Temporal Processing of Saccade Targets in Parietal Cortex Area LIP During Visual Search

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Thomas NW, Paré M. Temporal processing of saccade targets in parietal cortex area LIP during visual search. *J Neurophysiol* 97: 942–947, 2007. First published November 1, 2006; doi:10.1152/jn.00413.2006. We studied whether the lateral intraparietal (LIP) area—a subdivision of parietal cortex anatomically interposed between visual cortical areas and saccade executive centers—contains neurons with activity patterns sufficient to contribute to the active process of selecting saccade targets in visual search. Visually responsive neurons were recorded while monkeys searched for a color-different target presented concurrently with seven distractors evenly distributed in a circular search array. We found that LIP neurons initially responded indiscriminately to the presentation of a visual stimulus in their response fields, regardless of its feature and identity. Their activation nevertheless evolved to signal the search target before saccade initiation: an ideal observer could reliably discriminate the target from the individual activation of 60% of neurons, on average, 138 ms after stimulus presentation and 26 ms before saccade initiation. Importantly, the timing of LIP neuronal discrimination varied proportionally with reaction times. These findings suggest that LIP activity reflects the selection of both the search target and the targeting saccade during active visual search.

INTRODUCTION

Saccade target selection entails an initial scene analysis that directs visual attention to a salient target and the subsequent planning of a saccade (Schall and Thompson 1999). Using the visual search paradigm—the search of a visual target among distractors—neurophysiological studies in monkeys have shown that these processes are reflected in the activity of neuronal populations in both the frontal eye field (FEF; Thompson et al. 1996) and the intermediate layers of the superior colliculus (SC; McPeek and Keller 2002). The dual capability of parietal cortex area lateral intraparietal (LIP) to integrate visual signals (Andersen et al. 1990; Baizer et al. 1991) and impact saccade executive centers (Ferraina et al. 2002; Paré and Wurtz 1997) puts it in an excellent position to participate in selecting saccade targets during visual search. Several studies using instructed delayed saccade tasks have already implicated area LIP in selective visual attention (Colby and Goldberg 1999) and saccade planning (Andersen et al. 1997; Platt and Glimcher 1997). Furthermore, Wardak et al. (2002) recently reported that visual search behavior is particularly impaired when area LIP is pharmacologically inactivated. Finally, visual search performance in humans has also been shown to depend on the integrity of the parietal cortex (Arguin et al. 1993; Ashbridge et al. 1997; Eglin et al. 1989).

Despite this body of evidence, the exact contribution of area LIP to the active process underlying saccade target selection in visual search is not known. We studied LIP neuronal activity during a color search task to gain insights into the temporal aspects of this process. Portions of this work were presented in abstract form (Paré 2001; Thomas and Paré 2005).

METHODS

Surgical and experimental procedures

Data were collected from two female rhesus monkeys (*Macaca mulatta*, 5–7 kg), cared for with protocols approved by Queen's University Animal Care Committee and in accordance with the Canadian Council on Animal Care guidelines and the U.S. Public Health Service Policy on the humane care and use of laboratory animals.

The surgical procedure, stimulus presentation, data acquisition, and behavioral data analyses have been described in detail (Shen and Paré 2006). To record from neurons within the lateral bank of the intraparietal sulcus, a recording cylinder tilted 30° lateral of vertical was positioned over a hole trephined in the right hemisphere and centered on stereotaxic coordinates P 5.0 and L 12.0 mm. Monkeys received both antibiotics and analgesic medications during the postsurgery recovery period, after which they were trained with operant conditioning and positive reinforcement to perform fixation and saccade tasks for a liquid reward until satiation.

We used previously described techniques (Paré and Wurtz 2001) to record the extracellular activity of single LIP neurons. Spike occurrences were sampled at 1 kHz, along with the gaze position measured with either magnetic search coils (DNI, Newark, DE) or high-speed infrared cameras (Eyelink II, SR Research, Osgoode, Ontario, Canada).

Behavioral paradigms

The discharge properties of LIP neurons were first characterized while the monkey performed the visual delayed saccade task described in Paré and Wurtz (2001). The main data of this report were collected while the monkey performed a visual search task based on color discrimination and described in Shen and Paré (2006). After sustained fixation (500–800 ms) of a central fixation spot, the latter disappeared simultaneously with the appearance of a concentric array of one target stimulus and seven distractor stimuli equidistant from each other on a dark background (<0.01 cd/m²). The target randomly appeared at each stimulus location with equal probability. We collected ≥10 target trials at each stimulus position; ~40 trials per position were, on average, collected in the ensemble of the recording sessions. The target was circular and identical in shape, size, and

luminance (25 cd/m^2) to the distractors, but randomly assigned to be either red (CIE: $x = 0.61$, $y = 0.38$) or green ($x = 0.20$, $y = 0.75$), and the distractors were green or red, respectively. The monkey was given 500 ms to respond with a saccade to the search display presentation. A single correct saccade landing on the search target and its subsequent fixation for 200–300 ms yielded a full liquid reward. If the first saccade was erroneously directed to a distractor, the monkey was given an extra 2,000 ms to foveate the target with additional saccades and received a partial reward, which amounted to no more than one third of the full reward; all liquid rewards were delivered with an auditory reinforcement tone. This visual search task therefore did not stress accuracy as much as in previous monkey studies (McPeek and Keller 2002; Schall et al. 1995; Thompson et al. 1996), but the probability that the first saccade correctly landed on target was nevertheless high: 0.85 ± 0.10 (SD) across the recording sessions that constitute this report ($n = 50$). Although all these visual search tasks involve target foveation, the difference in reward contingency seems to be significant enough to promote different saccade strategies. We have recently presented evidence that saccades made by our animals can be viewed as rather "automatic" responses to the presentation of the search display because their latencies vary with neither the number of visual stimuli nor the difficulty of the search task (Shen and Paré 2006). The independence of these responses from visual context suggests that the visual behavior of these monkeys was less constrained than in previous studies.

An additional detection task was used to determine how activity related to the discrimination of a visual stimulus in the search array differs from that associated with the detection of a single stimulus. As in the visual search task, and unlike the delayed saccade task, the detection task stimulus was either green or red, and it was presented at one of the eight positions simultaneously with the disappearance of the central fixation spot. In all tasks, the stimulus size was scaled with the eccentricity of the response field and in proportion to striate cortex receptive field magnification (Van Essen et al. 1984): from 0.4° of visual angle at 5° of eccentricity to 1° of visual angle at 10° of eccentricity and 2.4° of visual angle at 20° of eccentricity.

Data analysis

We visualized the neuronal activation by building rasters of neuronal discharge and continuously varying spike density functions aligned on either the onset time of the visual stimulus presented in the neuron's response field or the onset of the first saccade. Spike density functions were constructed by convolving spike trains with a combination of growth (1-ms time constant) and decay (20-ms time constant) exponential functions that resembled a postsynaptic potential (Thompson et al. 1996). The initial, visually evoked response was defined as the mean value of the first 25 ms of activation, starting when the spike density function exceeded the mean baseline discharge rate by 3 SD (last 50 ms of activation before stimulus onset). The late, presaccade activity was defined as the mean value of the last 25 ms of activation before saccade initiation.

We used Signal Detection Theory (Green and Swets 1966) to determine how well an ideal observer of LIP activity can discriminate the target from distractors by estimating (during successive 5-ms intervals) the separation between the distribution of activity in target and distractor trials from the area under receiver operating characteristic (ROC) curves (Thompson et al. 1996); distractor trials were trials in which the target was at one of the three most distant positions from the response field. We quantified the time-course of neuronal discrimination by fitting the area under the ROC curves as a function of time with a Weibull function: $W(t) = \gamma - (\gamma - \delta) \times \exp[-(t/\alpha)^{\beta}]$, where t is time after stimulus onset, α is the time at which the function reaches 64% of its full growth, β is the slope, γ is the upper limit of the function, and δ is the lower limit of the function. The time at which the Weibull function reached the arbitrary criterion of 0.75 was taken as the time at which the neuron reliably discriminated the target

[discrimination time (DT)], whereas the upper limit (γ) defined the discrimination magnitude. A rank sum test was concurrently calculated for each of the same 5-ms intervals to determine the time at which the difference in neuronal activity between target and distractor trials reached statistical significance ($P < 0.01$). Only correct trials were considered in all analyses.

RESULTS

We studied the activity of 50 LIP neurons in two monkeys (42 in *monkey G* and 8 in *monkey F*). The discharge properties of these neurons in the visual delayed saccade task were comparable with those reported by Paré and Wurtz (2001). All neurons showed visually evoked responses within 100 ms of the onset of the visual stimulus in their response fields, which were restricted to the visual hemifield contralateral to the recording hemisphere. These initial responses remained sustained during the delay period, and the level of the activity before saccades (100 ms before saccade onset) was significantly greater (rank sum test, $P < 0.05$) than the corresponding delay activity (300-ms epoch before fixation spot disappearance) for 56% (28/50) of neurons.

We also calculated a visuo-movement index (VMI) to quantify the relative magnitude of visually evoked and saccade-related activity measured in the visual delayed saccade task and identify where each neuron in the sample was situated along the visuo-movement axis: $VMI = (vis - mov)/(vis + mov)$, where *vis* is the peak activity within 100 ms of visual stimulation (mean = 129 Hz, range = 17–370 Hz) and *mov* is the peak activity within ±40 ms of saccade initiation (mean = 114 Hz, range = 32–238) in the delayed saccade task. Neurons with stronger visually evoked responses would have a VMI closer to 1.0 and those with stronger saccade-related activity would have a VMI closer to -1.0. The mean VMI value of the neuronal sample was 0.04 ± 0.03 (SE; range = -0.49 to 0.57).

Figure 1 shows the activation of one representative LIP neuron in detection (Fig. 1, *A* and *C*) and visual search (Fig. 1, *B* and *D*) trials. In the detection task, the initial visually evoked responses were significantly tuned with respect to target direction. In the search task, the visually evoked responses were not significantly modulated by target direction, and their magnitudes were independent of whether the visual stimulus was a target or a distractor (Fig. 2*A*, open symbols; paired *t*-test, $P = 0.09$) and whether it was green or red (paired *t*-test, $P = 0.16$). These initial responses were, however, attenuated by, on average, 28% compared with those in the detection task (mean = 57 vs. 80 Hz; paired *t*-test, $P < 0.001$); even though the mean latency of the activation did not vary between detection and search tasks. The late presaccade activity (last 25 ms of activation before saccade initiation) also showed a significant, albeit weaker, attenuation (mean = 106 vs. 118 Hz; paired *t*-test, $P = 0.003$), suggesting that significant visual processing continues to take place until saccade initiation.[1]

Before the first saccades made in response to the search array, the neuronal activation eventually evolved to signal the presence of the search target in the neurons' response field: activity associated with the target became enhanced (Fig. 1*B*),

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[1] Significant attenuation was observed not only when measuring neuronal activity during a 25-ms interval before saccade onset but also during a 10-ms interval before saccade onset (an interval close to the LIP efferent delay), as well as when the decay time constant of the spike density function was set to 1 ms.
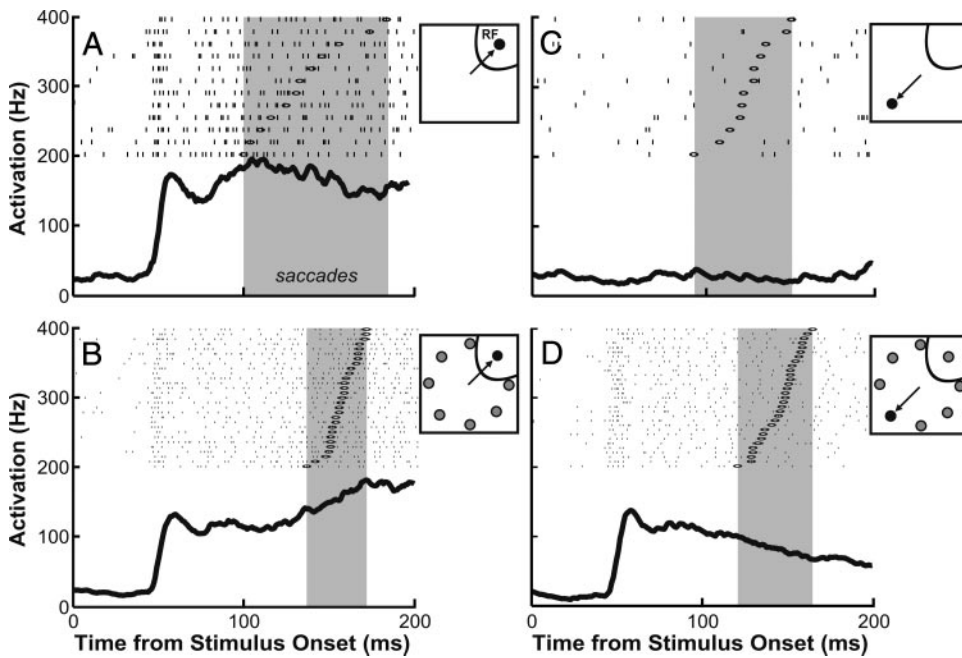
FIG. 1. Spike density functions and rasters of spike occurrences from 1 lateral intraparietal (LIP) neuron shown as a function of time in detection (*A* and *C*) and visual search (*B* and *D*) trials, in which the target appeared in the neuron's response field (*A* and *B*) or in a diametrically opposite position (*C* and *D*). Trials are rank-ordered according to saccade reaction times.

whereas that associated with distractors became suppressed (Fig. 1*D*). To quantify this discrimination process, we first examined the activation just before the initiation of correct saccades. Unlike their visual responses, the presaccade activity of LIP neurons was significantly tuned with respect to target direction, being significantly greater in target trials compared

with distractor trials (Fig. 2*A*, filled symbols; mean = 106 vs. 64 Hz; paired *t*-test, $P < 0.0001$).

According to the ideal observer analysis, the probability of discriminating the target from distractor stimuli for these neurons grew from chance level (0.5) during the initial activation to an asymptotic magnitude that fell short of perfect discrim-
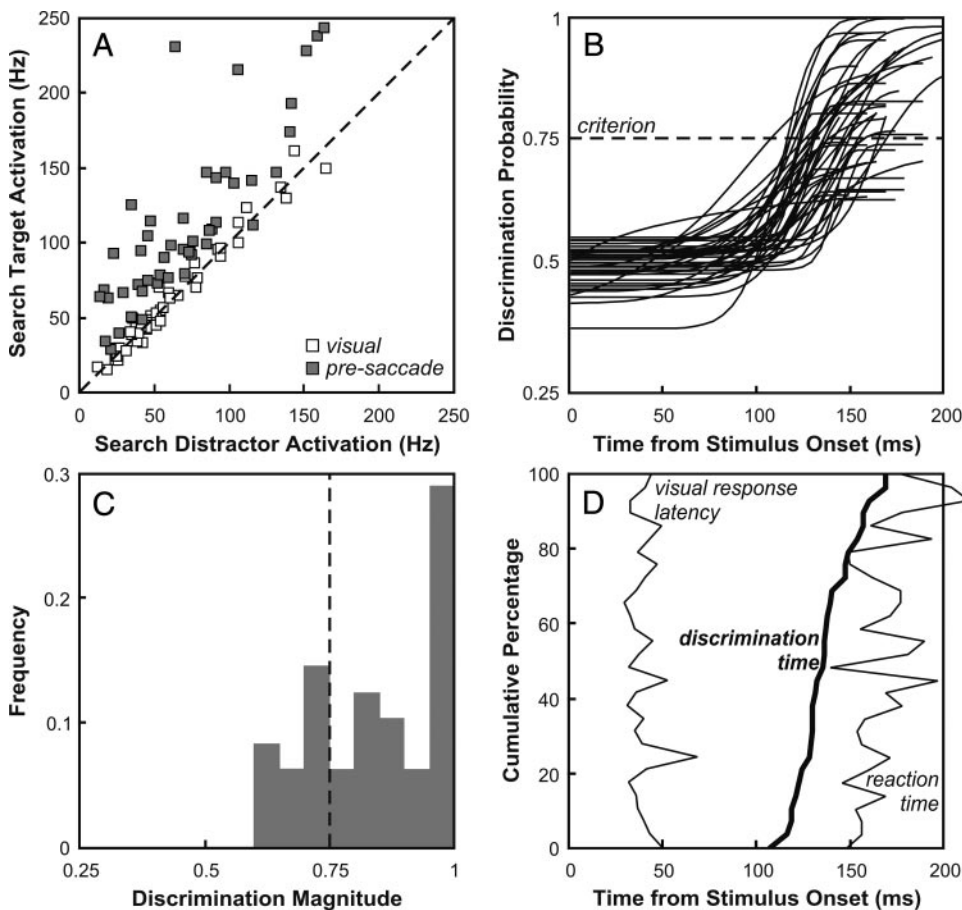

FIG. 2. *A*: Scatterplots of LIP neuronal activation in target trials against that in distractor trials (with target at a position opposite to response field) in visual search task ($n = 50$). *B*: time-course of discrimination probability (best-fit Weibull functions) from ideal observer analysis conducted on neurons with statistically (rank sum test, $P < 0.01$) greater activity in target trials ($n = 46$; r^2: mean = 0.85, range = 0.30–0.99). Functions were calculated only with activity before saccade onset and terminated when there were <5 target and distractor trials. The reaction time ranges for the 2 sets of trials were matched. *C*: distribution of discrimination magnitudes for neurons shown in *B*. *D*: distribution of discrimination times, along with the latency of visually evoked responses and saccade reaction times, for neurons with discrimination magnitudes exceeding criterion of 0.75 ($n = 30$).

ination (1.0), which would indicate distinct and greater target-related activity than distractor-related activity (Fig. 2B). The discrimination magnitude of our neuronal sample ranged from 0.40 to 1.0, with a mean of 0.81 ± 0.02, and it exceeded the criterion of 0.75 in 60% (30/50) of the neurons (Fig. 2C) at a time that did not exceed the mean reaction time (RT) of the monkey. The discrimination time (DT) of these 30 neurons ranged from 108 to 170 ms and occurred, on average, 138 ± 2.9 ms after stimulus presentation, 98 ± 3.3 ms after the onset of the initial visual response, and 32 ± 3.0 ms before saccade initiation (Fig. 3D); the DT obtained with neuronal activity aligned on the time of saccade initiation averaged 26 ± 3.3 ms. In the trials considered by this analysis, RT ranged from 122 to 249 ms, whereas the mean RT in individual sessions averaged 169 ± 3.3 ms and the probability that the first saccade correctly landed on target averaged 0.86 ± 0.02.

At the time of neuronal discrimination, the difference between activity in target and distractor trials was statistically different (rank sum test, $P < 0.01$) for all but 3 of those 30 neurons that reached the ROC criterion. Overall, all but four neurons of our sample ($n = 46$) were found to have statistically significant discriminating activity before saccade initiation. The time at which these 46 neurons reached significance was, on average, 132 ± 2.3 ms after stimulus presentation (range = 105–180 ms), 90 ± 2.7 ms after the initial visual response, and 34 ± 2.7 ms before saccade initiation. RT ranged from 122 to 249 ms in the trials considered in this analysis, and the mean RT in individual session averaged 166 ± 2.7 ms.

To determine the relationship between LIP neuronal discrimination and saccade initiation, we segregated trials into equal-sized groups of short or long RT trials, computed DT separately for each RT group, and calculated the slope of the curve connecting the paired DT-RT values (Fig. 3A). This analysis was done on 28 of the 30 LIP neurons that had discrimination magnitude >0.75; two neurons were excluded because DT could not be computed for both RT groups. Figure 3B shows that the distribution of the DT/RT slopes aligned on target presentation was unimodal and not significantly different from 1.0 (mean = 1.1 ± 0.1; t-test, $P = 0.56$), but it was significantly different from 0.0 ($P < 0.0001$). Consistent with this finding, the distribution of DT/RT slopes with activity aligned on the time of saccade initiation (Fig. 3, C and D) was not significantly different from 0.0 (mean = 0.1 ± 0.2; t-test, $P = 0.57$), but it was significantly different from −1.0 ($P < 0.0001$). LIP neuronal discrimination predicted saccade initiation.

The temporal aspects of the saccade target selection process observed in LIP neurons during visual search was a product of neither the discharge properties of an individual neuron nor its position on the visuo-movement axis. There was no significant correlation between individual DT/RT slopes and VMI ($r^2 = 0.02$; F-test, $P = 0.52$). In addition, the variance in DT/RT slopes could be accounted for by neither the peak visual activity ($P = 0.92$) nor the peak saccade activity ($P = 0.43$) measured in the delayed saccade task. We also found no correlation between DT and VMI ($P = 0.50$), visual activity
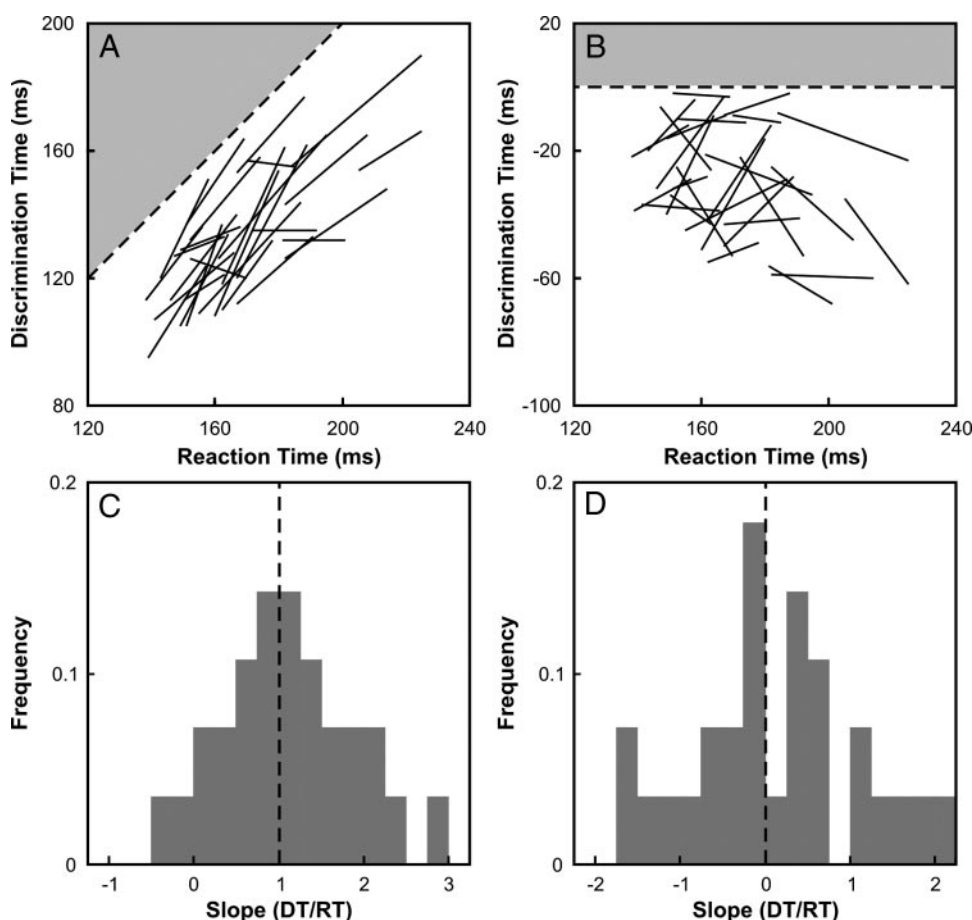

FIG. 3. Plots of discrimination times of short and long reaction time groups for activity aligned on stimulus onset (A) and saccade onset (B); shaded areas indicate time after saccade initiation. Distribution of slopes of relationship between discrimination time and reaction time for activity aligned on stimulus onset (C) and saccade onset (D). Data are from neurons with discrimination magnitude exceeding 0.75 in both reaction time groups ($n = 28$).

($P = 0.40$), or saccade activity ($P = 0.11$). However, the saccade activity of LIP neurons did predict their discrimination magnitudes ($r^2 = 0.17$; F-test, $P = 0.003$): the larger the saccade activity, the larger the discrimination.

DISCUSSION

We showed that, during a visual feature search task based on color discrimination, LIP neurons initially exhibited nonselective activation that in the majority of neurons evolved to reliably signal the search target at a fixed time before saccade initiation. Previous evidence that LIP neuronal activity evolves to discriminate visual stimuli was obtained with instructed, delayed saccade tasks (Paré and Wurtz 2001; Platt and Glimcher 1997; Toth and Assad 2002). Our observation that LIP activity represents all visual stimuli until a saccade goal is selected is consistent with these reports. Others have found LIP neurons to have negligible responses when visual stimuli are brought into their response fields by saccades unless the stimuli were cued, i.e., made behaviorally relevant (Gottlieb et al. 1998). The conclusion reached by these authors that area LIP contains a generally weak representation of the visual world except for salient stimuli may, however, only apply to conditions in which neuronal activity reflects the outcome of the already completed saccade target selection process, i.e., after the distractor representations have been suppressed. Our study adds to these previous studies of area LIP by documenting the time-course of this selection process during an active visual search task, in which the saccade target is specified by conspicuity.

Given the functional connection of area LIP with both the FEF and the intermediate layers of the SC (Ferraina et al. 2002; Paré and Wurtz 1997), the neuronal modulation we observed could be responsible for that reported in these brain regions during similar visual search tasks (McPeek and Keller 2002; Schall et al. 1995; Thompson et al. 1996). The direct comparison, afforded by the common ROC analysis used in all these studies, reveals that neurons across these brain regions reliably discriminate target from distractors with similar timing relative to the search display presentation [FEF: 140 ms, Thompson et al. 1996 (Table 1); SC: 138 ms, McPeek and Keller 2002 (exact figures graciously provided by R. M. McPeek); LIP: 138 ms]. However, FEF and SC neurons seem to discriminate in greater proportion and at earlier times with respect to saccade initiation [FEF: 78% and 53 ms; SC: 98% and 45 ms; LIP: 60% and 26 ms]. These proportion and timing differences could be caused by the shorter reaction times that we observed [FEF: 192 ms; SC: 189 ms; LIP: 169 ms], which could have provided insufficient time for neurons to reach criterion, even though the accuracy of the monkeys' responses were high. Alternatively, these differences could indicate a less efficient selection process in LIP, even though the discrimination in nearly all neurons was statistically significant. Despite these comparative differences, our finding indicates that LIP neurons have activity patterns sufficient to contribute to the active process of selecting saccade targets in visual search. This conclusion was also reached by a recently published study (Ipata et al. 2006), but the different analysis used by these authors did not permit a direct comparison with FEF and SC data. Their visual search task was also very different from the task used here, as well as in previous FEF and SC studies, in that it requested a manual response instead of target foveation, which eventually occurred after multiple saccades. Given these significant differences in task design and performance, the converging observations of these authors bolster our results.

Previous studies reported bimodal distributions of DT/RT slopes in FEF (Sato and Schall 2003; Thompson et al. 1996) and SC (McPeek and Keller 2002), which were interpreted as evidence that the selection of the search target (invariant DT, slope = 0.0) and targeting saccade (DT predictive of RT, slope = 1.0) was reflected in distinct populations of neurons. It could be that our neuronal sample is predominantly made of layer-five pyramidal neurons, because their larger sizes bias sampling. Since these neurons preferentially project to SC (Ferraina et al. 2002) and that many SC neurons have DT/RT slopes close to 1.0 (McPeek and Keller 2002), one could thus have expected the unimodal distribution of DT/RT slopes centered on 1.0 that we observed. This hypothesis is, however, at odds with the finding of Paré and Wurtz (1997 2001) that LIP neurons projecting to the SC do not have functionally distinct properties that are shared with SC neurons. The relatively small sample size of this study ($n = 28$) may also limit our conclusion, and whether a second mode of DT/RT slopes centered on 0.0 does exist will necessitate additional recording. Although Ipata et al. (2006) also obtained similar results with a larger sample ($n = 40$), the aforementioned differences in task design and performance render premature the conclusion that the role of area LIP in active visual search is limited to the selection of saccades. Rather, the dependence of LIP presaccade activity on the presence of additional stimuli within the search array suggests that LIP neuronal activity reflects both visual and saccade processing during the visual search task that we implemented. Perhaps the unconstrained nature of this visual search task does not allow visual and saccade selection processes to be dissociated, an alternative hypothesis consistent with the idea that the selective deployment of visual attention is not temporally distinct from the selection of the next saccade during free-viewing behavior (Findlay and Gilchrist 2003).

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