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Visuomotor Origins of Covert Spatial Attention

Review

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Covert spatial attention produces biases in perceptual performance and neural processing of behaviorally relevant stimuli in the absence of overt orienting movements. The neural mechanism that gives rise to these effects is poorly understood. This paper surveys past evidence of a relationship between oculomotor control and visual spatial attention and more recent evidence of a causal link between the control of saccadic eye movements by frontal cortex and covert visual selection. Both suggest that the mechanism of covert spatial attention emerges as a consequence of the reciprocal interactions between neural circuits primarily involved in specifying the visual properties of potential targets and those involved in specifying the movements needed to fixate them.

Introduction

The primate cerebral cortex is comprised of neurons that are largely involved in processing visual information (Felleman and Van Essen, 1991). The discovery that the visual world is represented within a mosaic of cortical areas organized more or less hierarchically beyond primary visual cortex (V1) has proven to be particularly important in that it establishes the relatively modular nature of visual feature extraction (Zeki, 1978; Felleman and Van Essen, 1991; Hilgetag et al., 1996). However, our knowledge of how signals conveyed by neurons within these modules are used to guide behavior is severely limited. Much of what is understood about the functional properties of visual cortical neurons of the macaque was established either in anesthetized preparations or in animals passively viewing visual displays (Van Essen, 1979; Desimone et al., 1985). Yet, analysis of the visual scene under normal circumstances is by no means passive. Instead, primate vision is an active process, consisting of a sequential sampling of the visual world with saccadic eye movements (Yarbus, 1967). Visual scenes typically contain far more information than can be gathered at any one time by the primate visual system and this necessitates a piecemeal interpretation of the visual environment. Saccades bring targets of interest from peripheral retinal locations, where visual acuity is relatively low, to the fovea, where acuity is greatest. Therefore, the interplay between visual coding and oculomotor control mechanisms during scanning eye movements is of particular importance to visual neurobiologists.

Just as our eyes are unable to simultaneously fixate all the elements contained within a scene, our perception of those elements is likewise limited. The tremendous volume of information impinging on the retina imposes a severe bottleneck, or limited capacity, on perception (Broadbent, 1958). As a result, we must selectively filter, or attend, to relevant targets, at the expense of unimportant ones. Under normal circumstances, the direction of gaze and the direction of attention are aligned. That is, we normally fixate objects of interest, overtly attending to them. But attention can be disengaged from the point of fixation, and a great deal has been made of this fact (Sperling and Melchner, 1978; Posner and Cohen 1984). Covert attention has intrigued physiologists and psychologists alike for more than a century. In more recent years, a great number of studies of the monkey and human visual systems have revealed a dependence of the strength of visual cortical signals on the locus of covert visual attention (for reviews, see Maunsell, 1995; Desimone and Duncan, 1995; Kastner and Ungerleider, 2000). However, the mechanism by which the processing of relevant visual information is selectively biased has eluded investigators. A wealth of indirect evidence suggests that the neural mechanisms of covert attention are largely overlapping with those controlling the programming of saccadic eye movements (Rizzolatti, 1983; Hoffman and Subramaniam, 1995; Rizzolatti et al., 1987; Kustov and Robinson, 1996; Kowler et al., 1995; Corbetta, et al., 1998; Nobre et al., 2000), at least when attention is directed spatially. This paper surveys evidence of a relationship between oculomotor control and spatial attention, including some recent tests of a causal link between the control of saccadic eye movements by frontal cortex and the gating of visual information. This work suggests that the filtering of visual signals is determined in part by the likelihood that a saccade will be made to a particular location, as compared to others. Here, we suggest that the mechanism of covert spatial attention emerges as a consequence of the feedback interactions between circuits primarily involved in specifying the visual properties of potential targets and those involved in specifying the movements needed to fixate them.

The Role of Motor Mechanisms in Attention: A Brief History

Fundamental insight into the nature of attention was afforded by inquiry more than a century old. William James (1890) suggested the key distinction between *involuntary* and *voluntary* attention, or what is more recently referred to as *bottom-up* and *top-down* attention, respectively (Egeth and Yantis, 1997). The distinction is key in that it provides a basis by which perception of an event can be biased either by virtue of the characteristics of a visual stimulus (involuntary) or by willful selection by the subject (voluntary). Other work from the 19th

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century provided hints of a motor source of voluntary perceptual biases. The overt behaviors associated with attention, such as moving the eyes and head and orienting to targets of interest, are by definition driven by motor control mechanisms. But the effect of motor commands on visual input is not restricted to the indirect consequences of changes in eye and head orientation. The idea that motor mechanisms might exert a direct influence on incoming sensory information has been around for more than a century. Noted physicist, physiologist, and philosopher Hermann von Helmholtz (1866) proposed perhaps the first hypothesis that eye movement commands affected incoming visual information. As a possible solution to the problem of how our perception of the world remains stable during saccades, Helmholtz suggested that copies of movement commands could effectively cancel the visual consequences of the eye movement. Later, physiological evidence of an involvement of eye movement mechanisms in visual attention per se was noted by the noted Scottish physiologist Sir David Ferrier. Although among visual neuroscientists Ferrier is mostly remembered for having incorrectly localized primary visual cortex in the parietal lobe instead of the occipital (Gross, 1997), his legacy is much less tainted among oculomotor physiologists (e.g., Schall, 1997). Ferrier used Fritsch and Hitzig's method of cortical stimulation (Fritsch and Hitzig, 1870) in a variety of species, including monkeys, to reveal a localized cortical zone for the control of saccades (Ferrier, 1876), known today as the frontal eye field (FEF). But it was Ferrier's lesion studies that led him to conclude that attention is intimately related to motor control:

> In addition to the paralysis of the movements of the head and eyes on destruction of the frontal lobes, I have also observed (and my observations have been confirmed by Hitzig and Goltz) a noteworthy psychical defect—a defect which I have endeavoured to correlate with the inability to look at, or direct the gaze towards, objects which do not spontaneously fall within the field of vision. It is a form of mental degradation which appears to me to depend on the loss of the faculty of attention, and my hypothesis is that the power of attention is intimately related to the volitional movements of the head and eyes. (Ferrier, 1890)

Ferrier's conclusions were influenced in part by earlier ideas of Alexander Bain, a Scottish psychologist and teacher of Ferrier. Later, the noted psychologist Ribot (1890) elaborated on the view that attention might emerge from movement preparation and its inhibition, drawing from Ferrier's data. Ribot's ideas reflected an influence of both Ferrier's work and the emerging belief that the frontal lobes served a unique role in the inhibition of inappropriate behaviors, the principle evidence being the famous case of Phineas Gage and his tragic encounter with a tamping iron (Harlow, 1868).

Despite a long history of both speculation and evidence of a role of oculomotor mechanisms in visual attention, much of the modern literature attributes the hypothesis that saccade programming provides the basis for covert visual attention to Rizzolatti and colleagues and the "premotor theory of attention" (Rizzolatti, 1983; Rizzolatti et al., 1987). This view, the most recent incarnation of the motor-based view of attention, is consistent with many results from psychophysical studies of the relationship between saccades and orienting of attention. Perhaps some of the most informative sets of experiments are those demonstrating a lack of separability of the point of covert orienting from the point of intended gaze. Hoffman and Subramaniam (1995), refining the methods of similar studies on the relationship between saccades and covert orienting (e.g., Remington, 1980; Shepherd et al., 1986), measured detection accuracy of subjects instructed to make saccades to specific locations while also detecting targets at the same or different locations before saccade initiation. Based on the subjects' detection performance, the results suggested that attention was necessarily shifted to the point of intended fixation. Subjects were unable to attend to one location while preparing to shift their gaze to another. The close linkage between covert attention shifts and the planning of eye movements is consistent with an oculomotor-based view of spatial attention.

Motor Commands and Visual Representations

Macaque visual cortex has been divided into two relatively separate, functional streams, one proceeding ventrally into inferior temporal (IT) cortex and consisting of areas involved primarily in object and pattern vision, and the other proceeding dorsally into posterior parietal cortex (PPC), comprising areas involved in coding space (Ungerleider and Mishkin, 1982). The relationship between the representation of motor plans and of visual attention by neurons has been studied primarily in dorsal stream areas, particularly within posterior parietal cortex. The initial studies of PPC neurons in behaving monkeys by Hyvarinen and Poranen (1974), Mountcastle, and colleagues (Mountcastle et al., 1975; Lynch et al., 1977) appeared to demonstrate a dependence of neural responses to visual events on an animal's intention to direct its gaze or reach to a stimulus (i.e., overt attention). But subsequent experiments by Goldberg and Robinson (Goldberg and Robinson, 1977; Robinson et al., 1978) showed that although the visual responses of PPC neurons were certainly related to saccade or reach plans, they could nonetheless be dissociated from those movements. Furthermore, the responses to peripheral visual stimuli could be enhanced during fixation if the stimulus was made behaviorally relevant, i.e., during covert attention (Bushnell et al., 1981). However, more recent studies have reestablished a role of PPC neurons in motor intention by virtue of the dependence of their activity on the particular motor effector; neurons in the lateral intraparietal area (LIP) responding primarily before saccades and neurons in the parietal reach region (PRR) responding primarily before reaches to visual targets (Snyder et al., 1997, 1998). Despite the controversy regarding the precise role of PPC in visually guided behavior, electrophysiological studies of macaque parietal neurons have been instrumental in providing clues to how the representation of the world is actively constructed during visual scanning. These studies suggest, for instance, that the representation of visual space is dynamic before, during, and after a saccade is made (e.g., Duhamel et al., 1992). These studies also suggest that the representation of visual stimuli is heavily biased in favor of behaviorally relevant targets at the time a saccade is made (Kusunoki et al., 2000).

Studies that have explored the dynamics of visual signals conveyed by ventral stream neurons during saccades have been relatively scarce. As a result, little is understood about how objects and their component features are represented in visual cortex across changes in gaze. A few studies have reported perisaccadic modulation of inferior temporal (IT) cortex neurons (Chelazzi et al., 1993; Ringo et al., 1994; Sheinberg and Logothetis, 2001). The results of these studies suggest that object representations are dynamically filtered according to which stimuli are the targets of saccades. There have also been several studies of the saccade-related activity in area V4. Area V4 occupies a well-established position within the ventral stream (Ungerleider and Mishkin, 1982; Desimone et al., 1985). V4 neurons are selective for color (Zeki, 1973, 1978; Schein and Desimone, 1990), orientation (Desimone and Schein, 1987), disparity (Hinkle and Connor, 2001; Watanabe et al., 2002), as well as 3D contour (Hinkle and Connor, 2002), and their outputs provide the principal visual inputs to the highly complex neurons in inferotemporal areas TEO and TE (Desimone et al., 1980; Distler et al., 1993). Damage to this area disrupts discrimination of hue (Heywood and Cowey, 1987), form (Merigan, 1996), and texture (Merigan, 2000). Studies have also found that V4 lesions disrupt the detection of low-salience stimuli and the filtering of distracters (Schiller and Lee, 1991; De Weerd et al., 1999).

In addition to a clear role in pattern vision, some earlier studies suggest that V4 neurons serve a function in visually guided saccades. These studies, carried out in the early 1980s by Fischer and Boch (1981a, 1981b, 1985), were based on the type of studies pioneered by Wurtz and colleagues to study the role of the superior colliculus (SC) in saccades (Wurtz and Goldberg, 1972; Mohler and Wurtz, 1976). In the V4 experiments, monkeys were trained to make saccades to visual targets immediately upon their appearance or after a delay. Similar to cells in the superficial layers of the SC, V4 neurons exhibit enhanced visual onset responses when a RF stimulus is used as a saccade target. This enhancement is spatially dependent; when saccades are directed to non-RF targets, there is no enhancement, also similar to superficial SC cells. Furthermore, V4 neurons are "reactivated" prior to delayed saccades to RF targets (Figure 1). That is, when monkeys are trained to withhold saccades to targets flashed into a RF, one observes an initial visual response that adapts but then resurges prior to a saccade to the stable target. The presaccadic response of V4 cells observed during delayed saccades depends on the presence of a visual stimulus and thus appears to be a "reactivated" visual response. Likewise, enhancing SC cells do not respond before saccades to their RF when there is no visual stimulus (Wurtz and Mohler, 1976).

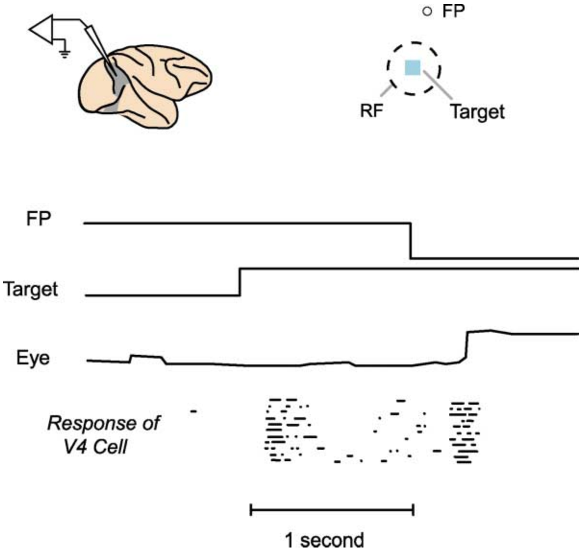

Figure 1. Presaccadic "Reactivation" of a V4 Neuron

The location of area V4 on the surface of the prelunate gyrus is shown in the side view of the macaque cerebral cortex. The response of the V4 neuron was recorded during a visually guided delayed saccade task. While the monkey fixated a central spot (FP), a visual target was presented inside the cell's receptive field (RF). After a delay, the fixation point was extinguished and the monkey made a saccade to the target. The eye position during each trial is shown by a representative horizontal position trace. The response of a single V4 neuron is illustrated in the raster below the event plots. The occurrence of a single action potential is denoted by a dot in the raster during each of 11 trials arranged vertically and aligned to the onset of the saccade. Note that not only is this neuron activated initially when the target first appears but also just before the saccade is made to the RF stimulus. (Adapted from Fischer and Boch, 1985.)

In the dominant view of V4's role in vision, evidence of saccade-related activity does not have a clear significance. (This might explain why this property of V4 neurons went unstudied for some 15 years.) Moreover, given that at least one view of ventral stream areas asserts that their role in vision is strictly passive (Goodale and Milner, 1992), the existence of presaccadic modulation seems even more curious. What function could presaccadic activity in V4 serve? Clearly, the absence of presaccadic enhancement prior to saccades to an empty RF indicates that this is not a purely *motor* signal. On the other hand, its dependence on the direction of impending saccades seems to rule out a purely *visual* signal as well. Thus, as with superficial SC neurons, it is necessary to consider a visuomotor role of this modulation as well as its relation to visual attention.

We might begin by asking how presaccadic activity differs from passive visual activity, i.e., the activity following the appearance of a visual stimulus in a cell's RF. Area V4 cells are highly selective to stimuli flashed within their RFs and to a variety of stimulus features. But is the presaccadic activity selective? If not, that result would imply a role of presaccadic activity only in triggering the eye movement. On the contrary, the presaccadic burst of V4 cells merely reestablishes the classical selectivity some 80 ms prior to saccade onset (Moore et al., 1998). This result is illustrated in Figure 2A. When a monkey makes saccades to a stable target presented at varying orientations, the reactivated response restores the orientation selectivity observed when the target first appears. Thus, the presaccadic signal effectively synchronizes a visually selective representation of the target with the saccade. These signals might facilitate the integration of pre and postsaccadic representations of the target (Irwin, 1991; Moore et al.,

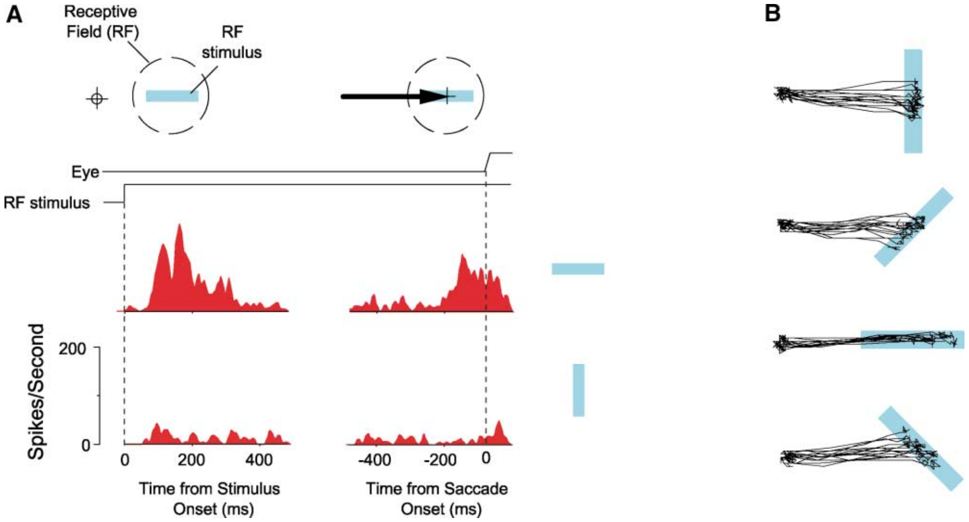

Figure 2. Activity of a V4 Neuron during Visually Guided Saccades, and the Degree of Visual Guidance of Saccades to Targets of Different Orientation

(A) The responses of a single V4 neuron during delayed saccadic eye movements to an oriented bar stimulus presented within a V4 cell's RF. Each plot shows the mean instantaneous firing rate of the cell when either the preferred (top) or nonpreferred (bottom) orientation was used as the target. The cell's activity during the first half of trials is aligned to the onset of the RF stimulus (left) and during the second half is aligned to the saccade (right). The cartoon above illustrates the two phases of the trial. In the first half, the point of fixation ("+") was on the fixation spot, and in the second half, the monkey made a saccade to the RF stimulus (arrow). When the preferred stimulus was presented, the neuron responded not only at the time of onset but also immediately before the monkey made a saccade to the stimulus. When the bar stimulus was presented at the nonpreferred orientation, the neuron failed to respond robustly at either time.

(B) Saccades made to oriented bar stimuli during the visually guided, delayed saccade task. Shown are individual saccade vectors (black lines) obtained from a single block of trials (13 trials/orientation). Note that the saccade end points fall along the axis of bar orientation.

1998). Moreover, robust presaccadic signals could also aid in the attenuation, by forward masking, of the "grey-out" or blur caused by rapid displacement of retinal stimuli (Campbell and Wurtz, 1978; Moore et al., 1998).

However, the fact that presaccadic signals are visually selective does not rule out a motor role. As is now widely appreciated, the degree to which saccades can be guided by the features of a target is tremendous. From merely examining the endpoints of a large number of saccades, one can often reconstruct the contours of the target (Yarbus, 1967). Studies of eye movements during reading have shown that movements to particular words in a line or phrase are idiosyncratic in their landing points and that often there are ideal landing points in terms of speed of comprehension (Vitu et al., 1990). Combined with the observation of enhanced presaccadic target representations in ventral stream areas, these facts suggest that pattern vision mechanisms play an active role in visually guided saccades. One study has sought and found evidence of this (Moore, 1999). Using saccades to oriented bars from the above V4 study, analyses revealed that these movements were guided by the target's orientation (Figure 2B). The endpoints of saccades tended to splay out along the axis of orientation. Moreover, the strength of the presaccadic response to each cell's preferred orientation in a population of cells correlated with the degree of visual guidance. In other words, the fovea's landing point along the target's contour could be predicted by the degree to which V4 cells coded that contour prior to saccade onset.

Consideration of the efferent projections of V4 neurons makes the above observation less surprising. As with most extrastriate visual areas, V4 projects directly to the SC and to the FEF in addition to its heavy input to inferotemporal cortical areas (Fries, 1984; Schall et al., 1995). The *visual* and *motor* accounts of presaccadic activation of V4 cells are by no means mutually exclusive. On the contrary, they are both suggestive of a reciprocal, visuomotor mechanism, out of which a more complex phenomenon may emerge, namely visual selection. As previously discussed, a wealth of psychophysical evidence has linked oculomotor control with spatial attention, both overt and covert. These studies suggest that visual selection may accompany planned changes in gaze even when those plans are not carried out. A comparison of the neural correlates of overt and covert visual selection sheds additional light on this issue.

Covert Attention Effects in Visual Cortex: Parallels with Overt Attention

Although most shifts of attention are accompanied by shifts in gaze, we are nonetheless able to attend to a stimulus without fixating it. Attention can be directed covertly as well as overtly (Figure 3). Although we usually bring targets of interest to the foveas, sometimes the required movements need to be suppressed. Gaze direction is often deliberately averted from the subject of attention, particularly during social interactions. For primates, direct gaze is often a sign of aggression. As a result, subdominant macaques, for example, often avoid the gaze of the more dominant ones, even while covertly monitoring them (Mendelson et al., 1982). To

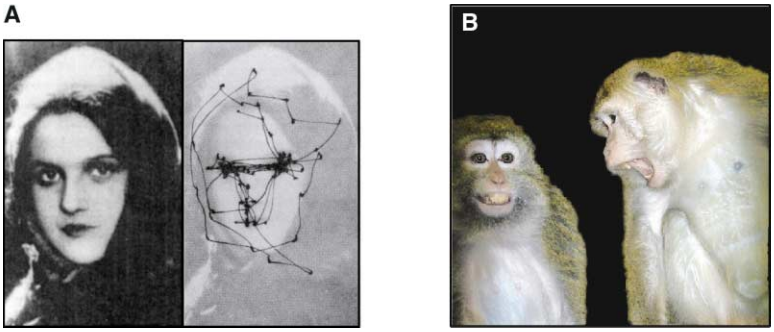

Figure 3. Overt and Covert Visual Attention

(A) Example of the overt selection of visual features contained within a portrait of a young woman as revealed by the scanning eye movements of a human subject. The figure on the right shows the subject's eye position traces superimposed on the portrait displayed by itself on the left. (Adapted from Yarbus, 1967.)

(B) An example of covert attention in macaque monkeys. The female monkey on the left is looking straight ahead and past the large threatening male on the right. However, it is apparent that the smaller monkey is fully attending to her neighbor.

date, several laboratories have found that the responses of neurons to covertly attended stimuli are enhanced above that of unattended stimuli in multiple extrastriate visual areas (see Desimone and Duncan, 1995; Maunsell, 1995, for reviews), and even some effects in V1 have been reported (Roelfsema, et al., 1998). In a typical experiment, a monkey is trained to attend to peripheral stimuli appearing at a particular location (e.g., Luck et al., 1997; McAdams and Maunsell, 1999) or to a particular stimulus, regardless of location (e.g., Chelazzi et al., 1998), while maintaining central fixation. The responses of neurons to physically identical stimuli are then compared across different states of attention. Although there are some exceptions (Motter, 1993), neural responses to attended stimuli are generally more robust.

More is known about the effects of covert attention on the visual responses of area V4 neurons than on any other area in macaque visual cortex. Separate studies have tested the effects of spatial attention on the RF profiles of single neurons (Connor et al., 1997), on their orientation tuning (Spitzer et al., 1988; McAdams and Maunsell, 1999), contrast thresholds (Reynolds et al., 2000), as well as on the representations of multiple, competing RF stimuli (Reynolds et al., 1999). Each of these studies provides evidence consistent with psychophysical data suggesting improved detection and discrimination of attended stimuli in the presence of distracters (e.g., Cheal and Gregory, 1997). Furthermore, evidence from studies of covert attention effects in this area also offers clues to the possible sources of biased signals in visual cortex.

In addition to offering compelling correlates of covert spatial attention, the above studies demonstrate intriguing parallels with studies of presaccadic activity in V4 (Figure 4A). The effects of overt and covert attention on cells in this area are similar in that in both cases responses to the target are enhanced (Fischer and Boch, 1981b; Motter, 1993). Moreover, this enhancement depends on how well the visual stimulus drives the activity of the studied neuron; the greatest enhancement is observed when attention is directed to the more effective stimulus in both the covert (Motter, 1993; Spitzer et al., 1988; McAdams and Maunsell, 1999) and overt cases (Moore et al., 1998; T. Moore, A.S. Tolias, and P.H. Schiller, 1998, Soc. Neurosci., abstract). Two separate studies have examined the effect of overt (Tolias et al., 2001) and covert (Connor et al., 1997) spatial attention on RF profiles of V4 neurons (Figure 4B). Both found that directing attention to locations near but outside a cell's RF was associated with increased responsiveness to stimuli at those locations. In both cases, the results suggest that the RFs of V4 neurons are not fixed rigidly in retinotopic space but can shift in the direction of attended targets. The similarities between the effects of overt and covert spatial attention on V4 activity could be explained by two independent mechanisms, saccade programming and visual selection, that happen to be temporally coupled during saccades (Thompson et al., 1997). On the other hand, it might be that the two are not independent and that the programming of saccades per se imposes a bias on incoming visual signals, even if the movement is not initiated.

Oculomotor Maps as "Salience Maps"

Some theoretical approaches to visual attention have employed the concept of a "salience map" to represent the differential weighting of incoming visual signals according to their featural or spatial characteristics (Koch and Ullman, 1985; Blaser et al., 1999). When attention is directed toward a location, such a map could bias visual representations in favor of stimuli at the attended position. Not surprisingly, the physiological instantiation of the salience map has been difficult to identify. What characteristics should neurons in a salience map possess if their activity is used to direct attention spatially? Presumably, such a map should accurately code the location of a visual stimulus, while failing to specify its featural characteristics. Thus, activation of a particular subset of the map would strengthen the representation of whatever stimulus is positioned at the corresponding point in space, while failing to alter its identity.

A common feature of neurons in structures uniquely involved in visually guided saccades is that they are seldom visually selective, although their activity can convey spatial information. This description applies to neurons in the SC (Wurtz and Goldberg, 1972), parietal area LIP (Colby and Duhamel, 1996, although see Sereno and Maunsell, 1998), the inferior and lateral pulvinar (Petersen et al., 1985), and the FEF (Mohler et al., 1973; Robinson et al., 1978). Neurons in these structures seem to relate the presence of visual targets to the command signals that shift the foveas to their location (Wurtz and Goldberg, 1972; Snyder et al., 1997; Robinson, 1993; Goldberg and Bushnell, 1981). However, the neural activity within these structures could simultaneously impose a saccade probability map onto incoming visual

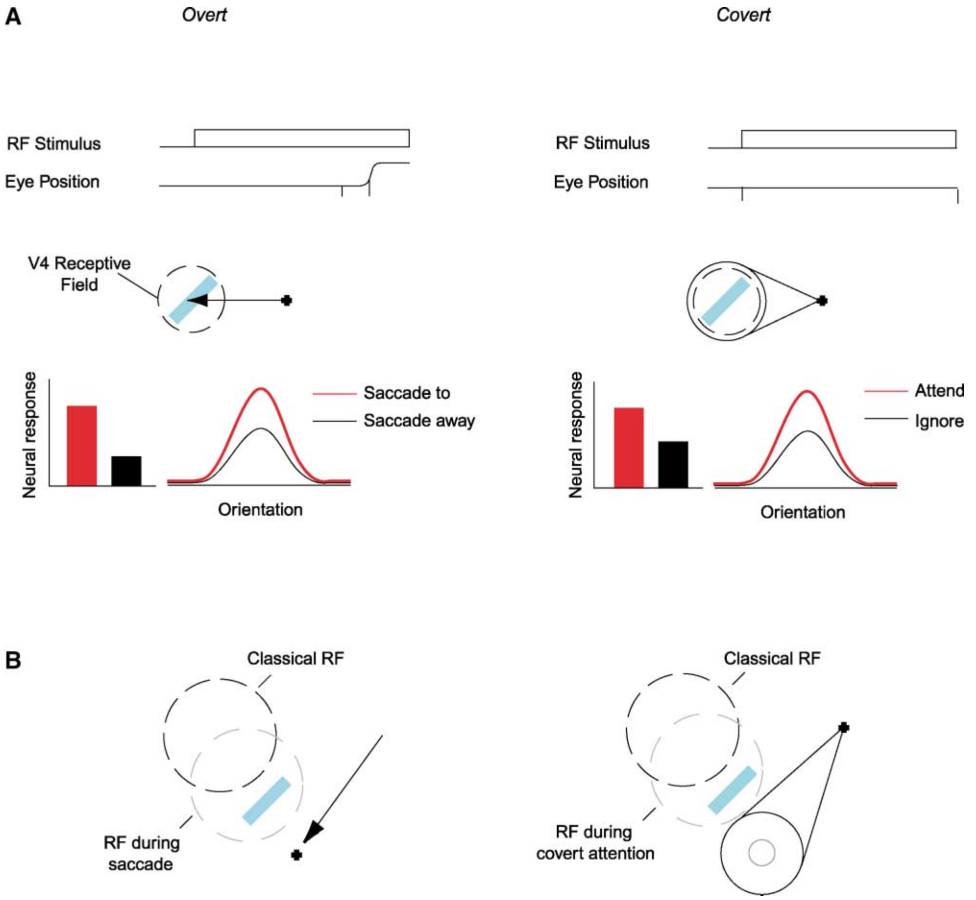

Figure 4. Overt and Covert Spatial Attention Effects in Area V4

(A) In studies of overt attention (left), a monkey is trained to make saccades to stable visual stimuli after a delay, and the effects on the presaccadic responses are compared between the different conditions. The event plot at the top indicates the period during which the activity of the cell is compared in the attended (saccade to RF) and unattended (saccade away) conditions (tick marks at time of saccade). The bottom plots summarize the basic results obtained, namely that overall visual responses are enhanced prior to saccades that target the RF stimulus and that the enhancement is greatest for the most effective stimuli (Fischer and Boch, 1981a, 1981b; Moore et al., 1998; T. Moore, A.S. Tolias, and P.H. Schiller, 1998, Soc. Neurosci., abstract). In studies of covert attention (right), monkeys are trained to attend to a peripheral stimulus while maintaining central fixation (spotlight). The attended stimulus can be placed within the RF of the V4 neuron under study, or at some other location, and the visual responses compared. The event plot at the top indicates the period over which the activity of the cell is compared in the attended and unattended conditions (tick marks on stable eye position). The bottom plots summarize the basic results obtained: overall visual responses are enhanced when the attention is directed to the RF stimulus (e.g., Motter, 1993) and that this enhancement is greatest for the most effective stimuli (McAdams and Maunsell, 1999).

(B) At the time overt attention (a saccade) is directed to a location outside of but near a cell's RF, the RF of some cells shifts toward the target location (Tolias et al., 2001). When covert attention is directed to a location outside of but near a cell's RF, the RF of some cells shifts toward the attended location (gray ring) (Connor et al., 1997).

signals, thereby modifying stimulus salience directly. For this to be true, there must be an anatomical basis by which motor command neurons, or neurons with efferent copies of those commands, provide recurrent inputs to neurons principally involved in representing the visual stimulus. Such an anatomical basis is evident for some structures involved in oculomotor control, particularly the FEF.

The FEF is reciprocally connected with many posterior visual areas, including areas V2, V3, V4, MT, MST, LIP, TEO, and TE (Stanton et al., 1995; Schall et al., 1995). Moreover, these connections are organized with respect to the amplitude of the saccades represented in FEF and the part of visual space represented in extrastriate cortex. Neurons in the lateral portion of the FEF, in which small saccades are represented, receive input from and project input to ventral visual areas where the central visual field is heavily represented. Neurons in the more medial portion of the FEF, where larger saccades are represented, are reciprocally connected with more dorsal visual areas where the peripheral visual field is heavily represented. Most of the feedback projections to posterior visual areas have a bilaminar pattern, with axons terminating in the superficial and deep layers, with the exception of projections to LIP and area MT that terminate in all laminae (Stanton et al., 1995). This anatomical relationship not only suggests a mechanism by which information about visual targets and their features can guide saccade metrics in a bottom-up fashion (e.g., Groh et al., 1997; Moore, 1999), but it also suggests a mechanism by which saccade-related signals can exert influences on visual representations. We next describe some recent experiments that begin to explore this possibility.

Focusing Spatial Attention with Microstimulation of the FEF

Despite an abundance of indirect evidence of a causal relationship between saccade programming and spatial attention, until recently there has been no direct test of such a relationship. Kustov and Robinson (1996) elegantly demonstrated that the direction of covert attention can influence the metrics of saccades evoked by microstimulation of the SC. In this study, the authors trained monkeys on a cue-target reaction time task in which the animal had to indicate the appearance of a target either with an eye movement or with a manual response. As with human subjects (Posner, 1980; Posner and Cohen, 1984), cues that correctly indicated the location of the impending target reliably lowered the monkey's reaction time. During the task, the investigators electrically stimulated sites within the SC to evoke saccades. They found that the direction of stimulation-evoked saccades was systematically shifted in the direction of the cued (attended) location. Moreover, these shifts had a time course that mirrored the time course of changes in reaction time to cued targets. This work demonstrates that involuntary shifts in attention, as measured by decreases in reaction time, are associated with eye movement preparation. What remains unclear, however, is whether attention shifts are *caused* by saccade preparation or vice versa.

If spatial attention shifts are a byproduct of preparation of saccades to a particular location, then it should be possible to direct attention by manipulating oculomotor signals. We recently explored this possibility by studying the effects of electrical microstimulation of the FEF on spatial attention (Moore and Fallah, 2001, 2003). As mentioned previously, the FEF contains a map of saccades coded in retinotopic space (Bruce et al., 1985). Microstimulation of the FEF evokes short-latency saccades, the metrics of which are constant for a given site and virtually indistinguishable from visually guided saccades (Figure 5A). As with other motor-related structures, at each FEF site the probability of evoking a saccade depends on the parameters of stimulation, most notably current and pulse frequency (for review, see Tehovnik, 1996). When stimulation current is varied, FEF sites can be characterized by easily obtained current threshold functions (Figure 5B). When an FEF site is stimulated below the current threshold, saccades are not evoked, but biases in the preparation of saccades can nonetheless be observed. For example, in the absence of a visual stimulus, subthreshold stimulation may fail to evoke a saccade. Yet, at the same current, the tendency of the monkey to saccade to a stimulus placed at the location represented by neurons at the stimulation site can be dramatically biased (Schiller and Tehovnik, 2001). We tested whether these oculomotor biases were accompanied by advantages in the processing of visual stimuli at corresponding locations.

We trained monkeys on an attention task in which they had to detect luminance changes of a peripheral target while ignoring a distracter (Figure 5C). Each monkey was required to maintain fixation throughout the task and indicate the target change with a manual response. In a block of trials, we measured the lowest luminance change the monkey could detect, i.e., the psychophysical threshold. Past studies of attention mechanisms involving monkeys have also employed tasks in which monkeys were trained to detect target luminance changes (Mohler and Wurtz, 1976; Bushnell et al., 1981). We modified this basic task to further require the monkey to attend to only one location by adding a distracter, which repeatedly flashed on and off at random locations in the display, except the region immediately surrounding the target stimulus. Flashing stimuli are potent distracters, drawing attention involuntarily (Remington et al., 1992). Thus, the monkey had to ignore the luminance changes at all locations but the target location. During each experiment, we located a site within the FEF from which we could evoke saccades with microstimulation. We then mapped the region of space to which FEF stimulation shifted the monkey's gaze, referred to as the "movement field" (MF), and determined the current threshold. We placed the target to be attended at the MF or at another location. During a fraction of behavioral trials, we preceded the target change with microstimulation of the FEF at current levels below that which evoked saccadic eye movements, while the monkey maintained fixation. On other trials, we stimulated the FEF when no target change took place to determine if it altered the monkey's tendency to report a target change.

We found that when the target change was preceded by microstimulation of the FEF, monkeys were more sensitive to changes in target luminance than during control trials (Figure 5D). Since our measurement of sensitivity depended on both the change and no-change trial performance, this improvement resulted both from an increased detection of target changes and a decrease in the rate of "false alarms." The increased sensitivity to the target change only occurred when the target was placed in the MF. When the task was performed with the target outside of the MF, there was no effect of microstimulation. Thus, the effect of stimulation was not merely to globally heighten sensitivity to target changes but to enhance detection performance at a discrete location.

But how could microstimulation improve performance at an already attended location? If we assume that the monkeys paid maximum attention to the target location, given prior knowledge that the target change would occur there, how could performance be enhanced? Presumably, one should not expect to increase the allocation of attention if it is already saturated. However, our ability to increase a monkey's sensitivity to the target change with microstimulation seems to have resulted partly from a withdrawal of attentional allocation during control trials. During some sessions, the monkey's sensitivity to the target change was measured in blocks with no microstimulation trials. Often, the monkey's sensitivity was greater during these control-only blocks than when microstimulation trials were interleaved (our unpublished data). Thus, the improvement in detection performance might have been achieved in part by reducing the monkey's need to allocate attention to the target

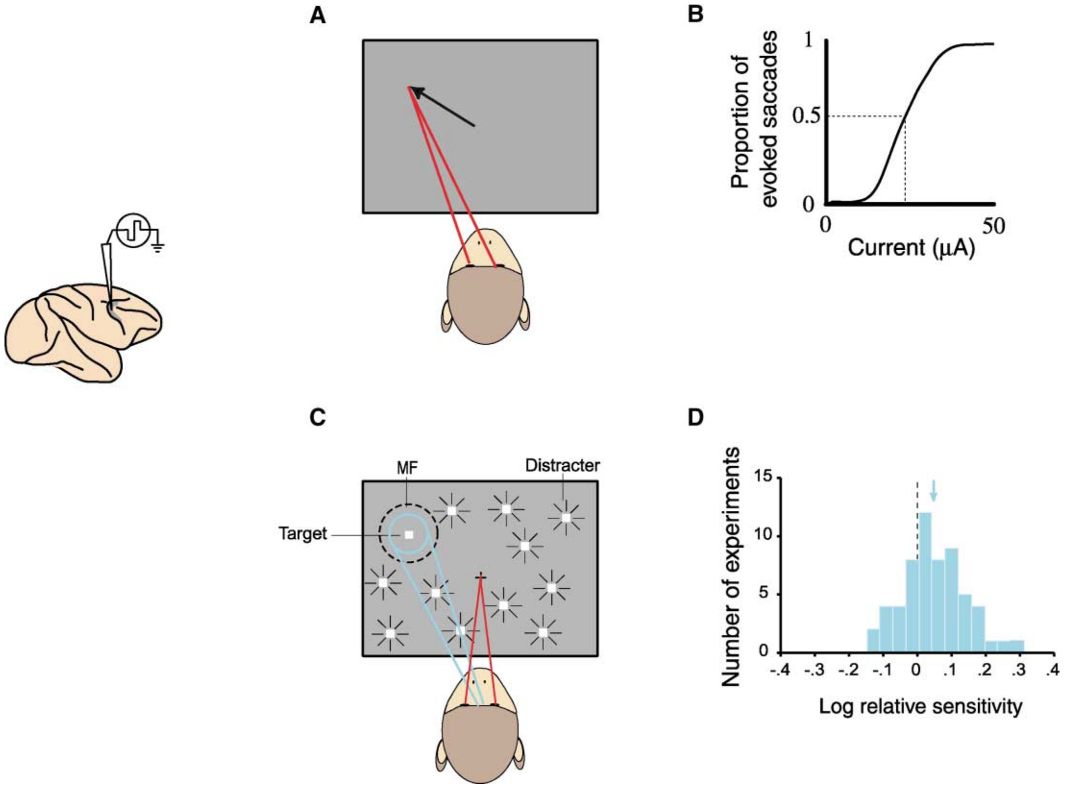

Figure 5. Microstimulation of the FEF and Its Effects on Covert Spatial Attention

The location of the FEF is shown in gray in the side view of the macaque brain. (A) Electrical stimulation of FEF sites can evoke saccades that shift a monkey's gaze to a fixed location with respect to the center of gaze (MF, or "movement field"). (B) The probability that a saccade will be evoked varies as a logistic function of current amplitude. In the example depicted, a saccade is evoked 50% of the time when the *threshold* current of 25 μA is applied to the FEF site. (C) Monkeys were trained on an attention task in which they had to detect the transient dimming of a visual stimulus (target) while ignoring a flashing distracter that appeared sequentially at random locations of the display. The target was placed at the location to which the monkey's gaze would be shifted with suprathreshold stimulation of the FEF site (part A). The attention task was performed with and without subthreshold stimulation of the FEF site on randomly interleaved trials. On stimulation trials, microstimulation occurred immediately prior to the dimming of the target stimulus. (D) Microstimulation increased the monkey's sensitivity to the target change, relative to nonstimulation trials. The distribution of relative sensitivity values (microstimulation/control, expressed logarithmically) is shifted above 0 (mean at arrow), indicating increased sensitivity during microstimulation. This effect was only observed when the target was positioned within the MF. (Adapted from Moore and Fallah, 2001, 2003.)

location for a given rate of reward. This would be consistent both with the interpretation that FEF microstimulation increased the salience of the target change and with previous observations of compensatory behavioral strategies in animals during electrical stimulation (Tehovnik et al., 1999).

Gating Signals in Visual Cortex with FEF Microstimulation

The above results indicate that, by activating networks capable of evoking saccades to a particular location, we can also improve a monkey's ability to extract visual information from that location. More recent experiments show that suprathreshold microstimulation of the FEF causes monkeys to select one of two moving targets for pursuit (Gardner and Lisberger, 2002), suggesting that activation of FEF triggers a commitment to a particular sensory interpretation and an appropriate motor plan (Shadlen, 2002). Aside from suggesting that the preparation of gaze shifts initiates corresponding shifts in spatial attention, these results suggest that the gain of visual representations may in part be a function of biases in the preparation of saccadic eye movements. If the latter is true, we should expect subthreshold FEF stimulation to gate responses in visual cortex, particularly in those areas in which attention effects have been observed. Moreover, it should be possible to initiate spatial attention-like neural effects in monkeys passively viewing stimuli.

In a broader attempt to understand the functional interactions between visual and oculomotor mechanisms, we studied the effects of microstimulation of FEF sites on the responses of single V4 neurons to visual stimuli in monkeys while they fixated a central point (Moore and Armstrong, 2003). In each experiment, we located sites within the FEF from which saccades could be evoked to points in visual space overlapping the RF of a simultaneously recorded V4 neuron (Figure 6A). As with the psychophysical experiments, we then lowered the stimulation current to well below the movement threshold and tested the effect of microstimulation on the responses of V4 cells to visual stimuli. While the monkey fixated, oriented bars were presented within a

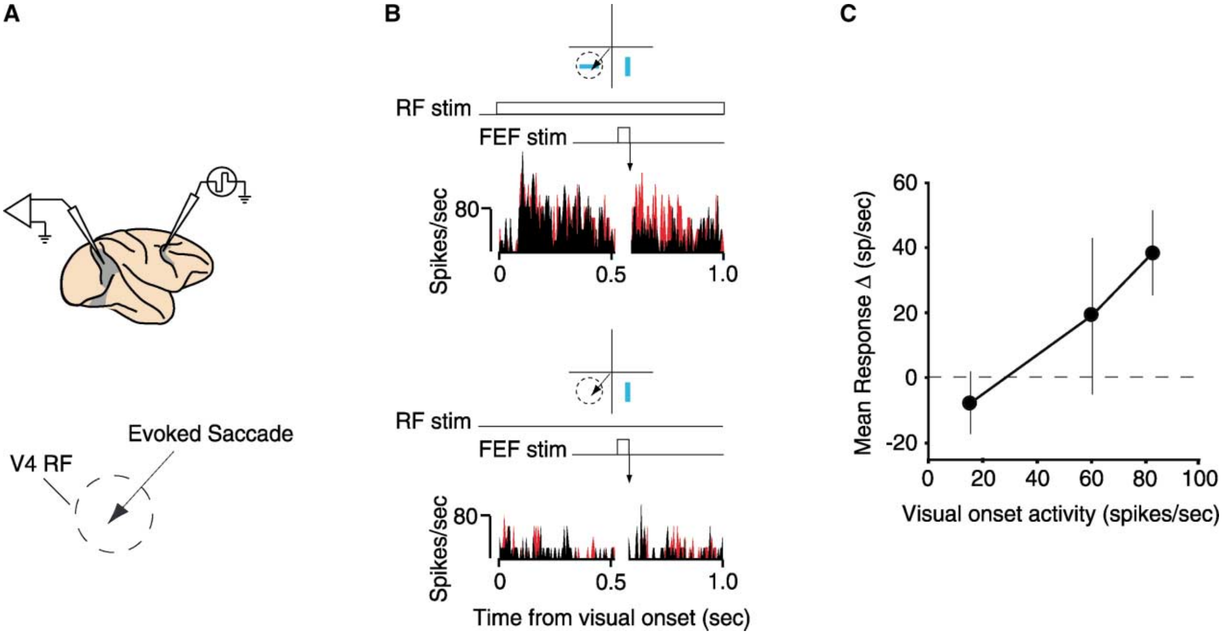

Figure 6. Effect of FEF Microstimulation on the Visual Response of V4 Neurons

(A) Microstimulation of sites within the FEF was carried out while simultaneously recording the responses of single V4 neurons to visual stimuli in monkeys performing a fixation task. The FEF microelectrode was positioned so as to align the evoked saccade vector with the RF position of the V4 cell under study (bottom cartoon).

(B) (Top) Example of the effect of FEF microstimulation on the response of a single V4 neuron to an oriented bar presented to the cell's RF (cartoon above) when the saccade vector represented at the FEF site (arrow) overlapped with the V4 RF. Mean response during control trials is shown in black, and the mean response of trials on which a 50 ms microstimulation train (FEF stim) was applied to the FEF site is shown in red. (Bottom) Same as in top, but histograms show responses during trials on which a visual stimulus is only presented outside of the RF. The response of the cell was elevated immediately following the stimulation train but only when the cell was being driven by a RF stimulus (i.e., top versus bottom histogram).

(C) The stimuation-driven enhancement of the cell's response depended critically on the effectiveness of the visual stimulus. When there was no RF stimulus, there was a near zero change in the cell's response, compared to control trials. When there was a nonoptimally oriented vertical bar in the RF, there was an intermediate enhancement. The greatest enhancement was observed when a horizontally oriented bar stimulus was presented inside the RF. (Adapted from Moore and Armstrong, 2003.)

V4 cell's RF, outside of it, or at both locations. On half of the trials, we delivered the subthreshold stimulation train to the FEF site 500 ms after the visual stimulus had appeared. This delay allowed us to examine the effect of microstimulation on the V4 response to a stable—as opposed to a flashed—visual stimulus. Thus, microstimulation of the FEF site could amplify, interfere with, or have no effect on the cell's representation of that stable stimulus.

When the evoked saccade vector overlapped the V4 RF, microstimulation of the FEF elicited a transient increase in the responsiveness of the V4 cell to visual stimuli (Figure 6B). Following the end of the stimulation train, there was an enhancement of the visual response which lasted 100—200 ms. When the visual stimulus did not appear in the RF, but only outside of it, microstimulation of the FEF site did not affect the cell's activity. The lack of an effect when the V4 cell was not visually driven rules out the possibility that FEF stimulation directly activated the cell under study, e.g., antidromically. Instead, it seems to show that the effect of FEF microstimulation was to raise the gain of the visually driven response, given that the difference between the cell's activity with and without a visual stimulus was increased above that of control trials. By using oriented bar stimuli, we were able to further examine the dependence of the stimulation effect on the amount of visual drive (Figure 6C). As would be expected by a simple (multiplicative) gain modulation (McAdams and Maunsell, 1999), the effect of FEF microstimulation on the responses to less-effective (nonpreferred) visual stimuli was intermediate to that of the most effective (preferred) stimulus and no stimulus conditions. For the example shown in Figure 6C, a particularly powerful example, the visual response was increased by about 1.5 times, both for preferred and nonpreferred stimuli.

As with the psychophysical experiments, it is crucial to know the degree to which the effect of FEF microstimulation is spatially dependent. Again, it might be that FEF stimulation heightens visual responses globally. To study the spatial dependence of the response gating effect, we conducted a set of stimulation experiments in which the evoked saccade vector shifted the monkey's gaze to a location outside of the RF of the recorded V4 cell. In these experiments, the visual stimulus placed outside of the RF was presented at the location to which suprathreshold stimulation shifted the monkey's gaze. Single-unit studies of attention have found that covert attention to one stimulus suppresses responses to nearby stimuli (Reynolds et al., 1999). Therefore, if subthreshold FEF stimulation initiates the covert selection of the non-RF stimulus rather than the RF stimulus, we might expect to observe a suppression of RF responses. Although the magnitude of the effect in the nonoverlap experiments was about half that of the overlap experiments, we indeed observed a significant suppression of visual responses to RF stimuli following brief microstimulation of FEF sites with nonoverlapping representations (Moore and Armstrong, 2003).

Somewhat to our surprise, the stimulation-driven enhancement and suppression of visual gain also depended critically on the presence of the non-RF stimulus. When the RF stimuli were presented singly, microstimulation effects were much reduced. In fact, in our sample of V4 neurons, the only significant effect of FEF stimulation on singly presented RF stimuli was found when the preferred stimulus was in the RF, and only during the *overlap* experiments. This result seems to add further evidence supporting the hypothesis that subthreshold stimulation of the FEF transiently shifts covert attention to the location represented by the FEF site. That is, if the hypothesis is true, the magnitude of the effect should depend critically on the presence (and number) of distracters (Treisman, 1969). Since single-unit recording studies have found that covert attention effects are often larger when multiple targets are present (e.g., Motter, 1993; Luck et al., 1997), the effects that we induced by microstimulation of FEF may represent a lower bound on the range of possible effects.

Interpretations and Future Directions

One straightforward interpretation of our psychophysical and physiological observations would be that biases in saccade preparation initiate spatially corresponding biases in the gain of visual representations. That is, by directly manipulating the probability that a saccade will be made to a particular visual stimulus, we appear to have correspondingly altered the gain of signals representing that stimulus. However, the FEF is not a strictly motor structure, and contains neurons exhibiting a broad spectrum of properties, from visual to motor, culminating in a map of visual space in which the amplitude and direction of saccades are organized in retinotopic coordinates (Bruce, 1990). Microstimulation of this area should be expected to excite the entire spectrum of FEF representations. It is possible that the attention-like effects were brought about by the coactivation of circuits completely separate and independent from those that trigger saccadic eye movements. Indeed, studies of FEF neurons seem to suggest the existence of a subpopulation of neurons specifically related to stimulus relevance but not an impending saccade (Schall, 1995; Thompson et al., 1997). Although it seems unlikely that specialized subpopulations within the FEF operate independently of one another, a more refined interpretation must take into account the collective visual and motor roles that FEF neurons, and neurons with FEF connections, play.

The fact that many FEF neurons, and neurons connecting to the FEF, have visual responses also raises important questions about the nature of signals introduced by microstimulation. Does microstimulation of FEF inject a *visual* signal? Clearly, what a monkey experiences during FEF microstimulation is all but impossible to determine, owing to the animal's inability to describe those experiences. Nonetheless, results from both the physiological and psychophysical manipulations suggest that the nature of the signal injected by FEF microstimulation is consistent with the response properties of FEF neurons. Visual responses exhibit little or no visual selectivity (Mohler et al., 1973), but presaccadic activity is highly tuned to the direction and amplitude of saccades (Bruce et al., 1985; Schall et al., 1995). These properties suggest that activation of sites within the FEF can specify a location in space without specifying a particular visual stimulus or stimulus attribute. This conclusion is supported by our failure to find any evidence that FEF stimulation altered the identity of the visual stimulus, particularly as measured by the responses of V4 neurons. In neither the psychophysical nor the physiological experiments was there evidence that FEF stimulation imposed a visual signal or visual percept. This finding is also consistent with the general failure of stimulation of FEF in humans to produce visual percepts, or phosphenes, while nonetheless evoking saccades (Penfield and Rasmussen, 1950; Blanke et al., 2000). Thus, the visual activity in this area may merely represent the salience of visual targets (Thompson et al., 1997). If so, the effect of FEF stimulation might be to increase the strength of visual representations via known feedback projections to posterior visual areas (Stanton et al., 1995) while simultaneously increasing the probability of the stimulated saccade representation. This view is consistent with both the *visual* and the *motor* properties of this area.

Although it is convenient to assume that the effects of stimulation on vision are principally due to the activation of top-down projections from the FEF to posterior visual areas, there is hardly a basis for choosing this over many other pathways. Even if one assumes that the microstimulation effects were solely orthodromic, there are several other possible pathways responsible for the observed phenomena. Aside from posterior visual areas, the FEF also projects directly to the SC (Sommer and Wurtz, 2000), which in turn projects to the pulvinar (Benevento and Standage, 1983; Kaas and Huerta, 1988). The pulvinar projects widely to extrastriate visual areas (Benevento and Rezak, 1976; Rockland, 1999) and has previously been implicated in the control of covert orienting (Robinson, 1993). In addition, the FEF and area LIP are highly and uniquely interconnected. FEF connections with the LIP for instance seem to be the only ones that violate the topography of feedforward and feedback circuits between the FEF and posterior cortical areas; both medial and lateral FEF project back to and receive input from LIP, whereas other areas tend to connect with only one part of the FEF (Schall et al., 1995; Stanton et al., 1995). Thus, in accordance with correlational evidence of LIP's involvement in spatial attention (e.g., Bisley and Goldberg, 2003), it may be that the stimulation-driven effects we observed operated solely via area LIP in parietal cortex. In fact, results from one human fMRI study demonstrated a selective activation of the FEF and the superior parietal lobule of subjects instructed to attend to a blank part of visual space (Kastner et al., 1999). The study also found activation of the supplementary eye field, another area heavily connected with the FEF. Future neurophysiological studies will need to further specify the circuits necessary and sufficient to alter the gain of visual signals. Evidence to date suggests that such studies will require a more refined account of visuomotor integration.

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