

8 From Attention to Action in Frontal Cortex

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8.1 Introduction

The purpose of the visual system is to transform light into action. For example, consider the visual search illustrated in figure 8.1, in which the observer must locate a T among many Ls. The observer makes a series of gaze shifts to inspect the elements in the array. Before each gaze shift, two selection processes have to take place (e.g., Allport 1987; Pashler 1991; Coles et al., 1995). The first process selects a stimulus to guide action, and the second selects the action. In this chapter, we will review our investigations into the processes by which visual stimuli are selected as targets for gaze shifts.

Recognition is growing that overt eye movements and covert shifts of visual attention are guided by a common mechanism. Several experiments have shown a cost in perceptual reliability or saccade latency if attention is directed away from the target for a saccade (e.g., Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996). In addition, directing attention seems to influence the production of saccades (Sheliga et al., 1995; Kustov and Robinson, 1996). Further evidence is the common manner in which bottom-up factors influence visual selection for attention and saccades. Visual conspicuity drives covert (e.g., Theeuwes, 1991) and overt (Theeuwes et al., 1998) selection. In fact, nontarget elements that resemble the target can be inadvertently selected covertly (e.g., Kim and Cave, 1995) or overtly (Findlay, 1997; Zelinsky and Sheinberg, 1997; Motter and Belky, 1998; Bichot and Schall, 1999b).

Top-down factors also influence visual selection. Cognitive strategies can override both covert (e.g., Bacon and Egeth, 1994) and overt (e.g., Bichot et al., 1996; Nodine et al., 1996) selection of conspicuous target stimuli. In addition, target selection is influenced by implicit memory representations arising through short-term priming of location or stimulus features for covert (e.g., Maljkovic and Nakayama, 1994, 1996) and overt orienting (Bichot and Schall, 1999a; McPeck et al., 1999). Target selection is also influenced by long-term priming of target properties across sessions (Bichot and Schall, 1999b). Finally, an explicit memory representation is needed to identify the unique target during conjunction search (e.g., Treisman and Sato 1990; Bacon and Egeth, 1997).

To explain all of these observations, most models of covert attention (e.g., Koch and Ullman, 1985; Treisman, 1988; Cave and Wolfe, 1990; Olshausen et al., 1993; Wolfe, 1994) and overt saccade generation (e.g., Findlay and Walker, 1999) postulate the existence of a map of salience derived from converging bottom-up and top-down influences. Peaks on the salience map that develop through winner-take-all competitive interactions represent locations that have been selected for further processing and can, but need not necessarily, lead to orienting saccadic eye movements.

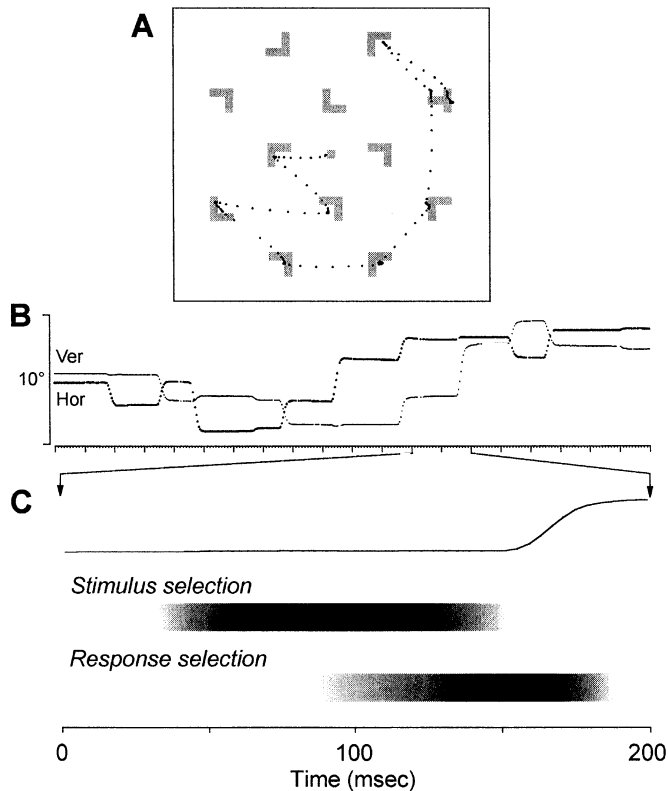


Figure 8.1

(A) Pattern of gaze shifts made by a monkey searching for a randomly oriented T among Ls. The T among L array appeared after the monkey fixated the central spot. On this trial the monkey's first saccade was to the left, followed by a sequence of eye movements around the perimeter of the array. (B) The same sequence of saccades plotted as horizontal (thick) and vertical (thin) eye position as a function of time. (C) A segment of the scan path, including the first saccade to the target, is expanded to illustrate the stimulus selection and response selection processes in (B). These processes precede each saccade. Modified from Schall and Thompson (1999).

8.2 Frontal Eye Field

This chapter focuses on our investigations of the frontal eye field (FEF), an area in prefrontal cortex that contributes to transforming visual signals into saccade commands (reviewed by Schall, 1997). FEF has two facets, one motor and the other sensory.

The evidence for the motor function of FEF is compelling. Low intensity microstimulation of FEF elicits saccades (e.g., Bruce et al., 1985). This direct influence is mediated by a population of neurons that discharge specifically before and during saccades (Bruce

and Goldberg, 1985; Hanes and Schall, 1996; Hanes et al., 1998). The neurons in FEF that generate movement-related activity are located in layer 5 and innervate the superior colliculus (Segraves and Goldberg, 1987) and parts of the neural circuit in the brain stem that generate saccades (Segraves, 1992). These neurons provide the motor plan for voluntary eye movements. In other words, their activity reflects the outcome of the motor response selection process, which is what movement to make. Electrophysiological data indicate the sufficiency of FEF activity to produce gaze shifts. Recent reversible inactivation studies provide evidence for the necessity of FEF to produce saccades. Recent work has demonstrated that reversible inactivation of FEF impairs monkeys' ability to make saccades (Dias et al., 1995; Sommer and Tehovnik, 1997). These findings complement earlier observations that ablation of FEF causes an initially severe impairment in saccade production that recovers in some respects over time (e.g., Schiller et al., 1987; Schiller and Chou, 1998; see also Rivaud et al., 1994).

The evidence for the visual function of FEF is equally compelling. FEF is connected with extrastriate visual areas in both the dorsal stream and the ventral stream (e.g., Baizer et al., 1991), and the projections between extrastriate visual cortex and FEF are topographically organized (Schall, Morel, et al., 1995; Stanton et al., 1995). The central field representation of retinotopically organized areas such as V4, TEO, and MT, as well as areas that overrepresent the *central* field (e.g., caudal TE), project to the ventrolateral portion of FEF. This part of FEF produces short amplitude saccades (Bruce et al., 1985). The peripheral field representation of retinotopically organized areas, as well as areas that overrepresent the *peripheral* visual field (e.g., PO and MSTd), project to the dorsomedial part of FEF. This part of FEF produces larger amplitude saccades. The anatomical evidence also reveals a large degree of convergence of afferents from multiple extrastriate visual areas in FEF. Specifically, the data suggest that individual neurons in FEF may receive signals representing the color, form, depth, and direction of motion of objects in the image. Such convergence seems desirable for a system to select targets for gaze shifts, regardless of the visual properties of the target. In addition to the connections with visual cortex, FEF is connected with prefrontal cortex areas 12, 46, and 9 (e.g., Stanton et al., 1993). In fact, quantitative analyses of the connectivity between cortical visual areas indicate that FEF is a uniquely well-connected node in the network (Jouve et al., 1998).

As a result of the extensive innervation from extrastriate visual cortical areas, physiological recordings in the FEF of monkeys trained to shift gaze to visual targets have found that roughly half of the neurons have visual responses (Mohler et al., 1973; Bruce and Goldberg, 1985; Schall, 1991). Consistent with the extensive convergence of visual signals in FEF, the neurons do not typically exhibit any selectivity for stimulus features like orientation, color, or direction of motion. The time at which FEF visual neurons respond to flashed stimuli coincides with the latencies of visual responses in dorsal stream areas such as MT (Nowak and Bullier, 1997; Schmolesky et al., 1998). In fact, many neurons

in FEF respond to visual stimuli before some neurons in area V1 do. Although FEF visual neurons do not respond selectively for stimulus features such as color or orientation, around half of the visually responsive neurons generate an enhanced response to stimuli that will be the target for a saccade (Goldberg and Bushnell, 1981). The research reviewed below demonstrates how these visually responsive neurons in FEF participate in the selection of visual targets for saccades (see also Schall and Bichot, 1998; Schall and Thompson, 1999). What does this selection process in FEF represent? In this chapter, we will develop the claim that the activation of FEF visual neurons represents a salience map in which stimulus locations are selected on the basis of visual conspicuousness, prior knowledge, and internal random variability (Thompson and Bichot, 1999).

8.3 The Role of Visual Conspicuousness in Selection

We will first review our work that addresses bottom-up influences on attention and eye movements. The term “bottom-up” refers to the usually automatic allocation of attention based exclusively on the properties of the image. A stimulus that is conspicuously different in one or more visual attributes from neighboring stimuli is most likely to be attended and fixated. The visual search paradigm has been used extensively to investigate visual selection and attention (Treisman, 1988; Wolfe, 1998). In a visual search task, multiple stimuli are presented, and from among them a target is discriminated. Search is efficient if stimuli differ along basic visual feature dimensions, for example, color, form, or direction of motion. This kind of search is referred to as “pop-out.” In contrast, if targets and distractors resemble each other, or no single feature clearly distinguishes the two types of stimuli, then search becomes less efficient (e.g., Duncan and Humphreys, 1989).

We have investigated how the brain selects targets for visually guided saccades by recording the activity of neurons in the FEF of monkeys trained to shift gaze to the pop-out target in either of two complementary visual search arrays (Schall and Hanes, 1993; Schall, Hanes, et al., 1995; Thompson et al., 1996). As shown in figure 8.2, we found that visually responsive neurons in FEF initially responded indiscriminately to the target or the distractor of the search array in their receptive field. The absence of feature-selective responses in FEF during visual search is consistent with earlier work (Mohler et al., 1973). However, before saccades were generated, a discrimination process proceeded by which most visually responsive cells in FEF ultimately signaled the location of the pop-out target stimulus. Thus, the activity of FEF visual neurons participates in the visual selection process. The movement-related activity in FEF was the same immediately before saccades to the target presented alone or with distractors (Hanes et al., 1995; Schall, Hanes, et al., 1995). But this should not be surprising, because the same saccade was generated in both conditions. Complementary observations in FEF have been made in monkeys scanning

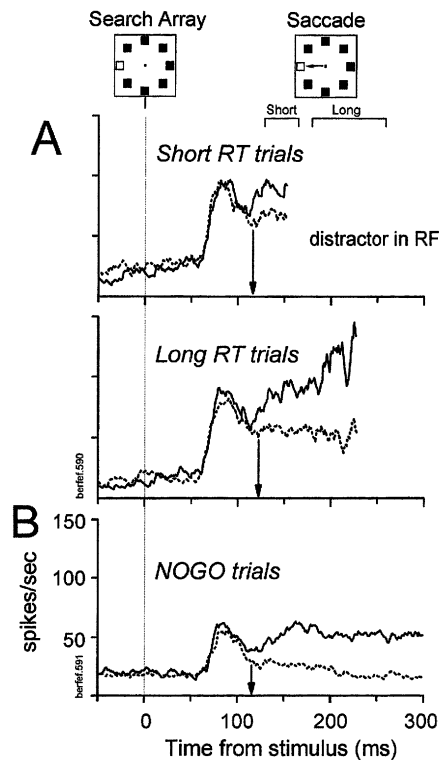


Figure 8.2

Visual selection of a conspicuous target. The neural activity of a single FEF visual neuron is shown following presentation of a pop-out search array during (A) GO search and (B) NOGO search. Each plot shows the activation when the oddball stimulus appeared in the receptive field (RF) (*solid line*) and when distractors appeared in the receptive field (*dotted line*). The trials are aligned on the time of search array (*top*) presentation. (A) The time course of activation during a block of GO search trials. The monkey was instructed to make saccades to the oddball of the search array. The activation during subsets of trials in which reaction times (RT) were short and long are shown separately. The plots of neural activity end at the mean reaction time for each group. The ranges of reaction times for the short and long trials are indicated across the top. (B) The time course of activity during a block of NOGO trials. The monkey was instructed to withhold eye movements. The times of target discrimination (arrows) were approximately the same in all three subsets of trials, showing a dissociation between the visual selection of a stimulus and the production of saccades. Modified from Thompson et al. (1996) and Thompson et al. (1997).

complex images (Burman and Segraves, 1994) and selecting a target based on a motion cue (Kim and Shadlen, 1999).

An obvious and important question about this selection process is, When does it occur? A corollary question is How does the time of target selection in FEF relate to when the saccade is made? These are particular instances of questions that have a long tradition in psychology because reaction time is one of the original and basic quantitative measures of behavior. A working hypothesis of experimental psychology is that behavioral response times are composed of more or less distinct stages of processing (Donders, 1868; Sternberg, 1969). For example, the time taken to identify and select a stimulus corresponds to the perceptual stage of processing, and the time taken to prepare and execute a movement corresponds to the motor stage of processing. We analyzed the time course of saccade target discrimination in FEF to evaluate the hypothesis that the random variability of saccade latency is due to variability in the time taken to select the target for the saccade. We found that the large majority of FEF visually responsive neurons discriminate the target from a distractor in a pop-out search at a fairly constant interval after search array presentation (figure 8.2A) (Thompson et al., 1996). This finding indicates that at least under the conditions of pop-out search, the visual system requires a relatively constant period of time to locate potential targets, and additional timing variability is introduced in the time to prepare and execute the eye movement. Other work has described how postperceptual response preparation processes (Hanes and Schall, 1996) and states of readiness (Everling et al., 1998; Pare and Munoz, 1996; Dorris and Munoz, 1998) contribute to reaction time variability.

To examine further the dissociation of visual selection in FEF from saccade production, we tested the hypothesis that the selection observed in FEF requires saccade planning and execution. FEF activity was recorded while monkeys were instructed to maintain fixation during presentation of a pop-out search array (Thompson et al., 1997). Although no saccade was made to the pop-out stimulus, FEF neurons still discriminated the oddball stimulus from distractors at the same time and to the same degree as when a gaze shift was produced (figure 8.2B). Thus, the visual selection observed in FEF does not require saccade planning. Coupled with the evidence that attention is allocated automatically to the pop-out target in a search array (reviewed by Egeth and Yantis, 1997), this finding suggests that FEF may play a role in covert orienting of visual attention. This conclusion is supported by recent brain imaging studies showing that a region in human frontal cortex including FEF is activated in association with both attention and saccade tasks (Nobre et al., 1997; Corbetta et al., 1998).

To summarize, current data indicate that the evolution of visually evoked activity in FEF represents the process of selecting conspicuous targets. This selection process seems to represent not only the target for an overt gaze shift but also the location of a covert

attention shift. The stimulus properties that distinguish a target from distractors are represented in appropriate areas of visual cortex in which a concomitant selection process occurs (e.g., Luck et al., 1997; Chelazzi et al., 1998; Treue and Maunsell, 1999; McAdams and Maunsell, 1999; Reynolds and Desimone, chapter 7 in this volume). Most likely, the selection observed in FEF is conveyed by the afferents from the various visual areas. However, FEF also provides feedback connections to extrastriate visual cortex (Baizer et al., 1991; Schall, Morel, et al., 1995), so we should not overlook the possibility that the state of neural activity in FEF can influence neural processing in visual cortex.

8.4 The Influence of Knowledge on the Selection Process

The influence of top-down factors on gaze behavior has been shown elegantly by Yarbus (1967), among other researchers (reviewed by Viviani, 1990). The term “top-down” is used to refer to internal influences, such as the memory and expectations of the observer. Although conspicuous objects attract gaze, knowledge of what to look for also strongly influences the guidance of gaze. The same type of selective visual behavior is observed in both humans and other primates, such as macaque monkeys (Keating and Keating, 1993; Burman and Segraves, 1994).

Numerous studies have demonstrated the influence of top-down factors on visual selection. Cognitive strategies can override both covert (e.g., Bacon and Egeth, 1994) and overt (e.g., Bichot et al., 1996; Nodine et al., 1996) selection of pop-out targets. Expectations can affect visual selection even when the stimuli of interest are conspicuous. Subjects are faster at finding a pop-out target when the feature distinguishing target from distractors remains constant than when it varies from trial to trial (Bravo and Nakayama, 1992; Maljkovic and Nakayama, 1994). Similar effects have been observed on eye movements (Bichot and Schall, 1999b; McPeck et al., 1999). Repetition of target position on successive trials also improves performance (Maljkovic and Nakayama, 1996). Recent work has shown that viewers detect targets faster if they are embedded in previously experienced visual display configurations even though observers do not recognize the repetition (Chun and Jiang, 1998).

In some cases, knowledge can override conspicuousness. For example, experts are more likely than novices to ignore conspicuous but irrelevant parts of a visual image from their field of expertise (e.g., Nodine et al., 1996; Chapman and Underwood, 1998; Nodine and Krupinski, 1998). Other work using simpler visual search displays also shows that, under some circumstances, cognitive strategies can prevent conspicuous stimuli from capturing attention (Bacon and Egeth, 1994). Such observations stress the extent to which visual selection is under voluntary control, and we have investigated how such control is expressed in the brain.

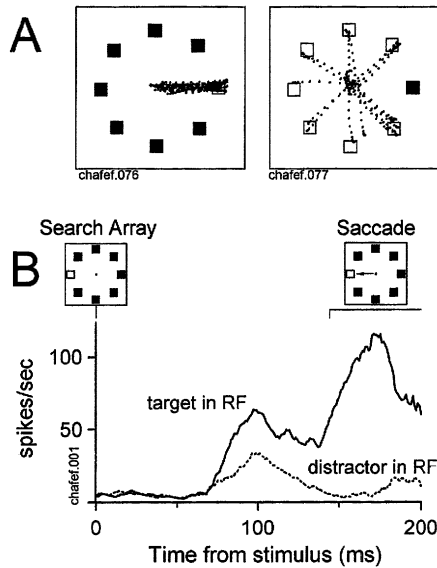


Figure 8.3

Visual selection of a learned target during pop-out search. (A) Saccades made by a monkey trained in only one instance of the visual search array, a red target among green distractors. When presented with an array in which the target and distractor colors were switched, instead of looking at the conspicuous green stimulus, this monkey looked only at one of the red distractors. (B) The time course of activation of a single FEF visual neuron in this monkey when the red target (solid line) was in the receptive field and when a green distractor (dotted line) was in the receptive field. Activity is plotted beginning at the time of search array presentation. The range of saccadic reaction times is shown. Unlike neurons recorded in monkeys that learned to perform generalized oddball search tasks (see figure 8.2), the initial visual response of this neuron discriminated the target from distractors. Modified from Bichot et al. (1996).

To study the effects of training experience on gaze behavior and associated neural activity, we trained monkeys exclusively with search arrays that contained a target of a constant color among distractor items of another constant color (Bichot et al., 1996). Control monkeys were trained to make a saccade to a target distinguished by the uniqueness of its color relative to all other items in the display (i.e., the display sometimes contained a red target among green distractors, and sometimes a green target among red distractors). Control monkeys shifted gaze according to visual salience, but the experimental monkeys persistently directed gaze to stimuli possessing the known target color (figure 8.3A). In other words, when experimental monkeys were presented with the search array complementary to that on which they had been trained, they shifted gaze to the distractors and not to the target, even though the target was of unique color. As described above, FEF neurons in monkeys trained to perform a general visual search do not exhibit color selectiv-

ity, but their activity evolves to signal the location of the unique stimulus. In monkeys trained exclusively on targets of one color, however, about half of FEF neurons show selectivity for stimuli of that color, which takes the form of a suppression of the initial visual responses to stimuli of the distractor color (figure 8.3B). How might this initial selective response arise in FEF? One possibility is that appropriate bias signals are delivered to FEF from other prefrontal areas responsible for executive control and strategy. Recent studies have demonstrated that the selective properties of prefrontal neurons can change according to rules or strategies (e.g., Asaad et al., 1998; Rainer et al., 1998, Rainer et al., 1999; White and Wise, 1999).

In many situations, objects of interest cannot be located solely on the basis of their visual features. In such cases, which are exemplified by a visual search for a conjunction of features such as color and shape, an explicit memory representation is needed to identify the target (e.g., Treisman and Sato, 1990; Bacon and Egeth, 1997). We investigated how the brain combines knowledge with visual processing to locate targets for eye movements by training monkeys to perform a visual search for a target defined by a unique combination of color and shape (feature conjunction) (figure 8.4). The color–shape combination defining the target was changed randomly between sessions. We observed two separate top-down influences on gaze behavior and the neural selection process: visual similarity to the target and the history of target properties (Bichot and Schall, 1999a, 1999b). The evidence for the influence of visual similarity was that monkeys made occasional errant saccades during this conjunction search that tended to direct gaze to distractors which resembled the current target. Similar observations have been made with human observers during covert (Kim and Cave, 1995) and overt orienting (Findlay, 1997; Motter and Belky, 1998; but see Zelinsky, 1996). Physiological recordings in FEF revealed that when monkeys successfully shifted gaze to the target, FEF neurons not only discriminated the target from distractors but also discriminated among the nonselected distractors exhibiting more activation for distractors that shared a target feature and a distractor that shared none.

Thus, the pattern of neural discrimination among nonselected distractors corresponded to the pattern of errors that reveal the allocation of attention. These behavioral and neurophysiological findings support the hypothesis that the target in at least some conjunction visual searches can be detected efficiently on the basis of visual similarity (Duncan and Humphreys, 1989), most likely through parallel processing of the individual features that define the stimuli (Wolfe et al., 1989; Cave and Wolfe, 1990; Treisman and Sato, 1990). The correspondence between the pattern of neural selection observed in FEF and the results of studies and predictions of models of visual attention (e.g., Cave et al., 1999) is further evidence that the selection in FEF predicts the allocation of visual attention.

The history of stimulus presentation across sessions also affected the selection process during conjunction search. If an error was made, monkeys showed a significant tendency

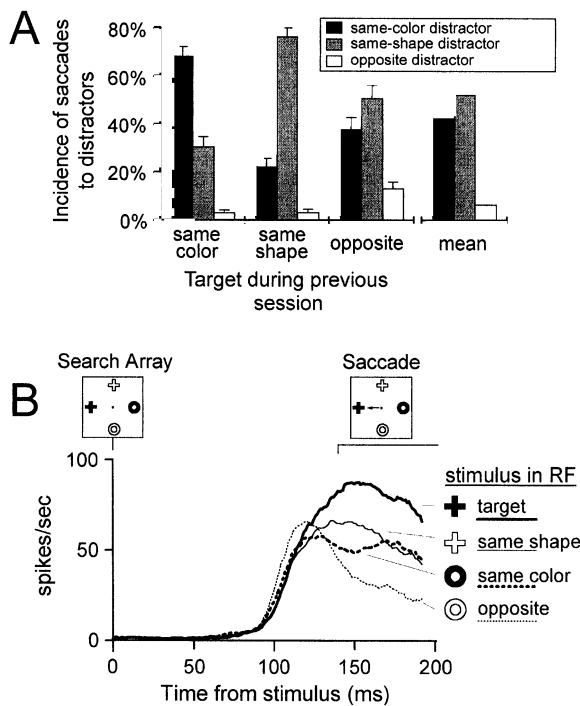


Figure 8.4

Visual selection during conjunction search. (A) Gaze pattern in conjunction search during neural recordings. Incidence of saccades to distractors having the same color (*black*) or the same shape (*gray*) as the target, or having features opposite to the target (*unfilled*) is shown as a function of the target properties in the previous session. Error bars show the standard error. If they made an error, monkeys tended to shift gaze to a distractor that resembled the target, especially if the distractor had been the target in the previous experimental session. (B) Time course of activity of an FEF neuron during conjunction search when the target stimulus (thick solid line), same-color distractor (thin solid line), same-shape distractor (thick dotted line), and opposite distractor (thin dotted line) fell in its receptive field. The plots begin at the time of search array presentation. The range of latencies of saccades to the target are indicated. When this neuron was recorded, the target was the same shape as the target of the previous session. Modified from Bichot and Schall (1999a).

(in addition to the visual similarity tendency just described) to shift gaze to the distractor that had been the target in the previous session. Recordings from FEF neurons during trials with correct saccades to the conjunction target revealed a corresponding difference in activation among distractors, resulting in more activation for distractors that had been the search target during the previous session. This effect, which may be a form of long-term priming, revealed itself across sessions that were at least a day apart and persisted throughout each experimental session. The longer duration of this influence distinguishes

this learning effect from the short-term priming during pop-out searches that lasts for about 10 trials or 30 seconds in humans (Maljkovic and Nakayama, 1994) as well as monkeys (Bichot and Schall, 1999b).

8.5 Selection of Ambiguous Targets

In the visual search studies just described and in other studies that have examined the neural processes involved in visual choices, the choice of behavioral response was dictated explicitly by differences in the visual stimuli (e.g., Glimcher and Sparks, 1992; di Pelli-grino and Wise, 1993; Schlag-Rey et al., 1997; Gottlieb et al., 1998; Asaad et al., 1998). In other words, the external stimuli completely dictated the correct response. The real world is rarely as clear as the laboratory. Often behavioral choices must be made on the basis of incomplete or unclear information. We have investigated the sensory and motor activity in FEF of monkeys responding to an ambiguous stimulus that could result in either of two mutually exclusive perceptual reports (Thompson and Schall, 1999; Thompson and Schall, 2000). The phenomenon of backward masking was used to create a condition in which the same physical stimulus might or might not be detected and localized. The experiment was designed to discourage guessing by requiring monkeys to report either the perceived presence or the absence of a target.

Figure 8.5 shows the activity of a visually responsive FEF neuron during *hit trials*, on which the target appeared and was correctly detected; *miss trials*, on which the target

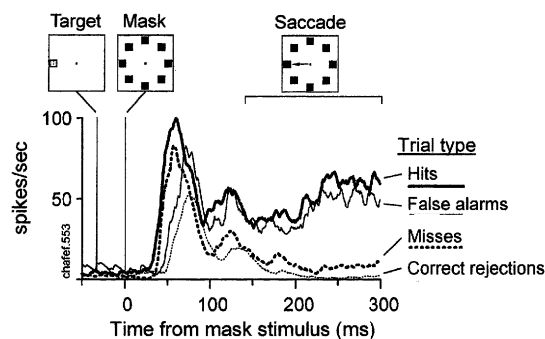


Figure 8.5

Visual selection of an ambiguous target during visual masking. The time course of activity of a single FEF visual neuron during the backward masking task is plotted separately for hits (thick solid lines), misses (thick dotted lines), false alarms (thin solid lines), and correct rejections (thin dotted lines). The activity is aligned on the time of mask presentation at 0 ms. The target appeared 33 ms before the mask on hits and misses. The range of saccade latencies during hits and false alarms is indicated at the top. Modified from Thompson and Schall (1999) and Thompson and Schall (2000).

appeared but was not detected; *false alarm trials*, on which no target appeared but the monkey reported one present; and *correct rejection trials*, on which no target appeared and the monkey correctly reported that no target was present. The monkey's behavior on hits and false alarms was the same; it made a saccade indicating perception of a target. Likewise, the monkey's behavior on misses and correct rejections was the same; it maintained fixation on the central spot, indicating a perceived absence of a target.

It is generally thought that visual responses in prefrontal cortex register sensory activity that reaches awareness to guide voluntary behavior (e.g., Crick and Koch, 1995). We were surprised to find that virtually all visually responsive neurons in FEF responded at short latencies to the target stimulus whether or not the monkey reported its presence (on hits and misses). Monkeys shifted gaze to the masked stimulus when the initial visual response to the target stimulus was only slightly stronger. Monkeys also made frequent errors of indicating target presence when there was none (false alarms), and we found that false alarms were made when visual neurons responded slightly more strongly to the mask stimulus. Thus, for nearly every visually responsive FEF neuron, when the early sensory responses were slightly greater, the target was reported as being present. This difference was small, often only one or two spikes in the period before the response to the mask. We believe it is unlikely that this difference in the initial visual activation arises *de novo* in FEF. Most likely, the difference observed reflects variations in visual activation in earlier stages of the visual pathway, perhaps even originating in the retina and propagating throughout the visual system.

Regardless of how the differences in activation came to be, the initial visual activation occurring immediately before the mask response predicts reasonably well whether monkeys will generate a "yes" or a "no" report (Thompson and Schall, 1999). We postulate that the initial visual responses in FEF represent the evidence upon which the detection decision is based. In terms of signal detection theory the early visual response is the dependent variable along a decision axis (Green and Swets, 1966). When this visual response is slightly greater than otherwise, it crosses a threshold on this axis such that the monkey responds that the target was there. Further studies are required to identify where in the visual system the differences in the initial visual responses arise, as well as the nature of the neural decision threshold.

In addition to the early visual response differences, many of the visually responsive FEF neurons exhibited a prolonged phase of elevated activity that occurred specifically during trials on which the target was reported as being present (hits and false alarms) but not during trials on which the target was reported as being absent (misses and correct rejections). For the neuron shown in figure 8.5, this second phase of differential activity began around 100 ms following mask presentation and continued until the saccade.

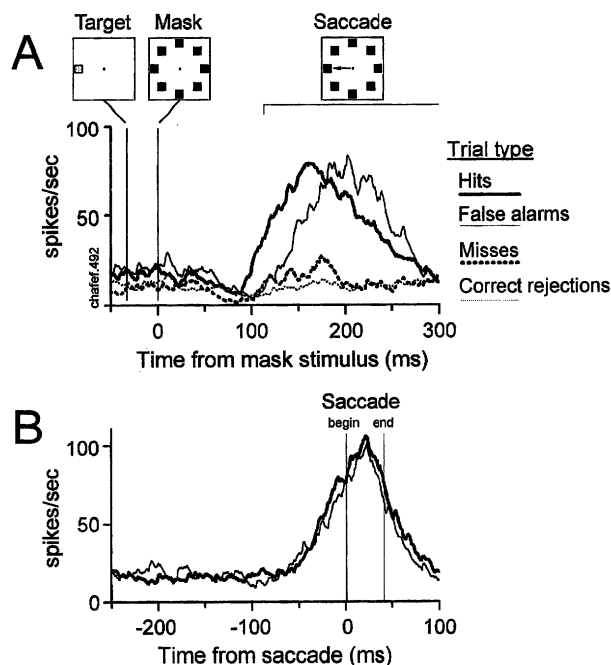


Figure 8.6

Response selection of an ambiguous target during visual masking. (A) The time course of activity of a single FEF movement neuron during the backward masking task is plotted separately for hits, misses, false alarms, and correct rejections. Conventions are the same as in figure 8.5. (B) The activity of the same FEF movement neuron associated with hits and false alarms aligned on the time of saccade initiation.

What does this late, enhanced activation on hits and false alarms represent? As reviewed above, FEF is commonly regarded as a motor area. Thus, one must ask whether the late activation after the mask response is related to visual processing or to motor programming. To address this question, we compared the selective activity of movement neurons against that of visual neurons.

Figure 8.6 shows the activity of a movement neuron during the visual masking task. Movement neurons in FEF are distinguishable from the visual neurons in several ways. First, movement neurons exhibited little or no modulation of activity on misses or on correct rejections, but exhibited strong activation associated with the saccade on hits and false alarms. Further, the magnitude and pattern of movement-related activity was the same for hits as it was for false alarms (figure 8.6B). And finally, the time of the late selective response in visual neurons was synchronized with the time of target presentation,

but onset of movement cell activity began progressively later on trials with progressively longer saccade latencies (Thompson and Schall, 2000).

These results indicate further that visual neurons and movement neurons in FEF are functionally distinct. FEF movement neurons provide a motor command appropriate to produce the overt behavioral report through a gaze shift. In contrast, the relationship of visual neurons to saccade execution appears to be more distal than that of the movement neurons. However, the later period of activity of the visual neurons was clearly related more to the behavioral response than to the physical stimulus. Therefore, we think that the selective signal observed in the visual neurons represents a signal that is not just visual but not quite motor, that is, the signal is not dictated solely by the retinal image but it is not an explicit motor command.

8.6 Conclusions

The findings we have reviewed suggest the following general conclusions. The data reveal neurophysiological correlates of two selection processes that have been theorized to be necessary for the execution of a voluntary movement: the selection of the *stimulus* that guides the action and the selection of the *action* itself. It seems clear that the activity of movement neurons in FEF corresponds to the selection and preparation of the action. We believe it is equally clear that the selection process observed in visual neurons in FEF corresponds to the selection of stimuli. This neural selection occurs during visual search for a conspicuous target as well as during visual search that requires a memory representation. The neural selection also occurs when an ambiguous sensory signal is selected for further processing. We hypothesize that this visual selection process corresponds to the allocation of covert attention that precedes purposive gaze shifts.

The data also indicate how the selection process observed in frontal cortex may be related to the selection processes observed in visual cortical areas. Whereas the role of visual cortex is to analyze what is where in the image, we suggest that one role of FEF is to represent locations that could receive orienting responses. Figure 8.7 (plate 5) diagrams the hypothesis that FEF contains a map of visual salience. To illustrate this, consider performance of a conjunction visual search. Each element in the array is distinct, but none is conspicuously different from the others. The properties of the elements in the image are processed by populations of neurons discriminating shape, color, and direction of motion, among other features. For the color–shape conjunction, the motion map does not contribute to the selection process, but the units responding to the particular color and shape at each location are activated. These feature maps correspond conceptually to the processing that occurs in striate and extrastriate visual cortex. In models of visual search,

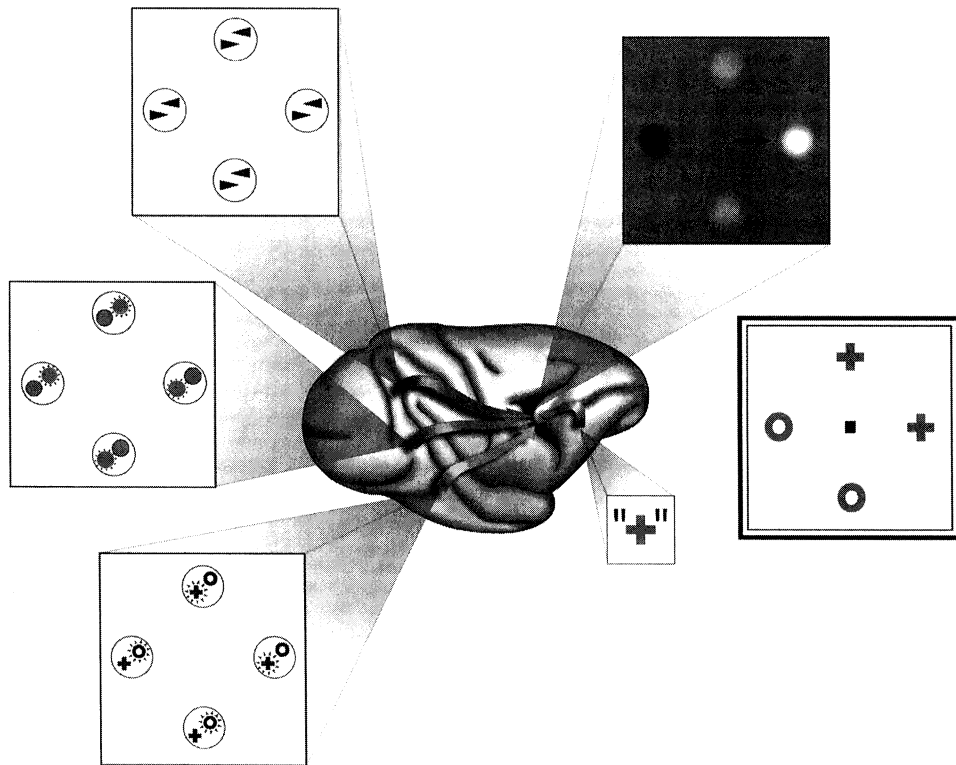


Figure 8.7

Frontal-eye fields as a saliency map. Consider the task of finding the target in the conjunction visual search display shown at the right in the double border. To locate the target, the elementary features of color and shape must be determined. Visual shape (*lower left*), color (*center left*), and motion (*upper left*) are portrayed as being analyzed across the visual field by topographic maps in different parts of extrastriate visual cortex. Each circle enclosing a pair of features represents a hypercolumn in the cortex; the actual organization is more complicated. The starburst design around one feature indicates activation at different locations in the color and shape maps resulting from the stimuli in the visual search display; the motion map is not activated because the search display is static. The convergence of the activation from the feature maps into FEF is portrayed on a rendering of a macaque brain. This search for a conjunction of color and shape cannot be accomplished with visual processing alone because the properties of the stimuli do not completely specify which is the target. To locate the target correctly, a memory representation must influence the activation in the saliency map. The square enclosing the red + symbolizes a memory representation of the correct target that is portrayed as influencing FEF through a projection from ventral prefrontal cortex. The panel issuing from FEF (*upper right*) indicates the state of activation in a saliency map that guides orienting in the search array. The location in the saliency map corresponding to the red + has the highest activation (white), the locations with stimuli that are the same shape or color as the target have intermediate activation (gray), and the location with the stimulus that is neither the same shape nor the same color as the target has minimal activation. Compare with figure 8.4B. The arrow in the saliency map (*upper right*) indicates the cover or overt orienting resulting from the pattern of activation. See text for discussion. (See plate 5 for color version.)

the feature maps converge onto another map of the visual field that represents the locations of targets for orienting.

Consistent with this architecture as reviewed above, FEF receives convergence from many extrastriate visual areas. When the desired target is distinctly different from other stimuli in the image, then these bottom-up projections are sufficient to guide action. In many situations, though, such as conjunction search, a memory representation must be combined with the outcome of visual processing to guide the search for the target. To perform this function, models of visual search include a top-down influence on the salience map. Similarly, FEF is also innervated by areas in prefrontal cortex that can represent the properties of the desired target as well as the influence of strategy and context. The level of activation in the salience map represents the likelihood that the represented stimulus will receive additional processing through covert or overt orienting. In figure 8.7 the correct target receives the highest activation and distractors that are the same shape or same color as the target receive some activation. Overall, the data we have reviewed suggest that the visually evoked activation in FEF represents the selection of stimuli for further action, whether the selection is guided by external stimulus properties, knowledge, or self-generated decision criteria.

We are not suggesting that FEF is the only map of visual salience in the brain. Several lines of evidence suggest a similar function for the superior colliculus (e.g., Basso and Wurtz, 1998; reviewed by Findlay and Walker, 1999) and posterior parietal cortex (e.g., Robinson et al., 1995; Steinmetz and Constantinides, 1995; Gottlieb et al., 1998). It seems clear, then, that the functional salience map is distributed among distinct, but interconnected, concurrently active visuomotor structures. Moreover, the representation of salience to select locations for further processing seems to be a useful theoretical construct that can organize current data and guide further empirical and theoretical efforts.

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