14 Saccade target selection in unconstrained visual search

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Our visual system is regularly faced with more information than it can process at once. As a result, our visual experience generally arises from the sequential sampling of visual details by overtly shifting perceptual resources through reorienting the fovea with saccadic eye movements. An emerging view is that this natural visual behavior can be promoted in visual search tasks that do not emphasize accuracy over speed. Here we review recent neurophysiological findings, which were obtained with such an approach, showing that the process of selecting a saccade target involves neurons within the "vision-for-action" processing stream of the cerebral cortex of monkeys. The visual responses of these posterior parietal cortex neurons evolve to signal both where the search target is located and when the targeting saccade will be made. Consistent with the involvement of attentional processes in saccade target selection, the magnitude of the enhancement of parietal activity in advance of a search saccade parallels what has been reported in neurons within the ventral "object-recognition" pathway when attention is covertly allocated.

14.1 Introduction

We see the world by shifting our perceptual resources either covertly by allocating visual attention to peripheral locations or overtly by reorienting the fovea with saccadic eye movements. Although these two processes can operate independently – it is undeniable that we can mentally scan a visual scene without moving our eyes (e.g., Sperling and Melchner, 1978) – experimental evidence suggests that they may be functionally coupled: shifting attention covertly to a spatial location facilitates the processing of saccades directed to that location, whereas planning a saccade to a spatial location facilitates perceptual processing of objects at that location (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996). Furthermore, the high rate of

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Cortical Mechanisms of Vision, ed. M. Jenkin and L. R. Harris. Published by Cambridge University Press.

saccades in natural tasks such as visual search, text reading and scene perception suggests that there are few attentional shifts besides those associated with the execution of saccades when the eyes are free to move (for a review see Findlay and Gilchrist, 2003). The current view that has emerged from these studies is that covert orienting may only assist overt orienting by analyzing the visual periphery during fixation intervals and contributing to the selection of the goal of each saccade (see Henderson, 1992; Schneider, 1995). Such a functional coupling between covert and overt shifts of attention may result from the overlapping of their respective neural circuits (Nobre et al., 1997; Corbetta et al., 1998) and from the massive connections between brain areas with visual and oculomotor functions (Schall et al., 1995a). Consistent with this interconnectivity, voluntary shifts in visual attention are associated with enhanced neural activity not only in visual cortical areas but also in the brain regions essential for saccade production: the frontal eye field (FEF) and the superior colliculus (SC) (see for review Moore et al., 2003; Awh et al., 2006).

A different picture has, however, emerged from studies that examined this coupling with controlled tasks that promote natural visual behavior, such as the visual search paradigm. Neurophysiological findings in FEF and SC studies with monkeys performing various visual search tasks suggest a dissociation of covert and overt processes. First, the activity of visually responsive neurons reflects the process of selecting a salient stimulus even when monkeys withhold directing their gaze to it (FEF: Schall et al., 1995b; Thompson et al., 1997, 2005a, b) or direct their gaze away from it (FEF: Murthy et al., 2001; Sato et al., 2001; Sato and Schall, 2003; SC: Shen and Paré, 2007). Second, the allocation of visual attention to the target and the subsequent planning of the saccade appear to correspond to the selective activity of distinct neuronal populations within both the FEF (Thompson et al., 1996; Sato and Schall, 2003) and the SC (McPeek and Keller, 2002). Although these findings are very valuable, as they inform us about the neural signatures of the sequential unfolding of decision processing stages that experimental psychology has long identified (e.g., Theios, 1975; Allport, 1987; Laberge and Brown, 1989; Schall and Thompson, 1999), they are difficult to reconcile with the idea that covert attention only assists overt orienting during free viewing of visual scenes.

It is reasonable to presume that this uncoupling of covert and overt processes in the above studies is an outcome of the constrained nature of the visual search tasks that were used. Given their emphasis on accuracy, these tasks explicitly enforced the strategy to withhold the rapid orienting behavior that is frequently observed in response to the presentation of visual search displays (Findlay, 1997; Williams et al., 1997; Maioli et al., 2001). In sum, the very different response times observed in discrimination tasks when accuracy versus speed is emphasized must reflect different strategies and increased accuracy demands may require extensive training that can modify the neural substrate of the behavior. Here we review recent studies from our laboratory, as well as others, that have investigated the brain mechanisms underlying saccade target selection in visual search tasks that are less constrained than in previous monkey studies.

14.2 Automatic responses during visual search

The visual search paradigm has been developed to study the deployment of visual attention in humans (see for review Wolfe and Horowitz, 2004). This approach requires subjects to indicate the presence of a search target within a multi-stimulus display with a manual response without them being instructed to foveate that target, but several studies have also monitored where subjects look while performing this task (e.g., Binello et al., 1995; Zelinsky and Sheinberg, 1995; Williams et al., 1997; Scialfa and Joffe, 1998; Maioli et al., 2001). Generally, the number of saccades is highly correlated with the time it takes to report the presence of the search target. The latency of the initial response to the search display, however, does not necessarily vary with task difficulty. In contrast, previous monkey studies have required the explicit foveation of the search target after a single saccade and they have reported longer response times with increasing task difficulty (Bichot and Schall, 1999; Buracas and Albright, 1999; Sato et al., 2001; Thompson et al., 2005a; but see Motter and Belky, 1998a).

To study the processes underlying the deployment of visual attention and the guidance of saccades during natural visual behavior, and to reconcile the differences between the human and monkey visual search literature, Shen and Paré (2006) examined the gaze behavior of monkeys trained to perform visual search tasks more akin to the human studies. These experiments did not demand high immediate performance accuracy and thus required relatively little training. Monkeys had to foveate a target stimulus and they received a full liquid reward (and a reinforcement tone) if their first saccade landed on that stimulus. Nevertheless, they were granted a generous length of time (>2 s) to freely visit whichever stimuli they wished to examine. In those trials, in which they foveated the target after sever saccades they received a partial reward, which amounted practically to only the reinforcement tone. In all tasks, the target was identified either solely by color (Fig. 14.1A) or by a conjunction of color and shape (Fig. 14.1B).

Human performance studies have shown that the search for a target stimulus defined by a conjunction of features is typically less efficient than when that target is defined by a single feature and performance is usually impaired by the addition of distractors, as if the display stimuli were being processed serially (Treisman and Gelade, 1980). In line with these previous observations from human subjects, Shen and Paré (2006) found that monkey's search time – the total amount of time needed to foveate the target – was longer during conjunction search and lengthened with increasing display size, whereas it remained unchanged by display size in feature search (Fig. 14.2A). Correspondingly, the accuracy of the first saccades during feature search did not vary with increasing display size, but it was significantly less during conjunction search and gradually fell with increasing display size (Fig. 14.2B). The latency of these first correct saccades, however, varied with neither the number of visual stimuli nor the difficulty of the search task (Fig. 14.2C); the average response time was 167 ms. The independence of these initial responses from the visual context of the search displays demonstrates that the visual behavior of these monkeys was less constrained than in previous monkey studies, and it suggests that these responses were largely independent of voluntary control (Jonides et al., 1985). Consequently, the monkey's decision about where and when to make a saccade to a visual stimulus within the search display was presumably based

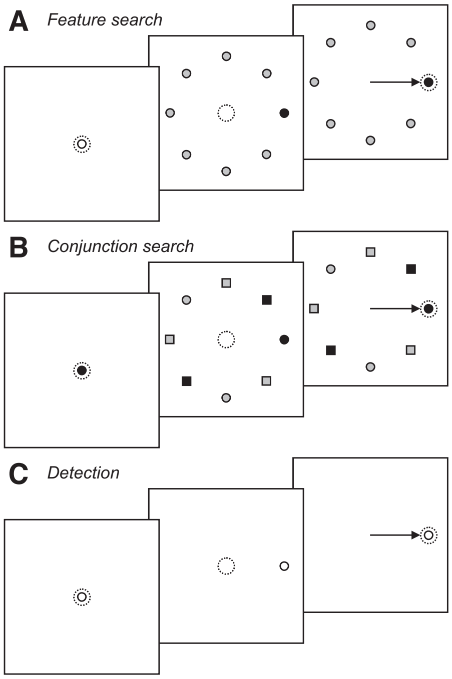

Figure 14.1. All behavioral tasks were initiated by the fixation of a central spot. After monkeys maintained fixation for 500-800 ms, the fixation spot disappeared simultaneously with the appearance of a saccade target at one of eight locations. In the visual feature search task (A), the saccade target was identified solely by color (red or green). In the visual conjunction search task (B), the target was identified by a conjunction of color (red or green) and shape (circle or square). In the visual detection task (C), the target was presented singly. Monkeys had to generate a targeting saccade within 500 ms. If their first saccade failed to land on target, they were given an additional 2 s to foveate the target. The dotted circle and arrow indicate current gaze position and saccade vector, respectively.

on limited processing of the available visual information. This was further evidenced by the uniformly distributed landing positions of the erroneous first saccades made in the more difficult visual (conjunction) search task as well as by the lack of significant differences in response time between correct and incorrect trials (Shen and Paré, 2006). Such an imperfect decision process was also observed by Ludwig et al. (2005) in human subjects, whose response times were best accounted for by a temporal filter model that integrates only the earliest visual information (first 100 ms) following the search display onset. Altogether, it appears that attentional resources beyond those recruited for regulating saccades are not required when subjects are “free” to search.

Although the visual search tasks of Shen and Paré (2006) did not stress accuracy as much as in previous monkey studies, the probability that the first saccade correctly landed on target was high (>0.80). While all the above visual search tasks involved

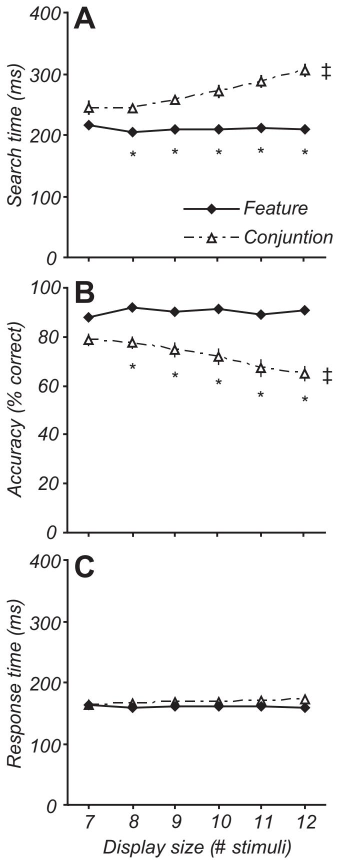

Figure 14.2. Behavioral performance across feature (solid line) and conjunction (dashed line) search tasks. Average search time (A), accuracy of the first saccade (B), and response time of correct saccades (C) are plotted as a function of display size. Data were obtained from three monkeys, each performing a total of eight conjunction search sessions (30,804 trials) and three feature search sessions (10,632 trials). Statistical differences within each task (display size effect) were assessed with one-way ANOVA tests, whereas between-task differences at each display size (task effect) were assessed with pair-wise rank sum tests ($p = 0.0083$ after correction). $*$, significant task effect; ‡, significant display size effect. Error bars, SE.

explicit target foveation, the difference in reward contingency appears to be significant enough to promote different search strategies. Eliminating all reward contingency on saccade production (as it was done by Ipata and colleagues, in a study discussed below) may not be necessary to promote in monkeys the natural rapid and invariant responses usually observed in humans performing visual search tasks.

14.3 Visual processing during visual search

Most previous studies of saccade target selection in visual search were conducted either in saccade executive centers (FEF: Schall and Hanes, 1993; Schall et al., 1995b; Thompson et al., 1996; Bichot and Schall, 1999; SC: McPeek and Keller, 2002; Shen and Paré, 2007) or in visual cortical areas (area V4: Chelazzi et al., 2001; Mazer and Gallant, 2003; Ogawa and Komatsu, 2004, 2006; Bichot et al., 2005; area TEO: Chelazzi et al., 1993). A comprehensive understanding of saccade target selection is, however, still wanting because little is known about the selection mechanisms operating at the interface between visual and saccade processes. Thomas and Paré (2007) recently addressed this need by examining the activity of visually responsive neurons within the posterior parietal cortex of monkeys performing the unconstrained visual feature search task described above (Fig. 14.1A). Specifically, single neurons were recorded in the lateral intraparietal (LIP) area, a key area in the dorsal "vision-for-action" stream, where neurons can integrate a variety of visual signals from converging inputs from visual cortical areas (Andersen et al., 1990; Baizer et al., 1991) and influence saccade production via direct projections to saccade executive centers (Paré and Wurtz, 1997; Ferrainia et al., 2002). The posterior parietal cortex in general and area LIP in particular are ideally positioned to participate in the process of selecting saccade targets during visual search. Human imaging studies have provided considerable evidence in support of this hypothesis (Corbetta et al., 1993; Donner et al., 2000, 2002), and human performance studies have shown that visual search depends on the integrity of the posterior parietal cortex (Riddoch and Humphreys, 1987; Eglin et al., 1989; Arguin et al., 1993; Ashbridge et al., 1997). In the monkey, several studies using instructed delayed saccade tasks have implicated area LIP in selective visual attention (see for review Goldberg et al., 2006) and saccade planning (see for review Andersen and Buneo, 2002), two processes closely associated with visual search. Furthermore, Wardak and colleagues (2002) recently reported that visual search behavior is particularly impaired when area LIP is pharmacologically inactivated. Despite this body of evidence, the contribution of LIP neuronal activity to the active process underlying saccade target selection in visual search had not been directly investigated.

To study the visual processing of multi-stimulus search displays in area LIP, Thomas and Paré (2007) examined the initial activation of LIP neurons while two of the monkeys studied in Shen and Paré (2006) performed a feature search task (Fig. 14.1A and Fig. 14.3, top), in which the target was identified by color, and a single-stimulus detection task (Fig. 14.1C and Fig. 14.3, bottom). With receptive fields restricted to the contralateral visual hemifield, these neurons had visually evoked responses significantly tuned with respect to target location in the detection task. In the search task, these responses were independent of whether the stimulus presented in their receptive fields was a target or a distractor (Fig. 14.4A, solid symbols), suggesting that area LIP does not initially represent stimulus identity. In any given trial, the search target could be either green or red and the sensitivity to local stimulus irregularities found in visual cortical neurons (e.g., Knierim and Van Essen, 1992) could serve to locate the conspicuous stimuli in those displays. To test for feature selectivity in LIP neurons, Thomas and Paré (2007) examined whether their responses were modulated by the target color.

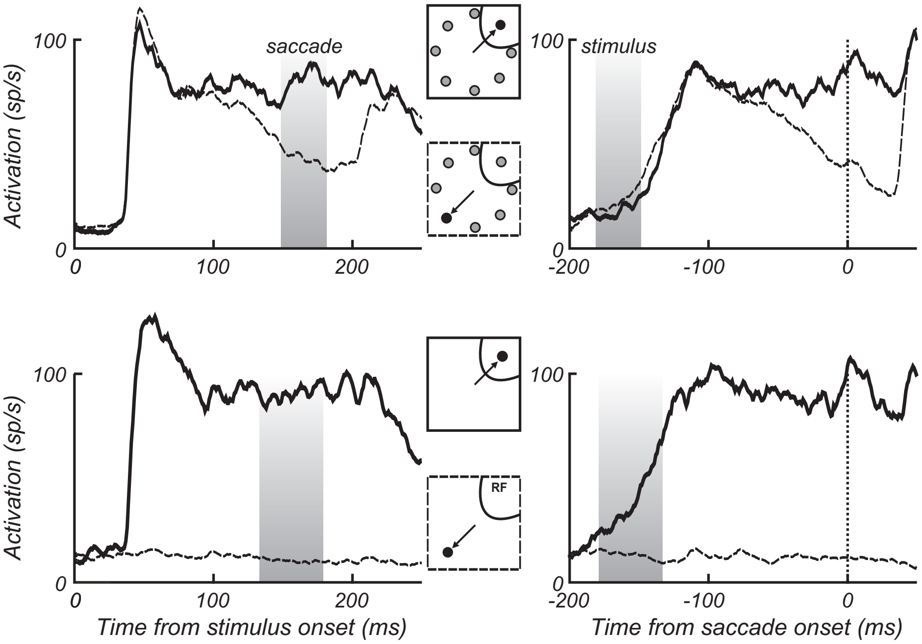

Figure 14.3. Representative LIP neuronal activity in visual feature search (top) and detection (bottom) trials, in which the target appeared in one neuron's receptive field (solid line) or in a diametrically opposite position (dashed line). Average activity of one neuron is depicted as spike density functions computed from data aligned with the presentation of the stimulus (left) or the onset of the targeting saccade (right). 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 (see Thompson et al., 1996).

Only 6% (3/50) neurons had some color selectivity, suggesting that area LIP is virtually featureless. An influence of visual context was also observed, as the visually evoked responses in the search task were attenuated by 28% from what was observed in the detection task (Fig. 14.4B, solid symbols). Surprisingly, this attenuation subsided until the saccade was initiated (Fig. 14.4B, open symbols), even though there was no significant difference between the saccades produced in the two tasks; the changes in LIP pre-saccade activity between tasks was related neither to changes in saccade amplitude nor peak velocity. These results suggest that significant visual processing continues to take place until saccade initiation, thus questioning a direct contribution of area LIP to saccade production.

LIP neuronal activation eventually evolved to signal the presence of the search target in a neuron's receptive field in advance of correct targeting saccades: activity associated with the target became enhanced and that associated with distractors became suppressed (Fig. 14.3, top). Unlike their visually evoked responses, the pre-saccade activity of LIP neurons was tuned to target location, being significantly greater in target

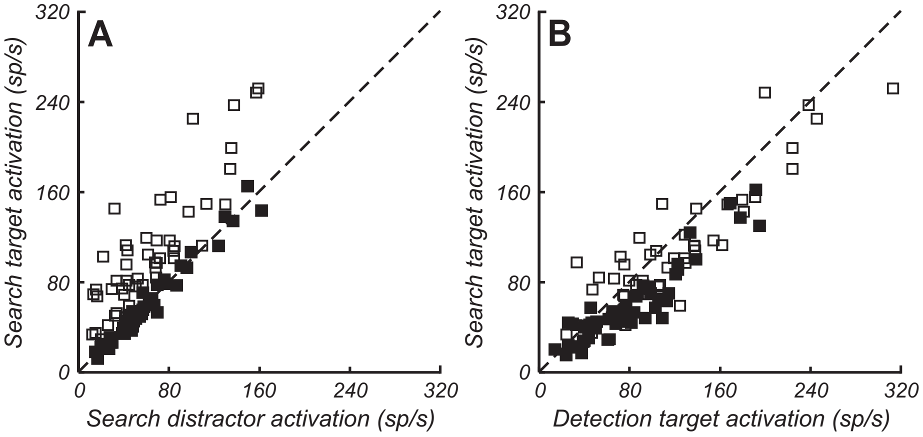

Figure 14.4. Scatterplot of LIP neuronal activation between target and distractor trials in the feature search task (A) and in target trials between feature search and detection tasks (B). Data from 50 neurons. Solid symbols: visually evoked responses (first 25 ms of significant activation after stimulus onset). Open symbols: pre-saccade activity (last 25 ms of activation before saccade initiation).

trials compared to distractor trials (Fig. 14.4A, open symbols). To estimate the time at which LIP neuronal activity became significantly greater in target trials than in distractor trials, Thomas and Paré (2007) applied successive *rank-sum tests* on this activity starting from the onset of the search display (Fig. 14.5, top). Nearly all LIP neurons (92%, 46/50) were found to have statistically significant discriminating activity before saccade initiation (Fig. 14.6A). These neurons reached a significant discrimination, on average, 132 ms (range 105–180 ms) after the search display onset and 34 ms before saccade initiation.

To permit a direct comparison with previous visual search studies in FEF (Thompson et al., 1996) and SC (McPeek and Keller, 2002), Thomas and Paré (2007) also used Signal Detection Theory (Green and Swets, 1966) to determine the time course of how well an ideal observer (or post-synaptic neurons) of LIP neuronal activity can discriminate the target from distractors by estimating the separation between the distribution of activity in correct target and distractor trials from the area under receiver operating characteristic (ROC) curves (Fig. 14.5, bottom). According to this *ideal observer analysis*, the probability of discriminating the target from distractor stimuli for many of these neurons grew from chance level (0.5) during the initial activation to an asymptotic magnitude that fell short of perfect discrimination (1.0), which would indicate distinctly greater activity in target trials. The discrimination magnitude of LIP neurons averaged 0.81, and it exceeded the standard criterion of 0.75 in 60% (30/50) of the neurons at a time that did not exceed the mean response time of the monkeys (Fig. 14.6B). The discrimination time (DT) of these 30 neurons occurred, on average, 138 ms (range 108–170 ms) after the search display onset and 32 ms before saccade initiation (Fig. 14.6C). Figure 14.6D shows that the estimate of LIP discrimination time

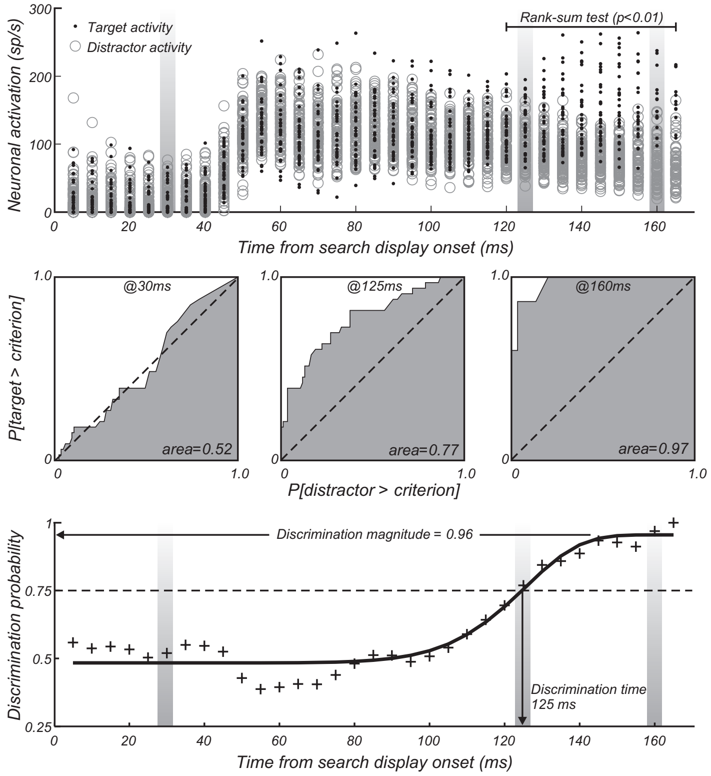

Figure 14.5. Estimation of LIP neuronal discrimination time. The activity of one neuron associated with target (•) and distractor (○) trials was compared every 5 ms (top) with the non-parametric *rank-sum test* to determine when the rate of activity in target trials became significantly greater ($p<0.01$) than that in distractor trials. In the ideal observer analysis, the same activity was compared to determine the probability that the rate of neuronal activity when a target fell within the receptive field is greater than a criterion rate as a function of the probability that the rate of neuronal activity associated with distractor trials is greater than that same criterion (middle). The area under the ROC curves was then plotted (+) as a function of time (bottom) and fit with a Weibull function (solid line) to describe the time course of neural discrimination. The point at which the best-fit Weibull function reached a criterion value of 0.75 represents the *discrimination time*. Functions were calculated only with activity occurring before saccade initiation and terminated when there were less than five target or distractor trials; the ranges of saccade response times for the two sets of trials were matched. Discrimination magnitude was defined by the upper limit of the best-fit Weibull function and represents the strength of discrimination. See Thompson et al. (1996) for further details.

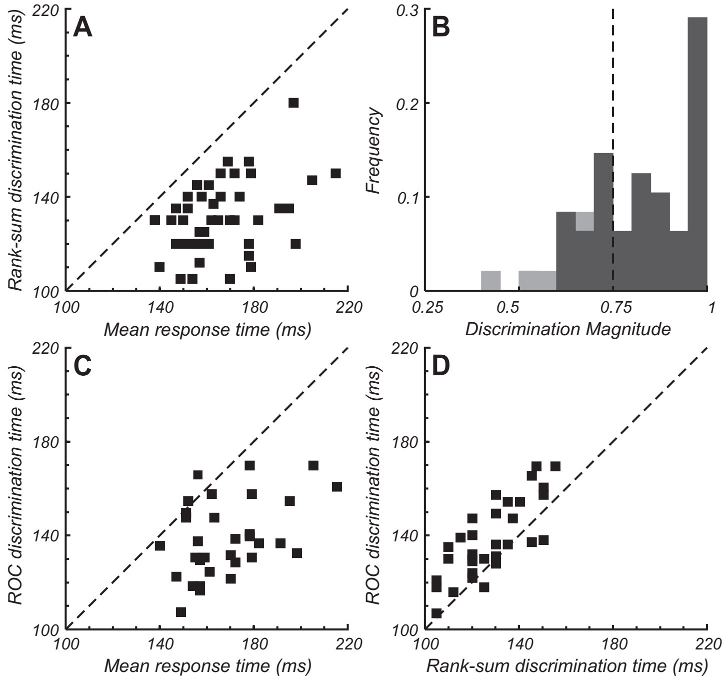

Figure 14.6. A: Relationship between LIP discrimination time and saccade response time in visual feature search; estimate of discrimination time was obtained by determining when each neuron's activity in target trials first became significantly greater than in distractor trials with a *rank-sum test* applied on successive 5-ms intervals from the onset of the search display (n=46). B: Distribution of discrimination magnitude for the sample of LIP neurons (n=50), as estimated with the *ideal observer analysis* (see Figure 14.5 for details); black, statistically significant discrimination (rank-sum test, $p<0.01$). C: Relationship between LIP discrimination time and saccade response time in visual feature search; estimate of discrimination time was defined as when the best-fit function across the ROC curves calculated from each neuron's activity in target and distractor trials first exceeded the standard criterion of 0.75 (see Figure 14.5 for details). Data from 32 neurons, two of which showing discrimination times that lagged the mean response time. D: Scatterplot of LIP discrimination times estimated with the ROC analysis against those estimated with the rank-sum test analysis (n=32).

obtained with the *ideal observer analysis* was closely related to that obtained with the *rank-sum test* ($R^2 = 0.60$), the former lagging by 11 ms on average.

The direct comparison afforded by the common *ideal observer analysis* used in the LIP, FEF and SC 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 (their Table 1); SC: 138 ms, McPeek and Keller, 2002 (exact figures graciously provided by R. M. McPeek); LIP: 138 ms) (see also Schall et al., 2007). However, FEF and SC neurons appear 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 due to the shorter response times that were observed in the LIP study (FEF: 192 ms; SC: 189 ms; LIP: 169 ms), which could have provided insufficient time for neurons to reach criterion. Alternatively, these differences could indicate a slower, less efficient selection process in LIP. Despite these comparative differences, the finding that nearly all LIP neurons had statistically significant discriminating activity indicates that LIP neurons do have activity patterns sufficient to contribute to the active process of selecting saccade targets in visual search, albeit perhaps only in its early stage.

Previous evidence that LIP neuronal activity evolves to discriminate visual stimuli was obtained with instructed, delayed saccade tasks (Platt and Glimcher, 1997; Paré and Wurtz, 2001; Toth and Assad, 2002). The observation of Thomas and Paré (2007) that LIP activity represents all visual stimuli until a saccade goal is selected is consistent with these reports and adds to these previous investigations 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. A similar time course was also reported by another recently published study (Ipata et al., 2006a) describing LIP activity in a free-viewing visual search task, which did not require foveation of the search target. In this study, two monkeys were presented with a display containing a single character – right side up (⊤) or upside down (⊥) – among seven distractors (+) and they were rewarded for indicating the orientation of the unique target character by releasing a lever in either the right or left hand. Although the monkeys eventually foveated the target stimulus in the great majority of trials (88–99% per session), they correctly selected and foveated the search target with a single saccade in only 56% and 44% of the trials (Ipata et al. 2006b). This lower saccade accuracy is not surprising given that saccades were not rewarded directly, but it suggests that the process of saccade target selection was only partially or infrequently completed. Nevertheless, LIP activity evolved to signal the location of the saccade target. Unfortunately, the different analysis of LIP discrimination time used by the authors of this study does not permit a direct comparison with FEF and SC data.

Another recent publication by Buschman and Miller (2007) describes LIP neuronal activity in feature and conjunction search tasks that emphasized accuracy over speed, as in previous monkey studies. Activity from neurons in FEF and lateral prefrontal cortex was also simultaneously recorded, but the discrimination time of all neuronal samples was estimated on a neuron-by-neuron basis with a method based on Information Theory (Shannon and Weaver, 1949), instead of Signal Detection Theory. Comparison with other studies of LIP with visual search tasks as well as with the previous FEF and SC studies is thus limited. Furthermore, serious difficulties with this study have been pointed out (Schall et al., 2007). First, the very early discrimination of LIP neurons found by Buschman and Miller (approximately 50 ms after the feature search display onset) is inconsistent with the observations made by Thomas and Paré (2007) that area LIP never discriminates before at least 100 ms after the onset of the search display as well as with the general finding that the initial activation of visually responsive neurons throughout the visual and oculomotor circuits is indiscriminant (e.g., Schall and Thompson, 1999). Second, the majority of neurons in the samples of Buschman and

Miller (2007), especially in the more difficult conjunction search task, do not discriminate before the initiation of the targeting saccades. This low proportion of discriminating neurons is again inconsistent with other LIP studies (Ipata et al., 2006a; Thomas and Paré, 2007) and it may be related to either heterogeneous sampling, because neurons were not selected on visual responsiveness, or sub-optimal activation of neurons, because the visual stimuli were not centered in their receptive fields. That these non-discriminating neurons could contribute to behavior is certainly unlikely and to include them in a sample is highly questionable, especially because only a minority of LIP neurons projecting to either FEF or SC has been found to have properties unrelated to sensory-motor processing (Paré and Wurtz, 1997; Ferrainia et al., 2002). The impact of the paper of Buschman and Miller (2007) on our understanding of the neural mechanisms underlying saccade target selection, particularly at the vision-action interface, appears to be marginal.

14.4 Attentional processing during visual search

Covert visual attention has been suggested to underlie the process of saccade target selection (e.g., Henderson, 1992; Schneider, 1995), and it may explain the enhanced activation of LIP neurons observed in visual search. Attention-related enhancement has been observed in neurons in several extrastriate areas (see for review Maunsell and Treue, 2006) as well as in posterior parietal cortex (see for review Constantinidis, 2006; Goldberg et al., 2006). Furthermore, visual attention is easily captured by the appearance of a salient stimulus (Yantis 1996), such as the conspicuous target in our feature search task, and this attentional capture has been shown to drive both covert (Theeuwes, 1991) and overt (Theeuwes et al., 1998) selection.

To determine the relationship between LIP neuronal selection and visual attention, we conducted an analysis introduced by Reynolds et al. (1999) to quantify the effect of attention on neuronal responses to multiple stimuli presented within the receptive fields of extrastriate neurons. This analysis examines how well responses to multiple stimuli are predicted by a weighted average of the responses to each single stimulus. The receptive fields of LIP neurons greatly encompass three of the eight stimuli presented in the visual search task. Using the results obtained in the detection trials, a neuron's selectivity for a given stimulus (presented either in the very center of the receptive field or in its periphery) was quantified by subtracting the neuron's responses to that stimulus from the responses elicited by the other stimulus. The impact of the additional stimuli presented simultaneously in the search trials on a neuron's responses to each of the stimuli considered above was then quantified by computing the interaction between that neuron's response to the stimulus together with the other stimuli (search trials) and that to the stimulus alone (detection trials); this was calculated by subtracting the neuron's responses in detection trials from the responses in search trials. In this analysis, if the responses to each of the stimuli presented in a neuron's receptive field were equally weighted during search trials, the relationship between stimulus selectivity and interaction should be positive with a slope of 0.5. Alternatively, if a stimulus were attended, its weight should increase (Moran and Desimone, 1985) and the selectivity and interaction relationship have a slope greater than 0.5.

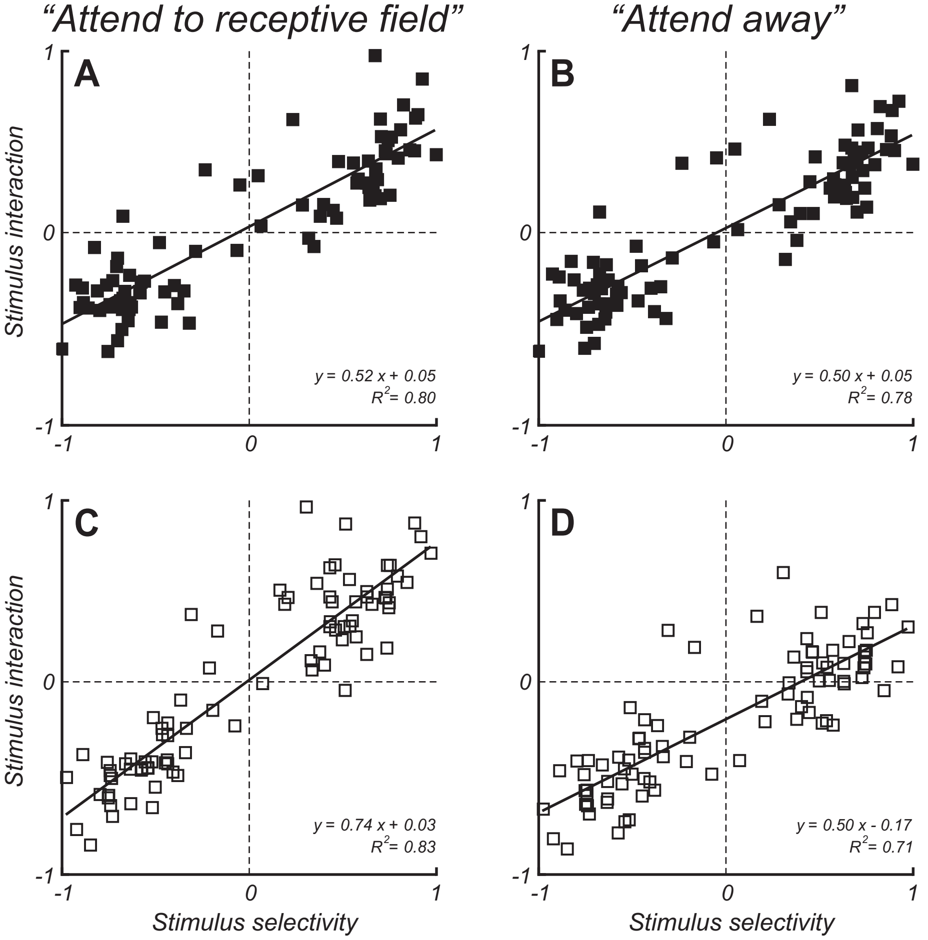

Figure 14.7. Correlation between stimulus selectivity and interaction of the visually evoked responses (A,B) and pre-saccade activity (C,D) of 50 LIP neurons for trials in which the search target appeared either within (A,C) or opposite to (B,D) the neurons' receptive fields. A neuron's selectivity for a given stimulus was quantified by subtracting the neuron's responses to that stimulus from the responses elicited by the other stimulus; this analysis considered the response to the stimulus presented in the very center of the receptive field in detection trials and the average response to the stimuli presented 45 degrees off that position, i.e., near the margin of the receptive field. The interaction between a neuron's response to each stimulus presented alone in detection trials and its response to the combined presentation of the stimuli in search trials was quantified by subtracting the neuron's responses in detection trials from the responses in search trials. Each neuron's response was normalized by dividing them by the highest discharge rate observed for that neuron in any of the conditions.

Figure 14.7 shows the results of our analysis of the LIP neurons recorded by Thomas and Paré (2007) during visual search. Linear regressions between stimulus selectivity and interaction of LIP neurons computed from their initial visually evoked responses (Fig. 14.7A, B) showed significant correlations with slopes near 0.5 and intercepts near zero ($\mathrm{R}^2 > 0.77, \mathrm{p}<0.001$). This was true whether we considered search trials in which the target stimulus was presented within the neuron's receptive field (Fig. 14.7A) – when visual attention would have been directed toward it – or at the diametrically opposite position (Fig. 14.7B) – when visual attention would then have been directed away. We conclude from these results that the initial LIP responses to the stimuli are averaged with equal weight during visual search, a finding consistent with the observation that these responses do not discriminate stimulus identity (cf. Fig. 14.4A, solid symbols).

When we consider the pre-saccade activity of the same LIP neurons, the slope of the linear fit between stimulus selectivity and interaction was 0.74 ($\mathrm{R}^2 = 0.83, p <0.001$), which was significantly greater than 0.5 (t-test, $p <0.001$). This relationship was observed when the search target stimulus fell in the neuron's receptive field (Fig. 14.7C), as if the overall neuronal responses were driven toward the responses associated with the appearance of the target stimulus alone. Most interestingly, the weight of this stimulus in driving the neuronal response to the search display (given by the relationship's slope) was increased by as much as that observed in V4 neurons with voluntary shifts in covert visual attention (Reynolds et al. 1999), thereby suggesting that the enhancement of the LIP representation of the search target is also driven by covert attention. When the search target stimulus fell outside the neuron's receptive field (Fig. 14.7D) – and attention was presumably directed away from that receptive field – the slope of the linear fit between stimulus selectivity and interaction was 0.5 ($\mathrm{R}^2 = 0.71, p <0.001$), indicating that stimuli exerted approximately equal influence over the responses in visual search. However, the large and significantly less than zero (t-test, $p < 0.001$) intercept of this regression reveals that the simultaneous presence of stimuli within the receptive field caused a reduction in mean response, indicating that the LIP representations of these distractor stimuli were suppressed. Altogether, these findings suggest that the modulation of the interaction between multiple stimulus representations prescribed by the "biased-competition model" of attention (Desimone and Duncan, 1995) is a plausible mechanism underlying saccade target selection within area LIP.

14.5 Saccade processing during visual search

Even though the latency of the first saccades made by monkeys during unconstrained visual search appears independent of the search difficulty (Shen and Paré, 2006), it shows a trial-by-trial variability within a given search task. Such response variability has long been attributed to decision processes (see for review Smith and Ratcliff, 2004) whose nature is still being investigated. The temporal relationship between the discriminating activity of LIP neurons and saccade initiation can address this issue and shed light on the nature of the processing occurring within this cortical area. On the one hand, LIP discriminating activity could be involved in the decision about both where and when to make a saccade, in which case it would be closely related to the program-

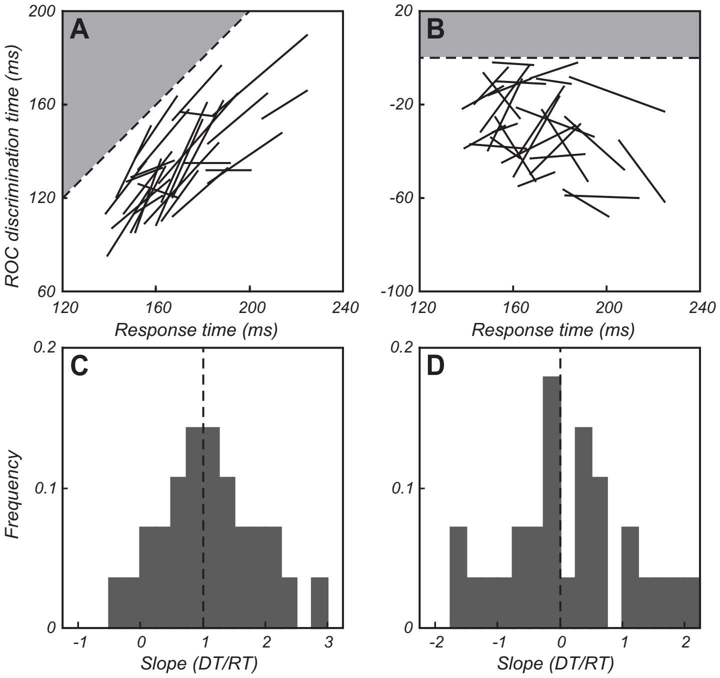

Figure 14.8. Plots of LIP discrimination times of short and long response time groups for activity aligned on stimulus onset (A) and saccade onset (B); shaded areas indicate time after saccade initiation. Distribution of the slopes of the relationships between ROC discrimination times and response times for activity aligned on stimulus onset (C) and saccade onset (D). Data are from neurons with discrimination magnitude exceeding 0.75 in both response time groups (n=28).

ming of the saccade and thus correlated with saccade initiation. On the other hand, it could strictly signal where (not when) to make a saccade, in which case it would occur irrespective of saccade initiation and perhaps reflect the aforementioned attentional process hypothesized to underlie the selection of the search target.

To test these alternatives, Thomas and Paré (2007) segregated their visual search trials into two equal-sized groups according to their response times (RT) and computed the discrimination time (DT) separately for short and long RT group (Fig. 14.8A, B). The slope of the curve connecting each paired DT/RT value was then used to quantify the relationship between these two variables (Fig. 14.8C, D). When the neural data were aligned on the search display onset, the distribution of these DT/RT slopes was unimodal and not significantly different from unity (Fig. 14.8C) but it was significantly different from zero. Consistent with LIP discriminating activity predicting saccade initiation, the distribution of DT/RT slopes calculated from neural data aligned on the time of saccade initiation (Fig. 14.8D) was not significantly different from zero, but it was significantly different from unity.

Previous studies reported bimodal distributions of DT/RT slopes in FEF (Thompson et al., 1996; Sato and Schall, 2003) and SC (McPeek and Keller, 2002), which were interpreted as evidence that the selection of the search target (invariant DT) and targeting saccade (DT predictive of RT) are instantiated by distinct populations of neurons. The neuronal sample of Thomas and Paré (2007) is presumably composed of infra-granular pyramidal neurons, because their recordings were largely confined to regions within the lateral bank of the intraparietal sulcus at which LIP neurons were antidromically activated by SC stimulation (Paré and Wurtz, 1997). Since these neurons preferentially project to SC (Ferrainia et al., 2002) and that many SC neurons have DT/RT slopes close to unity (McPeek and Keller, 2002), it may not be surprising that LIP discriminating activity shows a similar relationship with saccade initiation. 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 same prediction should apply to FEF, but the results in the FEF studies are in disagreement (Thompson et al., 1996; Sato and Schall, 2003). Interestingly, Thompson and Schall (2000) reported that the majority of anatomically localized FEF neurons from the sample of neurons studied by Thompson et al. (1996) were supra-granular pyramidal neurons potentially providing feedback to visual cortical areas. The higher proportion of cortico-cortical neurons recorded in the FEF studies could thus explain why this cortical area appeared predominantly involved in a visual selection process in contrast to area LIP, which appears more concerned with the selection of the targeting saccade perhaps because cortico-fugal neurons were primarily recorded in this area.

Ipata et al. (2006a) obtained similar results to Thomas and Paré (2007), thereby providing additional support for the hypothesis that the role of area LIP in active visual search is limited to the selection of saccades. This hypothesis is, however, difficult to reconcile with previous findings that LIP activity discriminates visual stimuli substantially in advance of saccade initiation in instructed, delayed saccade tasks (Platt and Glimcher, 1997; Paré and Wurtz, 2001; Toth and Assad, 2002). Instead, the dependence of LIP pre-saccade activity on the presence of additional stimuli within the search array suggests that LIP neuronal activity reflects both visual and saccade processing during visual search. The difference between visual search tasks may explain why the results obtained in the FEF (and SC) studies were not replicated in the studies of Thomas and Paré (2007) and Ipata et al. (2006a), whose “free-viewing” task did not emphasize accuracy over speed. It is our contention that visual and saccade selection processes are not distinguishable in natural situations, in which saccades are not associated directly with a reward or punishment. This hypothesis is 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.

14.6 Conclusion

We reviewed recent neurophysiological evidence that the process of selecting a saccade target involves neurons within the “vision-for-action” processing stream of the cerebral cortex of monkeys when they “freely” search for a visual target among distractor stimuli. The initial visual responses of these posterior parietal cortex neurons are neither feature selective nor do they represent whether a stimulus will later be selected, but their activity evolves to reflect this selection process as well as to predict when the targeting saccade is initiated. These results suggest that, during natural visual behavior, visual attention is shifted concomitantly with saccade planning. Consistent with this hypothesis, the enhancement of parietal activity in advance of a search saccade parallels what has been observed in neurons within the ventral "object-recognition" pathway when attention is covertly allocated.

Acknowledgements

The Canadian Institutes of Health Research, the EJLB Foundation, and the J. P. Bickell Foundation supported this work. M. P. was supported by a New Investigator Award from the Canadian Institutes of Health Research and an Early Researcher Award from the Ontario Ministry of Research and Innovation. K. Shen was supported by an Ontario Graduate Scholarship and a postgraduate scholarship from the Natural Sciences and Engineering Council of Canada.

References

Allport, A. (1987). Selection for action: Some behavioral and neurophysiological considerations of attention and action. In H. Heuer and A. Sanders (Eds.) *Perspectives on Perception and Action*. Hillsdale, NJ: Laurence Erlbaum, pp. 395–419.

Andersen, R. A., Asanuma, C., Essick, G. and Siegel, R. M. (1990). Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule. *J. Comp. Neurol.*, 296: 65–113.

Andersen, R. A. and Buneo, C. A. (2002) Intentional maps in posterior parietal cortex. *Ann. Rev. Neurosci.*, 25: 189–220.

Arguin, M., Joanette, Y. and Cavanagh, P. (1993). Visual search for feature and conjunction targets with an attention deficit. *J. Cogn. Neurosci.*, 5: 436–452.

Ashbridge, E., Walsh, V. and Cowey, A. (1997). Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia*, 35: 1121–1131.

Awh, E., Armstrong, K. M. and Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. *Trends Cogn. Sci.*, 10: 124–130.

Baizer, J. S., Ungerleider, L. G. and Desimone, R. (1991). Organization of visual inputs to the inferior temporal and posterior parietal cortex in macaques. *J. Neurosci.*, 11: 168–190.

Bichot, N. P. and Schall, J. D. (1999). Saccade target selection in macaque during feature and conjunction visual search. *Visual Neurosci.*, 16: 81–89.

Bichot, N. P., Rossi, A. F. and Desimone, R. (2005). Parallel and serial neural mechanisms for visual search in macaque area V4. *Science*, 308: 529–534.

Binello, A., Mannan, S. and Ruddock, K. H. (1995). The characteristics of eye movements made during visual search with multi-element stimuli. *Spatial Vis.*, 9: 343–362.

Buracas, G. T. and Albright, T. D. (1999). Covert visual search: A comparison of performance by humans and macaques (macaca mulatta). *Behav. Neurosci.*, 113: 451–464.

Buschman, T. J. and Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, 315: 1860–1862.

Chelazzi, L., Miller, E. K., Duncan, J. and Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, 363: 345–347.

Chelazzi, L., Miller, E. K., Duncan, J. and Desimone, R. (2001). Responses of neurons in macaque area V4 during memory-guided visual search. *Cerebral Cortex*, 11: 761–772.

Constantinidis, C. (2006). Posterior parietal mechanisms of visual attention. *Rev. Neurosci.*, 17: 415–427.

Corbetta, M., Miezin, F. M., Shulman, G. L. and Petersen, S. E. (1993). A PET study of visuospatial attention. *J. Neurosci.*, 13: 1202–1226.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., Petersen, S. E., Raichle, M. E., Van Essen, D. C. and Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, 21: 761–773.

Desimone, R. and Duncan, J. (1995). Neural mechanisms of selective visual attention. *Ann. Rev. Neurosci.*, 18: 193–222.

Deubel, H. and Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Res.*, 36: 1827–1837.

Donner, T., Kettermann, A., Diesch, E., Ostendorf, F., Villringer, A. and Brandt, S. A. (2000). Involvement of the human frontal eye field and multiple parietal areas in covert visual selection during conjunction search. *Eur. J. Neurosci.*, 12: 3407–3414.

Donner, T. H., Kettermann, A., Diesch, E., Ostendorf, F., Villringer, A. and Brandt, S. A. (2002). Visual feature and conjunction searches of equal difficulty engage only partially overlapping frontoparietal networks. *Neuroimage*, 15: 16–25.

Eglin, M., Roberson, L. and Knight, R. (1989). Visual search performance in the neglect syndrome. *J, Cogn. Neurosci.*, 1: 372–385.

Goldberg, M. E., Bisley, J. W., Powell, K. D. and Gottlieb, J. (2006). Saccades, salience and attention: the role of the lateral intraparietal area in visual behavior. *Prog. Brain Res.*, 155: 157–175.

Ferrainia, S., Paré, M. and Wurtz, R. H. (2002). Comparison of cortico-cortical and cortico-collicular signals for the generation of saccadic eye movements. *J. Neurophysiol.*, 87: 845–858.

Findlay, J. M. and Gilchrist, I. D. (2003). *Active Vision: The Psychology of Looking and Seeing*, New York, NY: Oxford University Press.

Findlay, J. M. (1997) Saccade target selection during visual search. *Vision Res.*, 37: 617–631.

Green, D. M. and Swets, J. A. (1966). *Signal Detection Theory and Psychophysics*. New York, NY: Wiley.

Henderson, J. (1992). Visual attention and eye movement control during reading and picture viewing. In K. Rayner (Ed.) *Eye Movements and Visual Cognition*. Berlin: Springer, pp. 261–283.

Hoffman, J. E. and Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Percept. Psychophys.*, 57: 787–795.

Ipata, A. E., Gee, A. L., Goldberg, M. E. and Bisley, J. W. (2006a). Activity in the lateral intraparietal area predicts the goal and latency of saccades in a free-viewing visual search task. *J. Neurosci.*, 26: 3656–3661.

Ipata, A. E., Gee, A. L., Gottlieb, J., Bisley, J. W. and Goldberg, M. E. (2006b). LIP responses to a popout stimulus are reduced if it is overtly ignored. *Nature Neurosci.*, 9: 1071–1076.

Jonides, J., Naveh-Benjamin, M. and Palmer, J. (1985). Assessing automaticity. *Acta Psychologica*, 60: 157–171.

Knierim, J. J. and van Essen, D. C. (1992). Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. *J. Neurophysiol.*, 67: 961–980.

Kowler, E., Anderson, E., Dosher, B. and Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Res.*, 35: 1897–1916.

LaBerge, D. and Brown, V. (1989). Theory of attentional operations in shape identification. *Psycholog. Rev.*, 96: 101–124.

Ludwig, C. J., Gilchrist, I. D., McSorley, E. and Baddeley, R. J. (2005). The temporal impulse response underlying saccadic decisions. *J. Neurosci.*, 25: 9907–9912.

Maioli, C., Benaglio, I., Siri, S., Sosta. K. and Cappa, S. (2001). The integration of parallel and serial processing mechanisms in visual search: Evidence from eye movement recording. *Eur. J. Neurosci.*, 13: 364–372.

Maunsell, J. H. and Treue, S. (2006). Feature-based attention in visual cortex. *Trends Neurosci.*, 29: 317–322.

Mazer, J. A. and Gallant, J. L. (2003). Goal-related activity in V4 during free viewing visual search. evidence for a ventral stream visual salience map. *Neuron*, 40: 1241–1250.

McPeek, R. M. and Keller, E. L. (2002). Saccade target selection in the superior colliculus during a visual search task. *J. Neurophysiol.*, 88: 2019–2034.

Moore, T. (2006) The neurobiology of visual attention: Finding sources. *Curr. Opin. Neurobiol.*, 16: 159–165.

Moore, T., Armstrong, K. M. and Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron*, 40: 671–683.

Moran, J. and Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science*, 229: 782–784.

Motter, B. C. and Belky, E. J. (1998a). The zone of focal attention during active visual search. *Vision Res.*, 38: 1007–1022.

Murthy, A., Thompson, K. G. and Schall, J. D. (2001). Dynamic dissociation of visual selection from saccade programming in frontal eye field. *J. Neurophysiol.*, 86: 2634–2637.

Nobre, A. C., Sebestyen, G. N., Gitelman, D. R., Mesulam, M. M., Frackowiak, R. S. and Frith, C. D. (1997). Functional localization of the system for visuospatial attention using positron emission tomography. *Brain*, 120: 515–533.

Ogawa, T. and Komatsu, H. (2004). Target selection in area V4 during a multidimensional visual search task. *J. Neurosci.*, 24: 6371–6382.

Ogawa, T. and Komatsu, H. (2006). Neuronal dynamics of bottom-up and top-down processes in area V4 of macaque monkeys performing a visual search. *Exp. Brain Res.*, 173: 1–13.

Paré, M. and Wurtz, R. H. (1997). Monkey posterior parietal cortex neurons antidromically activated from superior colliculus. *J. Neurophysiol.*, 78: 3493–3497.

Paré, M. and Wurtz, R. H. (2001). Progression in neuronal processing for saccadic eye movements from parietal cortex area lip to superior colliculus. *J. Neurophysiol.*, 85: 2545–2562.

Platt, M. L. and Glimcher, P. W. (1997). Responses of intraparietal neurons to saccadic targets and visual distractors. *J. Neurophysiol.*, 78: 1574–1589.

Reynolds, J. H., Chelazzi, L. and Desimone, R. (1999). Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.*, 19: 1736–1753.

Riddoch, M. J. and Humphreys, G. W. (1987). A case of integrative visual agnosia. *Brain*, 110: 1431–1462.

Sato, T., Murthy, A., Thompson, K. G. and Schall, J. D. (2001). Search efficiency but not response interference affects visual selection in frontal eye field. *Neuron*, 30: 583–591.

Sato, T. R. and Schall, J. D. (2003). Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron*, 38: 637–648.

Schall, J. D. and Hanes, D. P. (1993). Neural basis of saccade target selection in frontal eye field during visual search. *Nature*, 366: 467–469.

Schall, J. D. and Thompson, K. G. (1999). Neural selection and control of visually guided eye movements. *Ann. Rev. Neurosci.*, 22: 241–259.

Schall, J. D., Paré, M. and Woodman, G. F. (2007). Comment on "top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices". *Science*, 318: 44a-b.

Schall, J. D., Morel, A., King, D. J. and Bullier, J. (1995a). Topography of visual cortex connections with frontal eye field in macaque: Convergence and segregation of processing streams. *J. Neurosci.*, 15: 4464–4487.

Schall, J. D., Hanes, D. P., Thompson, K. G. and King, D. J. (1995b). Saccade target selection in frontal eye field of macaque. I. visual and premovement activation. *J. Neurosci.*, 15: 6905–6918.

Schneider, W. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition and space-based motor action. *Visual Cogn.*, 2: 331–376.

Scialfa, C. T. and Joffe, K. M. (1998). Response times and eye movements in feature and conjunction search as a function of target eccentricity. *Percept. Psychophys.*, 60: 1067–1082.

Shannon, C. and Weaver, W. (1949). *The Mathematical Theory of Communication*. Urbana, IL: University of Illinois.

Shen, K. and Paré, M. (2006). Guidance of eye movements during visual conjunction search: Local and global contextual effects on target discriminability. *J. Neurophysiol.*, 95: 2845–2855.

Shen, K. and Paré, M. (2007). Neuronal activity in superior colliculus signals both stimulus identity and saccade goals during visual conjunction search. *J. Vision*, (in press).

Smith, P. L. and Ratcliff, R. (2004). Psychology and neurobiology of simple decisions. *Trends Neurosci.*, 27: 161–168.

Sperling, G. and Melchner, M. J. (1978). The attention operating characteristic: Examples from visual search. *Science*, 202: 315–318.

Theeuwes, J., Kramer, A., Hahn, S. and Irwin, D. (1998). Our eyes do not always go where we want them to go: Capture of the eyes by new objects. *Psycholog. Sci.*, 9: 379–395.

Theeuwes, J. (1991). Exogenous and endogenous control of attention: The effect of visual onsets and offsets. *Percept. Psychophys.*, 49: 83–90.

Theios, J. (1975). The components of response latency in simple human information processing tasks. In P. Rabbitt and S. Dornic (Eds.) *Attention and Performance V*. London: Academic Press, pp. 418–440.

Thomas, N. W. and Paré, M. (2007). Temporal processing of saccade targets in parietal cortex area LIP during visual search. *J. Neurophysiol.*, 97: 942–947.

Thompson, K. G. and Schall, J. D. (2000). Antecedents and correlates of visual detection and awareness in macaque prefrontal cortex. *Vision Res.*, 40: 1523–1538.

Thompson, K. G., Bichot, N. P. and Schall, J. D. (1997). Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *J. Neurophysiol.*, 77: 1046–1050.

Thompson, K. G., Bichot, N. P. and Sato, T. R. (2005a). Frontal eye field activity before visual search errors reveals the integration of bottom-up and top-down salience. *J. Neurophysiol.*, 93: 337–351.

Thompson, K. G., Biscoe, K. L. and Sato, T. R. (2005b). Neuronal basis of covert spatial attention in the frontal eye field. *J. Neurosci.*, 25: 9479–9487.

Thompson, K. G., Hanes, D. P., Bichot, N. P. and Schall, J. D. (1996). Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *J. Neurophysiol.*, 76: 4040–4055.

Toth, L. J. and Assad, J. A. (2002). Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature*, 415: 165-168.

Treisman, A. M. and Gelade, G. (1980). A feature-integration theory of attention. *Cogn. Psychol.*, 12: 97–136.

Wardak, C., Olivier, E. and Duhamel, J. R. (2002). Saccadic target selection deficits after lateral intraparietal area inactivation in monkeys. *J. Neurosci.*, 22: 9877–9884.

Williams, D. E., Reingold, E. M., Moscovitch, M. and Behrmann, M. (1997). Patterns of eye movements during parallel and serial visual search tasks. *Can. J. Exp. Psychol.*, 51: 151–164.

Wolfe, J. M. and Horowitz, T. S. (2004). What attributes guide the deployment of visual attention and how do they do it? *Nature Rev. Neurosci.*, 5: 1–7.

Yantis, S. (1996). Attentional capture in vision. In A. Kramer A, M. Coles and G. Logan (Eds.) *Converging Operations in the Study of Selective Visual Attention*. Washington, DC: American Psychological Association, pp. 45–76.

Zelinsky, G. and Sheinberg, D. (1995). Why some search tasks take longer than others: Using eye movements to redefine reaction times. In J. M. Findlay, R. Walker and R. W. Kentridge (Eds.) *Eye Movement Research: Mechanisms, Processes and Applications*. New York, NY: Elsevier, Amsterdam, pp. 325–336.