of untrained subjects were installed, with only one being attached to the elastic bands. Finally, the 5-min pause between *parabola 22* and *parabola 23* was used to swap the elastic bands onto the last subject. Only subjects without elastic bands were tested during the 1.8g phases.

For each parabola, both subjects received the same sequential announcement of the targets they had to reach. Prior to the flight, one subject for each pair of subjects was designated for performing the movement immediately after the announced target. When this subject returned the arm toward the initial position after the movement, she/he had to say "OK" to indicate to the second subject to start her/his movement. Such sequencing of the movements facilitated the kinematics data analyses by preventing obstructions and misattributions of kinematics markers between subjects.

Altogether, within each experimental condition, the subjects performed eight arm movements for each of the three target orientations. No feedback was given to the subjects about their final accuracy throughout the whole experiment.

Data analysis. Off-line data processing carried out with the E.L.I.T.E. software system allowed for complete three-dimensional kinematic reconstruction of marker trajectories, which were low-pass filtered with a digital second-order dual-pass Butterworth filter (10-Hz cutoff frequency). A model of arm orientation in the pitch dimension was constructed from these markers. The arm movement onset was defined as the time when angular velocity in the sagittal plane reached 5% of its peak. Conversely, final arm position relative to the target was recorded when the angular velocity dropped under 5% of the peak velocity.

Typical outputs of this processing are illustrated in Fig. 2, representing the arm angular displacement in the sagittal plane toward the 135° target orientation and its derivative over time, for the different environment conditions.

Arm movements were analyzed by first focusing on the final accuracy, expressed as the mean angular errors obtained by subtracting the target angle from the arm angle at movement offset. Angular errors were therefore positive when the arm angle exceeded the target orientation (these errors being referred to as movement overshoots). Movement variability was analyzed by computing the within-subject standard deviations of the angular errors obtained for each condition. Movement kinematics were also analyzed by computing movement duration (MD), mean velocity (V_{mean}), peak velocity (V_{max}), the ratio $V_{\mathrm{max}}/V_{\mathrm{mean}}$ (C parameter; see Flash and Hogan 1985; Papaxanthis et al. 2005), as well as the relative time to peak velocity (rTPV, namely, the ratio time to peak velocity/movement duration). C and rTPV are known to respectively reflect inertial influences and gravitational constraints upon movement organization (Papaxanthis et al. 2005). Usually, C varies with movement speed under normogravity conditions, whereas rTPV essentially varies with gravity environment.

Statistics. Analyses of variance (ANOVAs) were performed to compare the means of these kinematics parameters across the experimental conditions, after having ensured that the assumptions of normality and variance homogeneity were not violated (χ^2 and Levene's tests). Unless specified, a 3 target orientations (45°, 90°, 135°) × 4 environment conditions (1g, 1.8g, 0g, 0gE) statistical design was used to assess the effect of the experiment conditions on the different computed variables. When significant, the effect size ($P\eta^2$) was computed to estimate the importance of the effect (α level fixed at $P < 0.05$). Post hoc comparisons (Newman-Keuls tests) were also conducted to determine significant differences between specific conditions relative to others.

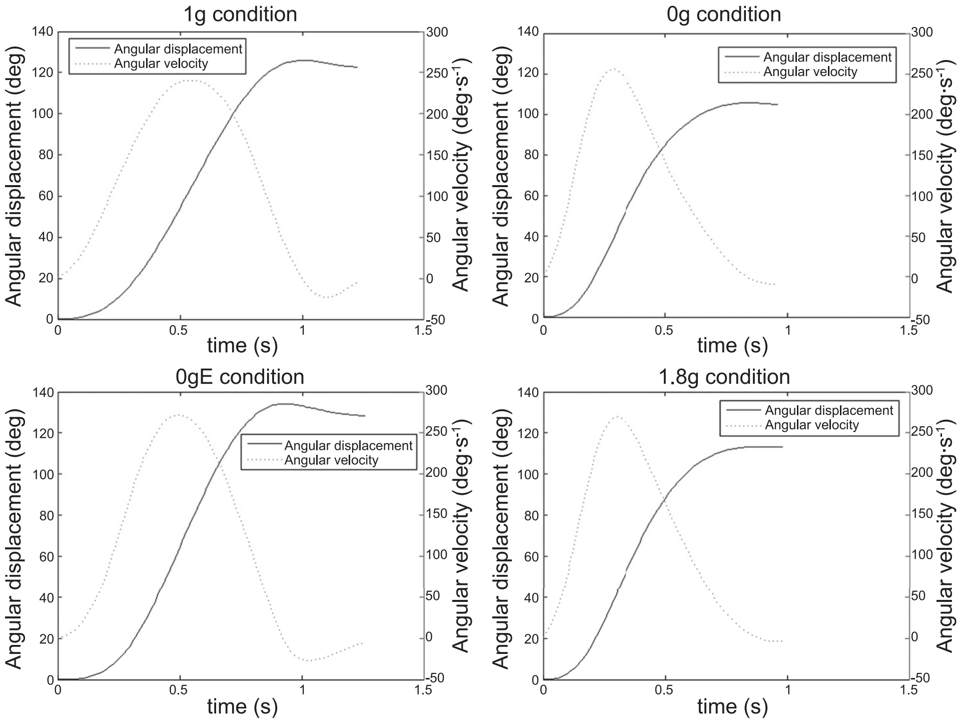

Fig. 2. Typical kinematic features of goal-directed arm movements performed toward a 135° target orientation in the different environment conditions. Angular displacement and angular velocity vs. time are represented for the 1g, 0g, 0gE, and 1.8g conditions.

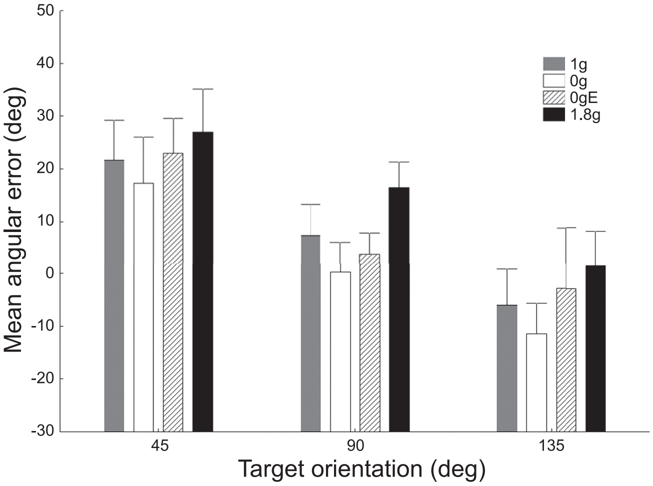

Fig. 3. Mean angular errors recorded on the final position of arm movements as a function of environment condition and target orientation. Error bars represent 95% confidence intervals.

RESULTS

First, for all measured variables, no significant differential influence of the experimental conditions was observed between subjects with and without parabolic flight experience [final position: $F(3,12) = 1.89$, $P = 0.18$; MD: $F(3,12) = 1.50$, $P = 0.27$; V_{mean}: $F(3,12) = 1.02$, $P = 0.42$; V_{max}: $F(3,12) = 0.62$, $P = 0.62$; C: $F(3,12) = 0.66$, $P = 0.59$; rTPV: $F(3,12) = 1.04$, $P = 0.41$]. Furthermore, there was no significant difference between the first and last reaching movements performed in the same experimental configuration (i.e., for each combination of target orientation and environment condition; $P > 0.05$ for all *t*-tests performed). This was expected because adaptive or learning effects are known to take place only in presence of an error-related feedback, for instance, from vision of the arm (Bourdin et al. 2001), which was unavailable in the present study (subjects having eyes closed throughout the experiment).

Final position. As predicted, the external forces markedly influenced the final arm orientation reached by the subjects (Fig. 3). This was confirmed by the ANOVA revealing a significant main effect of environment condition on the angular errors [$F(3,21) = 5.23$, $P < 0.01$, $P\eta^2 = 0.43$] as well as a significant target orientation × environment condition interaction [$F(6,42) = 2.50$, $P < 0.05$, $P\eta^2 = 0.26$]. Notably, post hoc analyses showed that the angular errors measured in the 0g and 1.8g conditions always differed from the 1g condition, while no difference was found between 0gE and 1g, irrespective of the target orientation (see Table 1 for post hoc analyses).

On the other hand, the angular errors significantly differed according to the target orientation [$F(2,14) = 54.82$, $P < 0.001$, $P\eta^2 = 0.89$]. The subjects notably overshot the 45° target orientation (global mean: +22°) and slightly undershot the 135° target orientation (global mean: −4.5°).

The variability of the reached arm orientation recorded for each condition was not found significantly different between environment conditions [$F(3,21) = 2.04$; $P = 0.14$] or between target orientations [$F(2,14) = 0.40$, $P = 0.68$]. On average, movement variability was 5.1°.

To specifically focus on the influence of the environment condition on movement accuracy, we rebased the angular errors relative to the 1g values obtained for each subject and for each target orientation. A one-way ANOVA comparing the mean rebased angular errors among the 1.8g, 0g, and 0gE conditions was then performed, irrespective of target orientation. It revealed a main effect of environment condition [$F(2,14) = 12.11$, $P < 0.001$, $P\eta^2 = 0.63$]. The mean angular error in 0gE was significantly different from that measured in 1.8g ($P < 0.001$) and 0g ($P < 0.05$) but did not significantly differ from the 1g baseline, as shown by the statistical comparison with a standard value of 0 ($t = 0.74$, $P = 0.94$). More precisely, the mean reached position in 1g was overshot in 1.8g (+7.3°) and undershot in 0g (−5.7°) but was not significantly different from that reached in 0gE.

Movement duration. The ANOVA conducted on movement duration did not reveal a significant effect of the environment condition [$F(3,21) = 0.96$, $P = 0.43$] or significant interaction between this factor and target orientation [$F(6,42) = 0.69$, $P = 0.66$]. This clearly indicates that the difference of final accuracy observed among environment conditions cannot be attributed to a difference in movement duration. On the other hand, movement duration was unsurprisingly affected by target orientation [$F(2,14) = 29.68$, $P < 0.001$, $P\eta^2 = 0.81$]. The greater the arm angle to be reached, the longer the movement duration (1.08 s, 1.19 s, and 1.28 s for 45°, 90°, and 135° target orientation, respectively; Fig. 4).

Mean velocity. The V_{mean} differences between environment conditions failed to reach significance [$F(3,21) = 2.96$, $P = 0.06$], and the interaction between environment conditions and target orientations was also nonsignificant [$F(6,42) = 1.75$, $P = 0.13$]. This suggests that the greater accuracy found in the 1g and 0gE conditions does not result from the slowing of the movements in these conditions (e.g., speed-accuracy trade-off). On the other hand, as generally observed, V_{mean} significantly varied with the amplitude of the movements [$F(2,14) = 107.35$, $P < 0.001$, $P\eta^2 = 0.94$]. The further the target, the greater V_{mean} (from 65°/s to 105°/s from 45° to 135° target orientations).

Peak velocity and C parameter. ANOVA revealed a significant main effect of environment condition on V_{max} [$F(3,21) = 6.03$, $P < 0.01$, $P\eta^2 = 0.46$]. Post hoc analyses revealed that the significant difference only concerned the 1.8g condition, V_{max} in 1.8g being greater than in the other conditions ($P < 0.01$). A main effect of target orientation was also found on V_{max} [$F(2,14) = 206.43$, $P < 0.001$, $P\eta^2 = 0.97$]. The larger

Table 1. *Post hoc analyses*

	1g	0g	0gE	1.8g
Target orientation: 45°				
1g	—	*	ns	*
0g		—	†	‡
0gE			—	*
1.8g				—
Target orientation: 90°				
1g	—	†	ns	‡
0g		—	ns	‡
0gE			—	‡
1.8g				—
Target orientation: 135°				
1g	—	†	ns	†
0g		—	‡	‡
0gE			—	ns
1.8g				—

*$P < 0.05$; †$P < 0.01$; ‡$P < 0.001$. ns, Not significant.

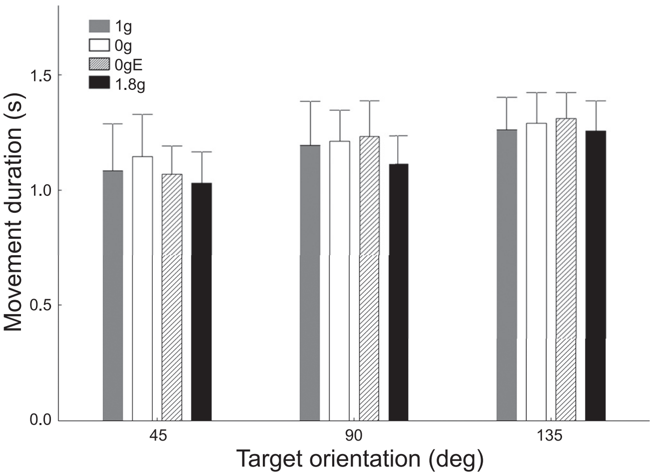

Fig. 4. Mean duration of arm movements as a function of environment condition and target orientation. Error bars represent 95% confidence intervals. Movement duration progressively increases for longer angular distances, but no significant difference appears across environment conditions.

the angle to be reached, the higher $V_{\max}$ (from 120°/s to 220°/s from 45° to 135° target orientations).

As expected, the C parameter was not significantly different across the environment conditions [mean: 1.9; $F(3,21) = 1.03$, $P = 0.40$] but varied with target orientation [$F(2,14) = 4.15$, $P < 0.05$, $P\eta^2 = 0.37$]. The further the target, the greater the C value (from 1.93 for 45° to 2.18 for 135°).

Relative time to peak velocity. Analyses of rTPV showed a significant main effect of environmental condition [$F(3,21) = 21.02$, $P < 0.001$, $P\eta^2 = 0.75$]. Specifically, rTPV was found significantly greater in both 1g and 0gE conditions compared with 0g and 1.8g conditions ($P < 0.001$), while no significant difference appeared between 0gE and 1g conditions ($P = 0.82$). On the other hand, ANOVA revealed no significant effect of target orientation [$F(2,14) = 1.88$, $P = 0.18$] and no significant interaction between this factor and environmental condition [$F(6,42) = 1.99$, $P = 0.09$].

Together, these results indicate that the temporal features of goal-directed arm movements performed in the 0gE condition did not differ from those observed in normogravity, contrary to those observed in the 0g and 1.8g conditions (Fig. 5).

DISCUSSION

The main purpose of the present study was to determine whether the decreased accuracy of goal-directed arm movements observed in microgravity could be counteracted by gravity-like arm loading. Although specific to this experimental context, our results clearly demonstrate that adding shoulder joint torque in microgravity allowed subjects to perform movements that were fully comparable to those performed in normogravity. This was true in terms of both movement accuracy and movement kinematics. These two important results strongly suggest that *1*) gravity-like arm torque contributes to arm estimation prior to and during reaching movements and *2*) the motor planning is tuned with respect to contextual information, which primarily includes arm loading.

Gravity-like arm loading improves perceived arm location. The present experiment unambiguously validates the use of gravity-related arm loading in microgravity to preserve the accuracy of movements performed in normogravity. When referred to the 1g baseline, the movement accuracy increased in the 0gE condition compared with the 0g condition, irrespective of the target orientation. This result provides support for arm position sense improvement due to gravity-related arm loading. To reach a specific location with the hand, the arm motor command must be tuned according to accurate estimates of the limb position prior to (Nougier et al. 1996; Rossetti 1995; Veilleux and Proteau 2011) and during (Blouin et al. 1996, Sainburg et al. 1995; Sarlegna et al. 2006) the movement. Taking this into consideration, the question then arises as to how gravity-related arm loading improves the perceived arm location.

Several studies have suggested that muscle spindle firing modifications during active contraction against a load strongly influence position sense on Earth (e.g., Allen et al. 2008; Ansems et al. 2006; Proske 2006). On the other hand, other works have insisted on the role of the central command necessary to overcome gravitational load in limb position sense (Gandevia et al. 2006; Smith et al. 2009; Walsh et al. 2009). In the framework of the present experiment, however, it proves difficult to favor one hypothesis over the other. According to the afferent explanation, the increased alpha activity required to counteract the gravity-like torque in the 0gE condition was presumably accompanied by an enhanced gamma coactivation at the fusimotor level. This higher gamma activity could neutralize the disturbing effect of microgravity on the arm movements (i.e., the decreased fusimotor drive mediated by vestibulospinal pathways; Lackner and DiZio 1992), keeping the muscle spindle sensible to muscle length changes. On the other hand, the motor command required to overcome the additional pseudogravitational torque induced by the elastic bands during arm reaching may have given rise to a better "sense of effort," which contributes to limb position sense (Gandevia et al. 2006). Most certainly, these interpretations are not exclusive, as afferent and efferent signals might contribute both to the position sense improvement and, consequently, to the increased reaching accuracy associated with gravity-like arm loading in microgravity.

Compared with the movements they performed in normogravity, subjects undershot and overshot the target orientations

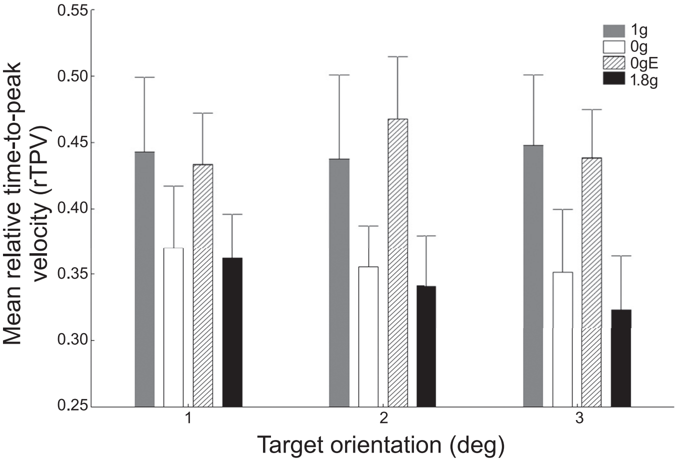

Fig. 5. Mean relative time to peak velocity (rTPV) of arm reaching movements as a function of environment condition and target orientation. Error bars represent 95% confidence intervals. If rTPV observed in 0gE significantly differs from that observed in 0g and 1.8g, it is not significantly different from TPV observed in 1g.

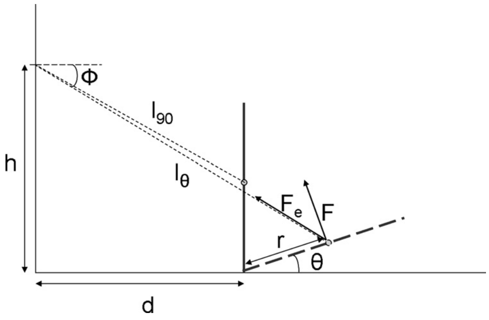

Fig. 6. Schematic illustration of the experimental setup with the parameters relevant to the calculation of the torque exerted on the subject's arm for angular positions ranging from 0° to 90° in 0gE. See APPENDIX for definitions.

in 0g and 1.8g conditions, respectively. These observations are contrary to those one could expect when considering the simple mechanical effects due to different gravitational force fields. The pattern of errors found here may suggest that subjects overestimated the expected consequences of arm loading/unloading in hyper- and microgravity, leading to a compensatory increase of movement amplitude in 1.8g and, conversely, to a compensatory decrease of movement amplitude in 0g, as already reported in a previous study (Carriot et al. 2004). The absence of visual feedback most likely decreased subjects' capacity to adapt to the new gravitoinertial fields (Lackner and DiZio 2000) and could explain the persistence of over/undershots across trials in hyper/hypogravity. However, in line with this hypothesis, the expected motor consequences associated with the gravity-like arm loading condition might have been very close to those expected in normogravity, precisely because of a comparable shoulder torque prior to movement onset. Interestingly, the present data recorded in the gravity-like arm loading condition show that not only the final accuracy but also the movement kinematics are tuned with respect to normogravity baseline.

Gravity-like arm loading allows for 1g-adapted motor planning. The finding that arm kinematics were similar in normogravity and in microgravity when a gravity-like torque was experimentally added at the shoulder joint is a key result of the present study. In particular, the temporal structure of the movements was similar in 1g and 0gE conditions (rTPV ~0.45), whereas it largely differed in both 0g and 1.8g conditions (rTPV ~0.35). This suggests that gravity-like arm loading in weightlessness helps to preserve the organization of the arm motor command generally observed in 1g. It has been proposed by Flash and Hogan (1985) that point-to-point movements respect the minimum jerk principle in which $C = 1.875$ and $rTPV = 0.5$. In that case, the hand trajectory is planned to maximize smoothness or to minimize execution variability. With C ~1.9 and rTPV ~0.45, the movements produced in 0gE and in 1g conditions therefore respected the principles underlying the organization of natural movements as described by Flash and Hogan (1985).

It is worth noting that rTPV is considered to be a reliable indicator of how gravitational constraints are implemented in motor commands (Papaxanthis et al. 2003, 2005). In our experiment, rTPV largely decreased in microgravity as well as in hypergravity (~0.35). This contrasts with the results obtained by Papaxanthis et al. (2005) and by Crevecoeur et al. (2009), who found a significant longer acceleration phase in microgravity and conversely an earlier rTPV in hypergravity compared with 1g, respectively. Movements with a longer deceleration phase are frequently found when accuracy constraints require a great deal of online control (Chua and Elliott 1993; Sarlegna et al. 2003; Terrier et al. 2011). In the present study, contrary to the experiments of Papaxanthis et al. (2005) and of Crevecoeur et al. (2009), subjects did not have visual feedback of their arm. The absence of vision, which is a powerful source of information for controlling reaching movements (Sarlegna et al. 2003; Veyrat-Masson et al. 2010), may have added stress on the online control of movements performed in such unusual gravitoinertial environments and caused the lengthening of the deceleration duration. According to current models of motor control, afferent signals that arise from self-generated movements are inhibited by a mechanism that compares the internal prediction of the sensory consequences by the brain to the actual resultant sensory feedback (Roy and Cullen 2004; Voss et al. 2006). In this framework, sensory attenuation may have been minimized in both the 0g and 1.8 conditions because of the putative mismatch between expected and current proprioceptive inputs evoked by the change of gravitoinertial constraints. This process may also have increased the importance of sensory processing during the deceleration phase. By contrast, the predicted and actual afferent signals presumably matched better in the 1g and 0gE conditions. This may have decreased the importance of feedback-based online control, leading to a bell-shaped velocity curve profile of the arm (i.e., rTPV ~0.5).

Overall, the present study, in line with others, strongly suggests that gravitational influences are taken into account for arm movement organization and execution in a predictive manner (Bockisch and Haslwanter 2007; Crevecoeur et al. 2009; Gentili et al. 2007; Guillaud et al. 2011; Papaxanthis et al. 1998a, 1998b, 2005). For instance, while the final accuracy of upward/downward arm reaching movements is impaired during initial exposure to microgravity, typical kinematic features (e.g., curvature differences between upward and downward movements) are maintained despite the absence of gravity-related biomechanical constraints (Papaxanthis et al. 1998a, 1998b). In the framework of optimal control strategy (Berret et

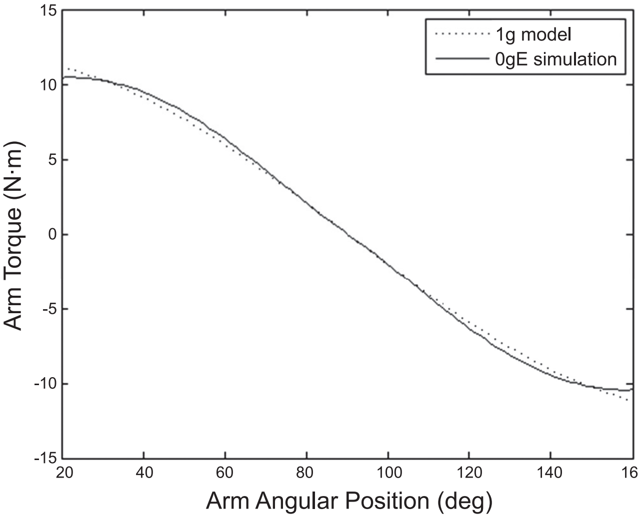

Fig. 7. Simulated torque values for the 0gE and 1g conditions within the experimental angular range for a subject of average mass (70 kg) and for an effective spring constant of 78 N·m.

al. 2008; Crevecoeur et al. 2009; Gaveau and Papaxanthis 2011), arm motor commands are optimized with respect to the action of gravity on the limb, whose consequences are integrated in motor planning and anticipated in terms of expected sensory states. It has been further hypothesized that gravity is encoded in the central nervous system and that the cerebellum may contain an internal representation of gravitational torques used for sensorimotor predictions (Gentili et al. 2009). Taking this idea further, it is tempting to hypothesize that reintroducing gravitational constraints on the moving limb by adding shoulder torque may reactivate forward internal models associated with 1g sensorimotor predictions, on the basis of an enhanced position sense. In turn, inverse dynamics of the movement could be computed in line with these sensorimotor predictions to yield a normogravity-like motor output. Here, the estimate of arm orientation could be specifically processed in proprioceptive coordinates, independently from a global state estimate of the whole-body orientation in space that may arise from a multisensory integration process (Merfeld et al. 1999).

Finally, the present data show that the additional information generated by gravity-like arm loading can be integrated in the motor commands. This integration appears effective from the very first movements performed in weightlessness, as the kinematics and accuracy of the first and last movements performed in microgravity did not significantly differ. Furthermore, the fact that gravity-related arm loading improved movement accuracy irrespective of whether participants had prior experience of microgravity suggests a wide and robust appropriateness of manipulating local torques to restore motor skills in microgravity.

Conclusions. Overall, the present study clearly shows that gravity-related constraints exerted on a moving limb may counteract the accuracy impairment observed in weightless environments in reference to normogravity baseline. This influence may be related to both position sense improvement and specific activation of a 1g-adapted motor plan. Future work is needed to question this directional effect of gravity-related arm loading, such as when gravitational constraints are not defined for prone body orientation in normogravity as in the present experiment but for supine or erect body orientation relative to the cabin floor. Other promising investigations may address the importance of gravity-related loading of body segments involved in postural control and locomotion, not only for reducing the deleterious effect of muscle atrophy during spaceflight as already considered but to help astronauts to recalibrate their motor behavior before landing back on Earth.

APPENDIX

Simulation of Torque Exerted on Arm in 0gE Condition

Extensive simulations were carried out prior to the experiment in order to ensure an acceptable correspondence between the torques exerted on the arm in the 0gE and 1g conditions. Given that the experimental setup was symmetrical about the vertical at the shoulder joint, the torques in the angular range of 90° to 180° could be determined (Fig. 6). θ is the arm angular position relative to the horizontal (starting position), Φ is the orientation of the elastic relative to the horizontal, h is the height of the attachment points of the elastic band on the metallic frame relative to shoulder joint center, d is the horizontal distance between the metallic frame and the center of the shoulder joint, r is the distance between the center of the shoulder joint and the elastic band attachment point on the arm, l_{90} is the length of the elastic band when the arm is oriented at 90° (i.e., no extension of the elastic), and l_θ is the length of the elastic band when the arm is oriented at $\theta° < 90°$.

The torque was calculated from the elastic force F_e, which was determined with Hooke's law, $F_e = -k \cdot \text{ext}$, where ext is the extension and k the spring constant of the elastic. *Equations 1–3* below show how the extension of the elastic can be derived from the geometry of the apparatus.

$$l_{90} = \sqrt{d^2 + (h - r)^2} \tag{1}$$

$$l_\theta = \sqrt{(d + r\cos\theta)^2 + (h - r\sin\theta)^2} \tag{2}$$

$$\text{ext} = l_\theta - l_{90} \tag{3}$$

$$\tau_{0gE} = r \cdot k \cdot \text{ext} \cdot \sin(\theta + \Phi) \tag{4}$$

$$\tau_{1g} = r \cdot m \cdot g \cdot \cos\theta \tag{5}$$

The spring constants of numerous elastic bands and cords were evaluated over the extension range of the arm anticipated in this experimental setup. The most linearly elastic band was selected and incorporated in such a way (bands in parallel) so as to give an appropriate mean effective spring constant over the extension range. The elastic force F_e was then resolved into its components to evaluate the actual turning force F and subsequently the total torque applied by the elastic (τ_{0gE}; see *Eq. 4*). The gravitational torque on the arm in the 1g control condition (τ_{1g}) was calculated with *Eq. 5*, the mass of the arm (m) determined from anthropometric tables (Zatsiorsky and Seluyanov 1983). As illustrated in Fig. 7, the shoulder torque generated in the 0gE condition was very close to the torque observed in the 1g condition for the different angulations tested.

GRANTS

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

Author contributions: L.B., J.B., H.R., and L.M. conception and design of research; L.B., J.B., T.C., H.R., and L.M. performed experiments; L.B., J.B., and T.C. analyzed data; L.B., J.B., and L.M. interpreted results of experiments; L.B. and T.C. prepared figures; L.B., J.B., and L.M. drafted manuscript; L.B., J.B., and L.M. edited and revised manuscript; L.B. approved final version of manuscript.

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Simulation microgravitaire en milieu subaquatique

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KINEMATIC FEATURES OF WHOLE-BODY REACHING MOVEMENTS UNDERWATER: NEUTRAL BUOYANCY EFFECTS

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Abstract—Astronauts' training is conventionally performed in a pool to reproduce weightlessness by exploiting buoyancy which is supposed to reduce the impact of gravity on the body. However, this training method has not been scientifically validated yet, and requires first to study the effects of underwater exposure on motor behavior. We examined the influence of neutral buoyancy on kinematic features of whole-body reaching underwater and compared them with those produced on land. Eight professional divers were asked to perform arm reaching movements toward visual targets while standing. Targets were presented either close or far from the subjects (requiring in the latter case an additional whole-body displacement). Reaching movements were performed on land or underwater in two different contexts of buoyancy. The divers either wore a diving suit only with neutral buoyancy applied to their center of mass or were additionally equipped with a submersible simulated space suit with neutral buoyancy applied to their body limbs. Results showed that underwater exposure impacted basic movement features, especially movement speed which was reduced. However, movement kinematics also differed according to the way buoyancy was exerted on the whole-body. When neutral buoyancy was applied to the center of mass only, some focal and postural components of whole-body reaching remained close to land observations, notably when considering the relative deceleration duration of arm elevation and concomitant forward trunk bending when reaching the far target. On the contrary, when neutral buoyancy was exerted on body segments, movement kinematics were close to those reported in weightlessness, as reflected by the arm deceleration phase and the whole-body forward displacement when reaching the far target. These results suggest that astronauts could benefit from the application of neutral buoyancy across the whole-body segments to optimize underwater training and acquire specific motor skills which will be used in space.

Key words: whole-body reaching, arm kinematics, postural strategy, underwater, neutral buoyancy.

INTRODUCTION

During space missions, astronauts evolve within unusual environments implying critical changes in the force field. For instance, they sustainably experience weightlessness on the International Space Station (ISS) or during Extra-Vehicular Activities (EVA), and must be ready to face other gravitational contexts such as on Moon and Mars surface for the upcoming decades of space exploration (Weiss et al., 2012). In these unusual environments, they often have to perform motor tasks in the framework of maintenance or scientific missions, requiring efficient sensorimotor behavior (see Lackner and Dizio, 2000 for a review). In order to overcome the impact of microgravity, they conventionally train underwater to learn the movements they will perform during their mission ('EVA training underwater'; Bolender et al., 2006). This training method exploits buoyancy (via the Archimedes principle) which is supposed to reduce the impact of gravity on the body by providing 'natural unweighting'. To approximate weightlessness, astronauts are immersed in training pools such that neutral buoyancy is usually applied to their Center of Mass (CoM). Neutral buoyancy is achieved when the upthrust exactly compensates for gravitational force. Despite this analogy with weightlessness, underwater exposure generates some additional viscous resistance acting on the moving limbs and does not affect vestibular signals as weightlessness does (Brown, 1961). Thus, in the field of motor control, the relevance of astronauts' underwater training remains to be further supported. To our knowledge, few studies investigated the influence of underwater exposure on sensorimotor and cognitive behavior (Brown, 1961; Ross et al., 1969; Dixon, 1985; Massion et al., 1995; Hoffmann and Chan, 2012; Dalecki and Bock, 2013, 2014; Schneider et al., 2014; Counil, 2015; Schaefer et al., 2015) but none of them specifically focused on its

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Abbreviations: ANOVAs, analyses of variances; CoM, Center of Mass; EVA, Extra-Vehicular Activities; LEDs, Light-Emitting Diodes; MD, movement duration; PV$_{ang}$, peak angular velocity; rDD$_{ang}$, relative angular deceleration duration.

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direct impact on goal-directed actions. Here, we addressed this issue and specifically examined the effect of neutral buoyancy on kinematic features of whole-body reaching movements.

Unweighting the body or some of its parts and questioning its effect upon motor control has been already achieved by means of robotic systems providing adjustable levels of arm-weight support (Coscia et al., 2014) or by microgravity exposure in parabolic and space flights (Mechtcheriakov et al., 2002; Carriot et al., 2004; Papaxanthis et al., 2005; Bringoux et al., 2012). In robot-assisted rehabilitation following stroke for instance, motor improvements were often reported (Prange et al., 2006) but Coscia et al. (2014) did not find distinct kinematic features with or without gravity compensation exerted by the robot on the arm in healthy subjects. When unweighting is achieved through microgravity, some studies reported a decreased mean and peak velocity of arm displacement during reaching movements (Berger et al., 1997; Mechtcheriakov et al., 2002; Papaxanthis et al., 2005; Crevecoeur et al., 2010). Such changes in weightlessness were often associated with similar movement accuracy as compared to normogravity observations (Berger et al., 1997; Mechtcheriakov et al., 2002), although other studies reported a decrease in final accuracy (Bock et al., 1992; Fisk et al., 1993; Watt, 1997; Carriot et al., 2004; Bringoux et al., 2012). Whole-body reaching tasks implying a postural involvement in the goal-directed action also led to contradictory results when performed in microgravity. Whereas Patron et al. (2005) reported a minimization of CoM displacements as it is usually observed in normogravity, Casellato et al. (2012) observed a new postural strategy characterized by a CoM projection beyond the base of support in microgravity. These contradictory findings may actually reveal that the task requirements must be accounted for when considering the impact of unweighting on motor behavior. Furthermore, in the case of underwater exposure for EVA training, the influence of the concomitant viscous fluid resistance is often neglected. Previous work dealing with how goal-directed arm movements are performed in transient or sustained modified force fields mainly used centrifugation (Lackner and Dizio, 1994; Bourdin et al., 2001, 2006) and robot manipulandum (Shadmehr and Mussa-Ivaldi, 1994; Goodbody and Wolpert, 1998). Compared to baseline, initial impairments such as final inaccuracy, altered trajectory and slower speed were reported but these tended to vanish after exposure to the field disturbance. These results suggest that humans are able to adapt their motor behavior when facing novel environments in order to keep the goal-directed actions functional. Nevertheless, neither the effect of underwater exposure on motor control nor the description of adaptive processes in this complex environment have been documented yet.

The purpose of the present study was thus to characterize the motor behavior of humans when reaching underwater compared to reaching on land. We examined the effect of task requirements by asking subjects to reach toward close versus far targets. In our experiment, reaching toward a far target required a whole-body displacement to successfully perform the task. This enabled us to investigate whether the postural component could serve the focal component for goal-directed actions in such unusual environments (Casellato et al., 2012). We also tested two different contexts of buoyancy since subjects were either immersed with their diving suit only (the neutral buoyancy was here only applied to the subjects CoM, but not to each body segment) or equipped with a submersible simulated space suit designed for astronauts training named 'Gandolfi'[†] (Hornet et al., 1990; Weiss et al., 2012). This unique space suit enabled the application of neutral buoyancy across body limbs and the adjustment of joint stiffness similar to that exerted in a pressurized space suit. Based on previous work, we expected underwater exposure to influence motor behavior but also expected this influence to vary with the experimental manipulation of buoyancy. Furthermore, we also hypothesized that target location (i.e., close versus far which determines the degree of postural involvement) could be critical in the way underwater exposure and buoyancy may affect whole-body reaching.

EXPERIMENTAL PROCEDURES

Participants

Eight right-handed professional divers (three women and five men, 1B-diving certificate holders, mean age = 38 ± 7.9 years) participated in the experiment on a voluntary basis. Security constraints excluded the possibility of testing naive participants in this environment. None of the subjects suffered from neuromuscular or sensory impairments. Vision was normal or corrected by lenses. All subjects were naive as to the specific purpose of the experiment, which was approved by the institutional review board of the Institute of Movement Sciences. They gave their signed informed consent prior to the study in accordance with the Helsinki Convention.

Experimental setup

Subjects stood upright in front of two targets, with their feet attached to the ground structure by means of footstraps (Fig. 1A). They had to press their right index finger on the start push-button positioned alongside. The height of the push-button was adjusted to each subject's height for initial posture standardization. Two circular targets (diameter: 10 cm) were presented to the subjects. They were oriented along the frontal plane and were positioned relative to subjects' anthropometric features. The close target was positioned at shoulder's height (i.e., the height of the target center corresponded to the horizontal projection of the height of the acromioclavicular joint in the sagittal plane) at a distance corresponding to arm length, allowing the subjects to reach this target without trunk displacement. The far target was positioned 25 cm away and 20 cm below the close target: in that case, subjects had to make an additional trunk displacement to reach this

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[†] Developed by COMEX S.A. & DASSAULT companies.

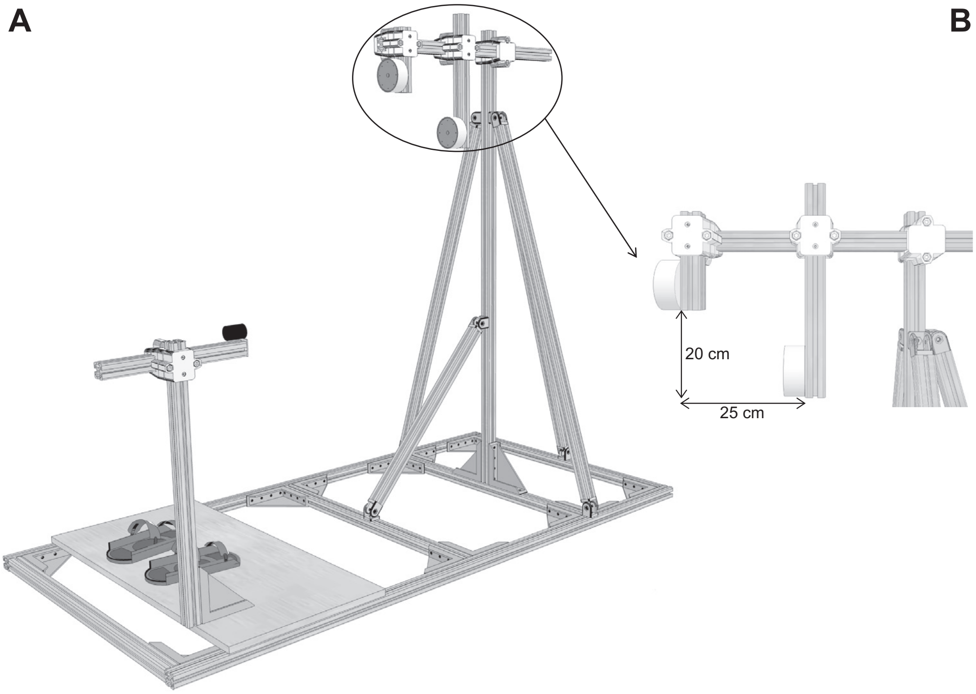

Fig. 1. Experimental setup. (A) Global view of the pointing structure including targets, start push-button (black array) and footstraps. (B) Side view of the targets which illustrates the position of the far target relative to the close target.

target (Fig. 1B). Each target could be illuminated through watertight Light-Emitting Diodes (LEDs) equally distributed around the border. Target switching and extinction were achieved by using a homemade software (Docometre©) piloting a real-time acquisition/control system running at 10 kHz (ADwin-Gold©, Jäger, Lorsch, Germany).

Luminescent markers (LED-type) were positioned onto the subjects' index, shoulder and hip. Markers position was recorded by a video motion capture system composed of three cameras sampled at 60 Hz (resolution: 848 × 480 pixels). These cameras were inserted in custom-made watertight housing for underwater acquisition.

Procedure

All the subjects were exposed to three environments: 1/on land (‘‘Land”), 2/underwater with neutral buoyancy applied to the CoM only (‘‘Aqua”), 3/underwater with neutral buoyancy applied to body limbs by using a ‘‘Submersible Simulated Space Suit” (‘‘AquaS”). In these three environments, subjects wore their diving suit to neutralize the effects of joint stiffness proper to the suit. Underwater conditions were performed in a specially-equipped pool (4 m deep) at COMEX SA. In Aqua, subjects wore their diving mask, air tank and wet suit with a weight belt, such that free floating was reached, but without specific control of buoyancy across the body segments. Conversely in AquaS, subjects also wore their diving mask and air tank, but were additionally equipped with the submersible simulated space suit (‘‘Gandolfi”) enabling us to apply neutral buoyancy across the body limbs. These buoyancy features were achieved by means of floats and weights specifically distributed into the simulated space suit to cancel out the gravitational force on each body part. Additionally, joint stiffness was tuned by means of adjustable springs to counteract the resultant torques yielded by the exoskeleton underwater (i.e. to minimize the influence of additional stiffness/inertia due to the exoskeleton upon motor output and subsequent kinematics). Subjects first performed the Land condition and four months later both underwater conditions whose order was counterbalanced.

Positions of the start push-button and the targets were adjusted for each subject before performing a calibration along the Z vertical axis (corresponding to arm movement elevation). Before each trial, subjects had to stand upright, the arms outstretched along the body, and the right index pressing on the start push-button. When one of the targets was illuminated, subjects were asked to perform an arm reaching movement toward the target while keeping the arm outstretched. Reaching movements had to be performed as quickly as possible while primarily respecting accuracy constraints related to the target area. The trial was validated when the index fingertip reached the target. The final position had to be maintained until target extinction (3 s after movement onset) which prompted the subjects to return to the starting position.

Subjects performed 42 pointing movements toward each of the two targets for a total of 84 trials per experimental session (during which the subjects were exposed to one of the three specific environments). The two targets were presented in a pseudorandom order, which was counterbalanced between the subjects. Each session included three specific blocks of four trials in which the order of target presentation was the same. These blocks were presented in the initial, middle and final part of the session to easily assess the potential evolution of motor performance in each session, which lasted about 45 min.

Data processing

For each trial, the time elapsed between target illumination and the release of the start push-button by the subjects defined the reaction time (RT). Video data from the three cameras were initially synchronized and sequenced (Kinovea© software), subsequently allowing for the appropriate tracking of the selected markers (i.e., XZ coordinates over time for index, shoulder and hip position). A 3D reconstruction method (Direct Linear Transformation; Abdel-Aziz and Karara, 1971) was used to merge XZ coordinates of a same marker from each camera (Labview™ software). This 3D reconstruction method enabled us to improve the accuracy of markers' position estimates to $3.3 \times 10^{-3} \pm 4 \times 10^{-3}$ m on average. Kinematic data presented below were obtained from this video processing and concerned the movement features in the sagittal plane.

First, we analyzed the fingertip trajectory, success rate, final accuracy, RT, movement duration (MD) and mean tangential velocity ($\mathrm{Vmean}_{\mathrm{endpoint}}$). The final accuracy was measured as the absolute error, i.e., the mean unsigned distance of the final position of the index fingertip relative to the target center along the Z vertical axis. Index position in the sagittal plane was filtered (digital second-order dual-pass Butterworth filter; 6 Hz cutoff frequency) and differentiated to obtain the endpoint tangential velocity in $\mathrm{m.s}^{-1}$. The movement onset was defined as the time when the index tangential velocity reached 1.5% of its peak. Conversely, movement end was defined when the tangential velocity dropped below 1.5% of its peak. Compared to higher cutoff values (5% of peak velocity) reported in other studies performed on land or in microgravity (Papaxanthis et al., 2005; Gentili et al., 2007; Gaveau and Papaxanthis, 2011; Bringoux et al., 2012), this threshold was chosen to avoid underestimation of movement duration considering the task constraints and their behavioral consequences underwater (e.g., slower velocity).

In this study, subjects performed reaching movements characterized by a single-joint arm elevation around the shoulder (i.e., with the arm outstretched). We therefore analyzed the focal component of whole-body reaching movements by considering the arm angular elevation over time (i.e., angle evolution of the extended arm relative to the shoulder with respect to its initial orientation). Arm angular elevation was computed from the index and shoulder XZ raw data, filtered (digital second-order dual-pass Butterworth filter; 6 Hz cutoff frequency) and differentiated to obtain angular velocity. From this, peak velocity ($\mathrm{PV}_{\mathrm{ang}}$ in $\mathrm{deg\,s}^{-1}$) and the relative angular deceleration duration ($\mathrm{rDD}_{\mathrm{ang}}$, defined as the duration between $\mathrm{PV}_{\mathrm{ang}}$ and movement end, in % of movement duration) were extracted.

In parallel, the postural component involved in the whole-body reaching movements (especially to reach the far target) was analyzed by considering trunk displacement. This latter was illustrated by the final angular position of trunk (hip-shoulder segment) relative to vertical ($\beta_f$trunk: trunk flexion in deg) at arm movement end, and by the forward displacement of subjects' shoulder and hip (translation in mm). Shoulder and hip movement onset/end were defined as the time when the translational velocity on the *X* axis respectively reached/dropped below 1.5% of its peak.

Statistical analyzes were based on mean comparisons. Repeated-measures analyses of variances (ANOVAs) were performed to compare the means of kinematic parameters mentioned above after having ensured that the assumption of normality and homogeneity of variance were not violated (Kolmogorov–Smirnov and Levene tests). Newman–Keuls tests were used for post hoc analyses and the significance threshold was set at .05 for all statistical tests.

RESULTS

Potential learning effects

Preliminary analyses investigated potential adaptive processes which might have been at work during a single session (84 trials). Repeated-measures ANOVAs including three Environment (Land, Aqua, AquaS) × 2 Target Position (Close, Far) × 3 Block (Initial, Middle, Final) were initially performed on all the selected parameters. The results did not show any significant main effect of Block or any interaction with the other factors ($p > .05$). Thus, the reported variables did not significantly change along a session depending on the moment of occurrence for a specific set of target presentation (see Experimental procedures). For the sake of clarity and statistical robustness, we thus removed the Block factor from our subsequent analyses.

Upper-limb displacement

We first examined arm displacement toward the targets in each environment. Fig. 2A illustrates endpoint trajectories (i.e., index fingertip) in the sagittal plane observed for a typical subject. It shows that final accuracy was comparable across conditions but that spatio-temporal characteristics of endpoint motion were impacted by the experimental conditions.

Success rate and final accuracy. Subjects never missed any targets (Close or Far), resulting in a 100% success rate in each experimental condition. Moreover, the ANOVA performed on the final accuracy (mean = 7.79 ± 3.65 mm) yielded no significant main effects (Environment: $p = .11$; Target Position: $p = .23$) and no interaction between these two factors ($p = .19$).

Reaction time (RT). The ANOVA performed on RT revealed a significant main effect of Environment ($F(2,14) = 12.60$; $p < .001$). Post-hoc analysis showed

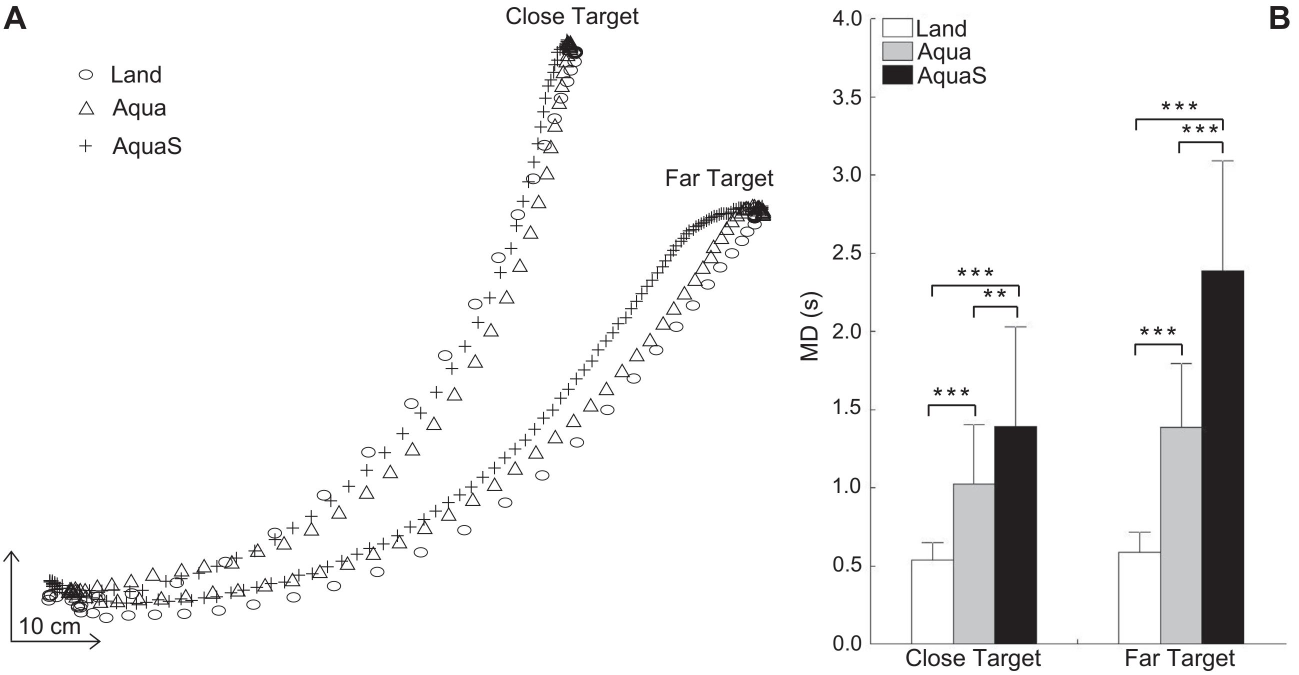

Fig. 2. (A) Representative endpoint trajectories for a typical subject in the sagittal plane in Land (circle), Aqua (triangle) and AquaS (cross) for the Close and Far targets. (B) Mean duration of endpoint movement as a function of Environment and Target Position. Error bars represent standard deviation of the mean. $^{***}p < .001$; $^{**}p < .01$.

more specifically that RT in Land (mean = 313 ± 34 ms) was shorter than in Aqua (mean = 444 ± 138 ms; $p < .01$) and AquaS (mean = 495 ± 115 ms; $p < .001$), while no significant difference was found between Aqua and AquaS regarding this variable ($p = .19$). No other significant main effect or interaction was found with regard to Target Position.

Movement duration (MD) and mean tangential velocity ($Vmean_{endpoint}$). The ANOVA conducted on MD yielded significant main effects of Environment ($F(2,14) = 28.05$; $p < .001$) and Target Position ($F(1,7) = 165.25$; $p < .001$) as well as a significant interaction between these two factors ($F(2,14) = 33.65$; $p < .001$; Fig. 2B). While MD in Land was shorter than in Aqua ($p < .001$) and AquaS ($p < .001$) for both Close and Far targets, MD in AquaS was even longer than in Aqua for the Far target ($p < .001$) as compared to the Close target ($p < .01$).

The ANOVA conducted on $Vmean_{endpoint}$ revealed a significant main effect of Environment ($F(2,14) = 105.57$; $p < .001$). Post hoc analyses showed that the mean tangential velocity differed in each of the three environments (mean = 1.94 m s^{-1}, 0.98 m s^{-1}, and 0.64 m s^{-1}, for Land, Aqua and AquaS respectively; $p < .01$). The analysis also showed a main effect of Target Position (Far target: 1.06 m s^{-1} vs. Close target: 1.31 m s^{-1}; $F(1,7) = 28.03$; $p < .01$). No significant interaction was found between these two factors.

Thus, our experimental conditions did influence the temporal execution of endpoint displacement during whole-body reaching movements. Next, we investigated the relative spatiotemporal organization of the focal component illustrated by the arm angular elevation over time.

Peak angular velocity (PV_{ang}) and relative angular deceleration duration (rDD_{ang}). Fig. 3A illustrates arm angular velocity profiles for both Close and Far targets in each environment. It shows that the experimental conditions appeared to impact the amplitude and the temporal structure of the velocity profiles. These modulations were well reflected by the analysis of PV_{ang} and rDD_{ang}.

The ANOVA conducted on PV_{ang} revealed significant main effects of Environment ($F(2,14) = 53.19$; $p < .001$) and Target Position ($F(1,7) = 28.14$; $p < .01$), as well as a significant interaction between both factors ($F(2,14) = 7.64$; $p < .01$; Fig. 3B). While PV_{ang} in Land was higher than in Aqua ($p < .001$) and AquaS ($p < .001$) for both Close and Far targets, PV_{ang} in AquaS was even lower than in Aqua for the Far target ($p < .001$) as compared to the Close target ($p < .01$).

The ANOVA performed on rDD_{ang} revealed significant main effects of Environment ($F(2,14) = 4.78$; $p < .05$) and Target Position ($F(1,7) = 19.06$; $p < .01$) as well as a significant interaction between these two factors ($F(2,14) = 6.10$; $p < .05$; Fig. 3C). For the Close target, rDD_{ang} was lower in Land than in Aqua ($p < .05$) and AquaS ($p < .05$), but did not significantly differ in the two latter environments ($p = .32$). Conversely for the Far target, rDD_{ang} in Land was lower than in AquaS ($p < .001$), but did not significantly differ from Aqua ($p = .13$). Most importantly, rDD_{ang} in AquaS was significantly higher than in Aqua ($p < .01$).

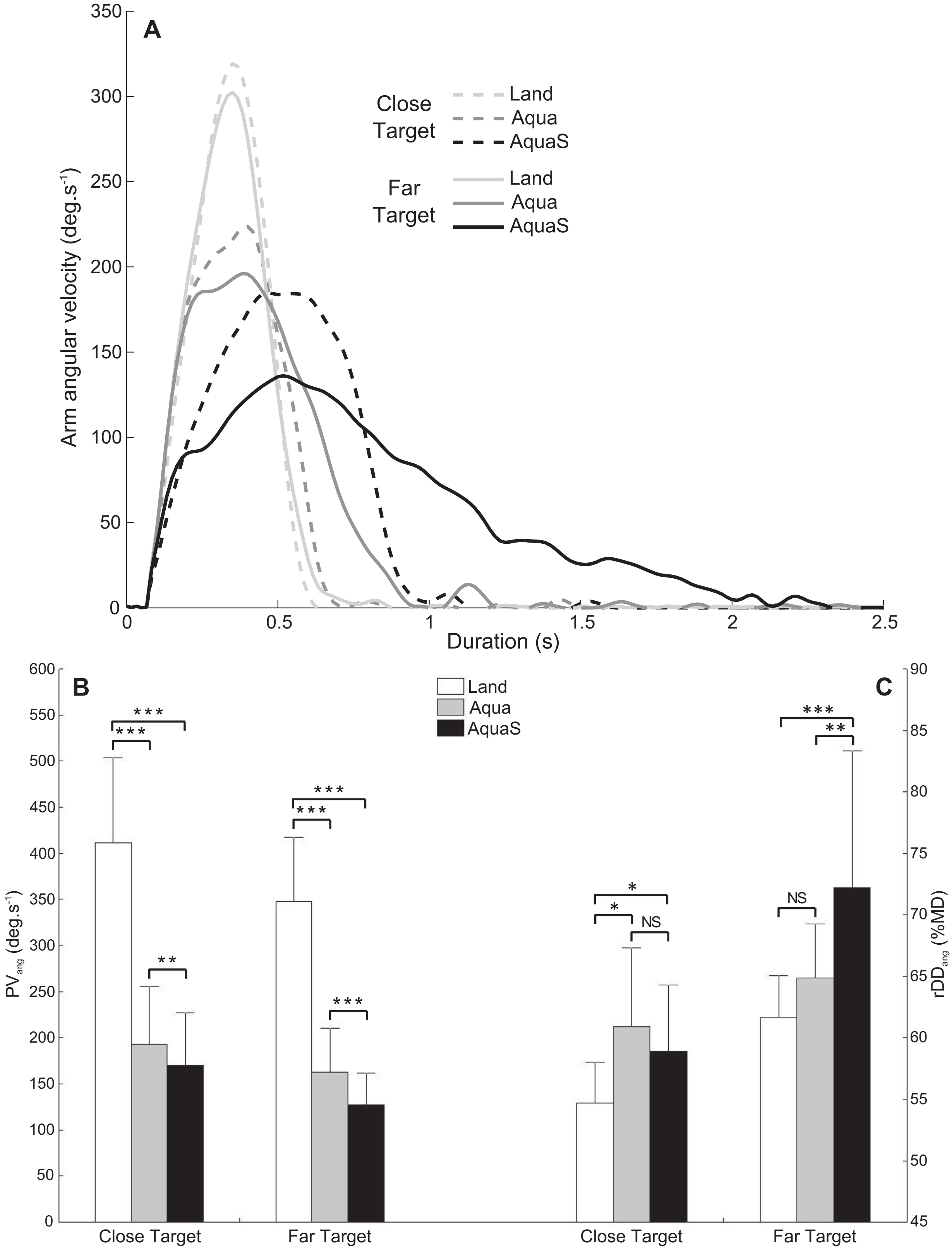

Fig. 3. (A) Representative arm angular velocity profiles for a typical subject in Land (light gray), Aqua (dark gray) and AquaS (black) for the Close and Far targets. (B) Mean arm angular peak velocity (PV) and C) Mean relative angular deceleration duration (rDDang) as a function of Environment and Target Position. Error bars represent standard deviation of the mean. $^{***}p < .001$; $^{**}p < .01$; $^{*}p < .05$; NS: non-significant difference.

Thus, the arm angular elevation reached slower maximal velocities underwater. This effect was accentuated when the neutral buoyancy was applied to body limbs by means of a simulated space suit as compared to when it was applied to the CoM only. In this former underwater condition (AquaS), the relative deceleration duration of arm angular elevation was substantially increased when reaching the Far target, when compared to both Land and Aqua conditions. The next part will focus on the postural component involved in whole-body reaching, especially when reaching the Far target.

Trunk displacement

Final angular position of trunk relative to vertical ($\beta_f$trunk). The ANOVA performed on $\beta_f$trunk revealed main effects of Environment ($F(2,14) = 6.77$; $p < .01$) and Target Position ($F(1,7) = 470.72$; $p < .001$). Moreover, the analysis yielded a significant interaction between these two factors ($F(2,14) = 37.68$; $p < .001$; Fig. 4). While no significant difference appeared between the three environments when reaching toward the Close target ($p > .05$), mean $\beta_f$trunk when reaching toward the Far target was significantly lower in AquaS as compared to Land ($p < .001$) and Aqua ($p < .001$), while no difference was found between these two latter environments ($p = .51$).

Shoulder and hip forward displacements. Unsurprisingly, no noticeable forward translation was observed for shoulder and hip when reaching toward the Close target (located at subjects arm length, see Methods). Although small movements of both joints were recorded during reaching execution, they were below the threshold we used for determining the start and end of a translational displacement. Therefore, we subsequently focused our analysis on the shoulder and hip forward displacements occurring when reaching toward the Far target.

The ANOVA conducted on shoulder displacement yielded a significant main effect of Environment ($F(2,14) = 6.79$; $p < .01$). Post hoc analyses showed that the shoulder displacement in AquaS (mean = 361 mm) was significantly higher than in Land (mean = 301 mm; $p < .01$) and Aqua (mean = 282 mm; $p < .05$) while no significant difference was found between these latter conditions ($p = .41$). Similarly, the ANOVA performed on hip displacement revealed a significant main effect of Environment ($F(2,14) = 34.49$; $p < .001$). Post hoc analyses showed that the hip displacement in AquaS (mean = 331 mm) was significantly higher than in Land (mean = 31 mm; $p < .001$) and Aqua (mean: 27 mm; $p < .001$) while no significant difference was found between these latter conditions ($p = .92$).

Overall, these analyses indicate that the postural involvement differed during whole-body reaching movements as a function of the Environment and Target Position. When neutral buoyancy was applied across the limbs underwater by means of a simulated space suit, reaching toward far targets led to smaller trunk bending associated to larger forward displacements of the shoulder and hip, as compared to land and underwater exposure without specific control of buoyancy across the body segments. The following discussion will address the main focal and postural differences previously reported and will propose possible interpretations for these observations.

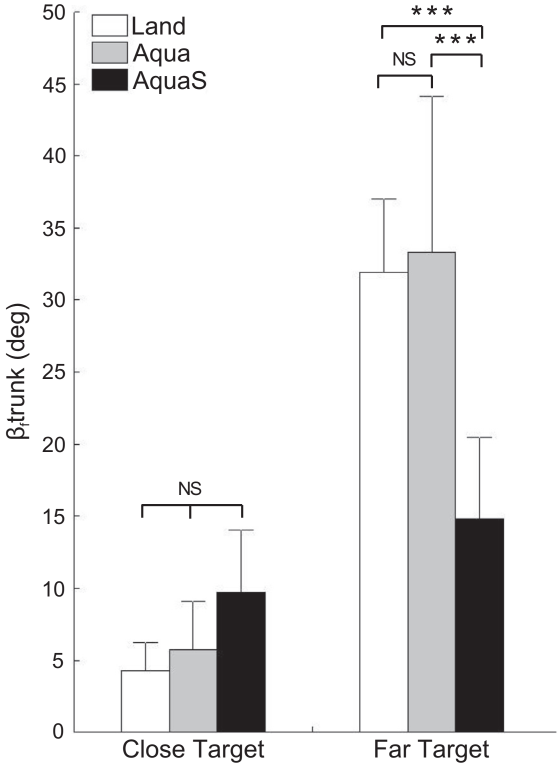

Fig. 4. Mean final angular position of trunk relative to the vertical as a function of Environment and Target Position. Error bars represent standard deviation of the mean. $^{***}p < .001$; NS: non-significant difference.

DISCUSSION

In this study, we investigated the influence of underwater exposure on motor behavior by testing subjects' performance in a whole-body reaching task, compared to a standard land condition. We also questioned the influence of neutral buoyancy and its specific application to body segments, as enabled by the use of a submersible simulated space suit. Analysis of the spatiotemporal characteristics of whole-body reaching movements demonstrated how underwater exposure by itself impacts basic movement features, especially in terms of speed reduction. However, movement kinematics also differed according to the way buoyancy was exerted across body limbs. Remarkably, some parameters reflecting the organization of focal and postural components of whole-body reaching were close to Land observations when neutral buoyancy was not specifically applied to each limb underwater (Aqua condition). Conversely, when subjects were equipped with the submersible simulated space suit, in which neutral buoyancy was exerted across the body segments (AquaS condition), substantial reorganizations of focal and postural components of the movement were found, resembling those reported in microgravity.

Basic influence of underwater exposure on motor behavior

Remarkably, we did not find any significant changes in the reported variables across the successive reaching movements performed underwater, thus suggesting the absence of any significant adaptation taking place during the experiment. Rather, we observed some motor reorganizations which took place at the earliest onset of exposure in Aqua and AquaS. Several hypotheses can be advanced to explain this observation. First, it is possible that the task constraints were not sufficient to yield adaptation along the experiment. Indeed, the subjects immediately succeeded in reaching the intended targets whatever the environment, thus implying no need to change the initial –successful– behavior. Moreover, the participants were all professional divers used to work and move underwater. The amount of experience gained by divers underwater could have been thus detrimental to the occurrence of adaptive effects in the study. However, it must be reminded that none of them had any experience with the submersible simulated space suit. In this latter condition, we could then argue that either the movements performed by the subjects during their installation on the pointing structure or prior expectancies of what it could be to move in a submersible suit favored motor pre-settings for immediate reorganization.

Overall, the substantial decrease of movement speed constitutes the most salient feature of motor reorganization underwater. This was reflected by higher movement duration and lower mean and peak velocity during movement execution, as compared to Land observations. These findings, observed both in Aqua and AquaS, are most likely related to the viscous resistance of the fluid during movement execution (Hoffmann and Chan, 2012). However, we cannot exclude that slowing down could reflect a *pre-established* strategy to face the anticipated disturbances underwater in order to maintain a given level of performance. Following this, the decrease in movement speed could be viewed as a natural response to the increase of task difficulty (i.e., to an unusual force field), according to Fitts' law (Fitts, 1954; Kerr, 1973, 1978). This hypothesis is supported by higher reaction times in Aqua and AquaS, thus suggesting that not only movement execution but also motor planning is modified underwater. This is consistent with a previous study also reporting an increase of reaction time during discrete reaching movements similar to Fitts' task performed in a pool (Dixon, 1985). As mentioned earlier, movement speed reduction, whether it could partly arise from an active reorganization in motor planning at the CNS level or from water resistance, could aim at keeping some aspects of motor performance unaffected. In this regard, we noticed a maximal success rate (100%) and similar final accuracy in Land, Aqua and AquaS. As requested, the subjects have thus favored the spatial constraints of the task, even when facing unusual environments. Interestingly, as we will detail in the following part, keeping this high level of accuracy underwater implied more subtle changes in motor behavior, depending on the way buoyancy is applied across the body and the Target Position to be reached.

Underwater motor features when neutral buoyancy is not specifically applied to body limbs

When participants wore only their diving suit with a weight belt and reached toward the far target, the relative length of deceleration phase of arm angular elevation as well as the final trunk flexion were close to those recorded on land. In other words, the motor behavior exhibited in Aqua may also reflect some spatiotemporal characteristics observed on land when considering the focal and postural components of whole-body reaching.

With regard to the focal component, arm elevation exhibited asymmetric bell-shaped velocity profiles (i.e., the relative deceleration duration of upward arm movements being longer that the relative acceleration duration), in line with previous reports on land (Gentili et al., 2007; Gaveau and Papaxanthis, 2011). Interestingly, while this asymmetry increased in Aqua with respect to Land when reaching toward the close target, it did not differ between these two conditions when reaching toward the far target. In other words, as soon as a postural motion was necessary to perform the whole-body reaching task, the relative spatiotemporal organization of the focal kinematics was comparable between Land and Aqua.

With regard to the postural component involved during whole-body reaching, one may hypothesize that a common postural strategy was used in Land and Aqua, which consisted in bending the trunk forward to assist the focal part of the movement (Massion, 1992; Vernazza et al., 1999). Such a posturo-kinetic strategy was also illustrated in our study by a large forward displacement of the shoulder associated to a very small displacement of the hip to reach the far target, both in Land and Aqua. This would favor equilibrium maintenance at the cost of mechanical energy minimization (i.e., higher absolute work) and joint smoothness maximization (i.e., higher angular jerk). In line with the optimal control theory, the combination of these cost functions (energy/smoothness) has been previously shown to characterize the control of reaching in sitting (Berret et al., 2011) and standing postures (Hilt et al., 2016) on land. The replication of this ''on land-strategy'' underwater, when neutral buoyancy is not specifically applied to body limbs, is also consistent with a study conducted by Massion et al. (1995) who reported a persistence of the terrestrial postural control during movements involving trunk flexion underwater. However, as discussed below, this strategy did not persist underwater when neutral buoyancy was applied across the body segments.

Motor reorganizations associated with distributed neutral buoyancy across body limbs

When neutral buoyancy was applied at the level of each body segment by means of a unique submersible simulated space suit, substantial motor reorganizations were noticed regarding focal kinematics and postural strategy. First, arm elevation in AquaS was characterized by a longer relative deceleration phase as compared to Land and Aqua. Neutral buoyancy homogeneously applied to the whole-body segments substantially changed the force field as compared to ‘‘raw” underwater exposure with the diving suit only. In AquaS, the use of pre-established internal models for sensorimotor planning and execution, acquired on Earth from past experience, may have become irrelevant (Wolpert and Kawato, 1998; Wolpert and Ghahramani, 2000). Also, to be activated, these representations strongly depend on the initial state of the sensorimotor system which provides useful information to elaborate the upcoming motor plan (Starkes et al., 2002; Flanagan et al., 2006; White et al., 2012). Here, the distributed neutral buoyancy in AquaS deeply modified the effect of gravitational force acting on upper limb joints. Several studies demonstrated that gravity is integrated in motor planning and anticipated in terms of expected sensory states (Berret et al., 2008; Crevecoeur et al., 2009; Gaveau et al., 2011, 2014). We therefore suggest that in AquaS, the uncertainty regarding these novel environmental constraints could disrupt the use of predictive mechanisms based on initial state estimates, as the latter could not be related to any previous experience. Accordingly, this would lead to a greater use of feedback processes (Bringoux et al., 2012; Franklin et al., 2012). Supporting this hypothesis, we found lower peak velocity and increased relative deceleration duration in AquaS, which would allow more time for sensory feedback control (Chua and Elliott, 1993; Sarlegna et al., 2003; Terrier et al., 2011). Thus, as feedforward predictions could be insufficient or incorrect in this context, the upregulation of feedback gains could help dealing with the unexpected disturbances and maintain movement accuracy (Franklin et al., 2012).

A second main finding relates to the postural reorganization observed in AquaS. Subjects seemed to adopt a new postural strategy illustrated in our study by a smaller trunk flexion than in Land and Aqua to reach the far target. This smaller trunk flexion suggests a whole-body forward displacement which would correspond to the ankle strategy evoked by Nashner and McCollum (1985), though with greater amplitude. In our study, this is supported by larger hip and shoulder forward displacements in AquaS than in Land and Aqua (while no significant difference was observed between these latter conditions). Such a strategy may help reducing the degrees of freedom (Bernstein, 1967) by minimizing the number of ‘free-to-move’ joints. Moreover, it could also minimize the mechanical energy expenditure and maximize joint smoothness, in line with the optimal control theory (Berret et al., 2011). The combination of these cost functions would thus enable the postural component to support more efficiently the focal part of the reaching movement. According to Hilt et al. (2016), a postural strategy based on whole-body forward displacement reduces the equilibrium safety margin in land. In AquaS however, the neutral buoyancy applied across the whole-body seems to decrease the gravitational constraints and the risk of falling, even when the CoM projection was presumably outside the base of support. Therefore, the postural strategy specifically used in this condition may reflect the interactions between cost functions which led to a tradeoff between efficient reaching and equilibrium maintenance (Hilt et al., 2016).

Behavioral similarities between AquaS and microgravity: a perspective of motor transfer?

As compared to Land observations, underwater exposure resulted in a decrease of movement speed which appears to be greater than that usually reported in weightlessness (Berger et al., 1997; Papaxanthis et al., 2005). This observation may be mainly explained by the additional presence of fluid resistance underwater (Hoffmann and Chan, 2012). However, when focusing on the kinematics of arm elevation normalized with respect to movement duration, similar reorganizations could be pointed out between AquaS and microgravity. Indeed, we previously reported an increase of the normalized deceleration phase of arm elevation in microgravity comparable to that observed here in AquaS (Bringoux et al., 2012). This longer relative deceleration phase would allow for a greater use of feedback corrective processes to compensate for incorrect initial state estimates prior to movement onset. Indeed, the simulation of a gravity-like shoulder torque in weightlessness, by means of elastic bands attached to the forearm, has been found to provide sufficient prior information to reactivate gravity-related internal models and thus restore kinematics and final accuracy of arm reaching (Bringoux et al., 2012).

Casellato et al. (2012) observed that when reaching movements required trunk mobilization in microgravity (whole-body reaching), subjects adopted a new postural strategy illustrated by a whole-body forward displacement toward the target, as in the present study. In Casellato et al. (2012) study, a biomechanical model revealed that this strategy was based on a CoM projection beyond the base of support. Notably, the subjects were not constrained by the gravitational force which would impose a reduction of the displacement of the CoM projection by some compensatory mechanisms. These main postural features led Casellato et al. (2012) to suggest the existence of an ‘‘oversimplification” of postural control to perform reaching movements. This would favor the fine control of the focal component during whole-body reaching, ensuring its final accuracy despite the degraded initial state estimates. We here postulate that similar processes were operating underwater when the subjects where immersed in the simulated space suit (AquaS).

The behavioral similarities that could be reported between AquaS and the microgravity environment strongly suggest that the neutral buoyancy, when uniformly exerted across the whole-body, could help reproducing a microgravity-like environment, despite the presence of additional fluid resistance. In the framework of astronauts’ training, it could be of value to test whether motor skills learned in this particular immersive environment could be transferred and used during extra-vehicular activities in space. Likely, a fine control of buoyancy across the whole-body may be advantageous to underwater training methods, by providing a more realistic EVA environment. Most importantly, the motor reorganizations observed in AquaS were observed at the early stage of exposure to the novel environmental constraints, and thus may not require adaptive processes to become functional. The occurrence of such early functional motor reorganizations must however be challenged in tasks involving higher accuracy constraints and tested with less experienced divers.

CONCLUSION

Although underwater exposure by itself influences some basic features of motor behavior during arm reaching movements as compared to land observations, the present study shows that some focal and postural components of the motor output underwater remain close to standard normogravity behavior when neutral buoyancy is not exerted across whole-body segments. On the contrary, when neutral buoyancy is applied to each body limb, by means of a submersible simulated space suit, subjects tend to produce focal and postural kinematics close to those observed in weightlessness. In other words, the fine control of neutral buoyancy, may improve the quality of the simulation of microgravity environments, thus optimizing astronauts' training before space missions.

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