Neural Mechanisms of Selective Visual Attention

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Keywords

orienting, cognition, visual perception, neural circuits, sensory processing

Abstract

Selective visual attention describes the tendency of visual processing to be
confined largely to stimuli that are relevant to behavior. It is among the
most fundamental of cognitive functions, particularly in humans and other
primates for whom vision is the dominant sense. We review recent progress
in identifying the neural mechanisms of selective visual attention. We discuss
evidence from studies of different varieties of selective attention and examine
how these varieties alter the processing of stimuli by neurons within the visual
system, current knowledge of their causal basis, and methods for assessing
attentional dysfunctions. In addition, we identify some key questions that
remain in identifying the neural mechanisms that give rise to the selective
processing of visual information.

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INTRODUCTION

Although we experience a complete image of the visual world, our capacity to process all facets of available visual information is extremely limited. These limitations are made compellingly evident in a number of widely popularized perceptual demonstrations, including demonstrations of change blindness (e.g., see **http://cogsci.uci.edu/~ddhoff/cb.html**). However, the limitations in our perception are also apparent when simply considering how much of a typical visual scene we fail to notice or recollect. When considering these limitations in the context of our visual system, which, as in other primates, involves a proportion of subcortical and cortical structures that vastly outstrips that of the other senses, it may seem striking that so much neural machinery frequently goes unused. Visual information that is first transduced in the retina and then conveyed through the visual system is encoded by neurons along numerous spatial and featural dimensions such that the output of populations of neurons at some stages can signal the identity and location of a seemingly infinite number of stimuli. Yet it appears that, under most circumstances, that information goes unused. However, one must also consider the largely adaptive consequences of these limitations, given that what we tend to perceive is the information most relevant to our behavioral goals. Although the visual system carries out a more or less exhaustive extraction of visual information from the environment, at least at early stages, our behavior is driven only by the small subset of that information that is most pertinent. This aspect of visually guided behavior is broadly referred to as selective visual attention, and it is among the more fundamental cognitive functions. In this review, we discuss recent evidence that elucidates the neural mechanisms of visual selective attention. In doing so, we attempt to consider all aspects and types of visual selective attention and discuss how they alter visual processing, their causal basis, and how to assess dysfunctions of attentional control.

VARIETIES OF SELECTIVE VISUAL ATTENTION AND THEIR CORRESPONDING NEURAL CORRELATES

Organisms have a tendency to selectively process only a subset of sensory input. This selective processing comes in multiple forms, and in considering the neural circuitry of attention it is important to consider each of them separately. Although it may seem likely that the different forms of attention should share common mechanisms or consequences at some basic level (e.g., effects on neural coding), as is frequently implied in some models (e.g., Lee & Maunsell 2009, Reynolds & Heeger 2009), the different forms should also be expected to be quite different at other levels (e.g., neuronal source). In the visual modality, a useful starting point is the division of selective attention into three (presumably orthogonal) dichotomies, i.e., three pairs of contrasting types of attention. The first of these is top-down versus bottom-up selective attention, the former describing selective visual processing due to an endogenously generated signal (e.g., representation of a rule, strategy, or motivational state) and the latter describing selective processing based solely on the physical salience of the visual stimulus (e.g., bright or moving objects). In recent years, several investigators have described the combination of top-down and bottom-up factors as stimulus priority, given evidence that neurons in some structures signal both types of attention (Bisley & Goldberg 2010). The second dichotomy distinguishes spatially directed selective attention from attention directed toward particular classes of visual features or objects. The third dichotomy distinguishes between the selective processing of stimuli in the absence of any orienting movements (covert attention) from that which occurs in conjunction with orienting movements (e.g., eye movements, reaching, or grasping). As we discuss in the following sections, by definition these dichotomies already suggest divergent neural mechanisms (e.g., absence of motor commands in covert attention); however, there is still surprisingly little known about the mechanistic basis of these different manifestations of attentional selection.

Top-Down and Bottom-Up Attention

As described above, the deployment of attention can occur either by virtue of the physical salience of a stimulus or according to internal, behavioral goals. Most neurophysiological studies in the past, particularly those aimed at identifying neural circuits controlling attention, have focused primarily on top-down attention. Although it is clear that both top-down and bottom-up attention modulate neuronal activity within the visual system, both the neurophysiological effects and the underlying circuitry of these forms of attention are less understood. In the following sections, we discuss evidence for both forms.

Neural correlates of top-down attention. The primary focus of research on visual selective attention has been on the influence that top-down, covert attention has on visually driven signals throughout the primate visual system, and this research has included parallel work in humans (Corbetta et al. 1991, Hillyard 1993, Heinze et al. 1994, Luck et al. 2000, Pessoa et al. 2003) and nonhuman primates (Desimone & Duncan 1995, Reynolds & Chelazzi 2004, Noudoost et al. 2010). In neurophysiological studies of the latter, the basic observation is that selective visual attention increases visually driven firing rates of neurons encoding the attending stimulus; this modulation is present as early as the dorsal lateral geniculate nucleus (dLGN) (McAlonan et al. 2008) and increases in magnitude at subsequent stages of visual processing (Moran & Desimone 1985, Luck et al. 1997, Maunsell & Cook 2002, Buffalo et al. 2010, Noudoost et al. 2010). The results from human functional brain imaging largely parallel these general observations from neurophysiological studies (Kastner & Ungerleider 2001, Pessoa et al. 2003). In addition, these

observations appear to be consistent for both spatial and feature/object-based attention (e.g., Treue & Martínez-Trujillo 1999, Sàenz et al. 2002).

Within the past decade, an increasing number of studies have focused on testing other aspects of neural activity that are affected by selective attention, again largely in the context of top-down, covert attention. Given that selective attention is defined behaviorally as a relative improvement in psychophysical performance for attended versus unattended stimuli (e.g., Carrasco 2011), it is, of course, important to measure the extent to which neural correlates of attention involve corresponding relative improvements in neural coding, particularly because an increase in the neuronal firing rate does not necessarily signify an increase in neural coding. If the objective of attention is to increase the signal-to-noise ratio of the readout from populations of neurons encoding the attended stimulus, then, in theory, this can be accomplished in a number of ways, including strengthening of selected signals, improvements in the efficacy of inputs to the readout stage, and the reduction of noise. A number of studies have measured the influence of selective attention on the coding of visual stimuli by single neurons (e.g., Spitzer et al. 1988; McAdams & Maunsell 1999, 2000; Reynolds & Chelazzi 2004) and populations of single neurons (Cohen & Maunsell 2009, 2010), and they have discovered that attention appears to increase the information conveyed about stimuli. Moreover, attention-driven increases in coding appear to be specific to behavioral conditions in which an animal's perceptual sensitivity per se, rather than simple response bias, is increased (Luo & Maunsell 2015). However, the means by which these increases are accomplished remains somewhat unclear. In addition to changing the firing rate, attention reduces the variability of responses to repeated stimuli (Mitchell et al. 2007) and can reduce the covariability of neuronal responses to repeated stimuli in simultaneously recorded neurons (Cohen & Maunsell 2009, Mitchell et al. 2009). Reductions in firing rate variability increase the information available in stimulus-driven activity by effectively diminishing the noise in the neural signal. Reductions in spiking covariability, by contrast, are expected to reduce the redundancy in signals from populations of neurons (Cohen & Maunsell 2009), at least for neurons with similar stimulus preferences (positive signal correlations) (Averbeck et al. 2006, Ruff & Cohen 2014). However, the relationship between neuronal spiking covariability and the strength of information in the population code is not entirely straightforward (Hu et al. 2014).

In addition to increasing the information available in the spiking activity, attention can potentially enhance signal efficacy via synchrony among neurons encoding the attended stimulus. In particular, some researchers have argued that high frequency (γ-band) synchronization in the spiking output from projection neurons can increase the influence of spikes on downstream neurons (Salinas & Sejnowski 2001, Azouz & Gray 2003; for a contrasting view, see Martin & Schröder 2016). At least within the rodent somatosensory system, evidence exists of a direct influence of γ synchrony among fast-spiking interneurons on both sensory coding (Cardin et al. 2009) and tactile detection (Siegle et al. 2014). In neurophysiological recordings in behaving animals, coherence among spikes and between spikes and local field potentials (LFPs) provides a measure of phase locking within local groups of neurons. A near-zero phase lag in the spiking synchrony among neurons could facilitate the integration of spikes from these populations converging on postsynaptic targets. Studies have generally found increases both in local γ-band LFP power and in synchrony between spiking and the γ-band phase (Fries et al. 2001, Bichot et al. 2005, Fries 2009). Related changes occur within other LFP frequency bands (Fries 2009), and those changes appear to depend on the cortical layer in which they are recorded (Buffalo et al. 2011).

Although observations of increased γ-band synchrony lend support to the notion of a functional role of synchrony in attentional selection, evidence that attentional modulation results in greater postsynaptic efficacy is only now emerging. Briggs et al. (2013) tested the influence of attention on

the synaptic efficacy of dLGN inputs to visual area 1 (V1) in monkeys. To accomplish this, they stimulated dLGN neurons while simultaneously measuring the stimulation-evoked responses in V1. They observed that when attention was directed to the receptive fields (RFs) of V1 neurons, those neurons were more likely to be activated by dLGN stimulation. These results are particularly exciting in that they provide a direct approach for testing how attention alters the transmission of signals across stages of the visual system.

Modulation of visual activity by other endogenous factors. Although the evidence in the previous section is largely consistent with the supposition that (top-down) attention should increase the fidelity of neural signals related to the attended stimulus, it nonetheless remains unclear whether the changes that correlate with attentional deployment are actually necessary and sufficient to improve perceptual performance. In fact, this remains one of the more fundamental open questions in study of the neural mechanisms of attention (see the section Future Issues). In recent years, an increased interest in addressing this question has not only necessitated more rigorous measurements of perceptual performance in animal models (e.g., Sridharan et al. 2014) but also prompted investigators to test the degree to which factors other than selective attention modulate visual activity. For example, Baruni et al. (2015) found that, although the relative reward value determined discrimination performance at a given location, the absolute reward amount determined the extent of activity modulation in visual area 4 (V4) (see the section Future Issues). This dissociation indicates that selective attention, or at least its top-down component, is not the only factor contributing to the modulation of sensory responses. Another study demonstrated that the planning of saccadic eye movements to the RFs of V4 neurons was sufficient to modulate visually driven responses, even when saccade planning was spatially dissociated from the direction of covert attention (Steinmetz & Moore 2014) (**Figure 1**). Importantly, the effects of saccade planning on V4 activity were actually greater than the effects associated with attention. The above results demonstrate the potency of endogenous factors other than covert selective attention in regulating sensory driven signals. However, both reward value and motor preparation are generally expected to be coupled with adaptive changes in sensory representations. In later sections of this review (Gaze Control Mechanisms and Their Role in Visual Spatial Attention; Overt Attention and Perisaccadic Perception), we return to the latter of these two factors (motor preparation), as it appears to reveal a great deal about the mechanisms underlying both covert and overt spatial attention.

Neural correlates of bottom-up attention. In contrast to the extensive studies demonstrating the modulation of signals throughout the visual system during top-down attention, details about the influence of bottom-up attention on visual processing are notably less clear. In particular, the degree to which physical, non-task-driven salience can bias visual responses at early stages of the visual system remains ambiguous. Psychophysical studies have established that visual targets composed of features that differ from surrounding distracters are more salient and thus more easily located during visual search (Egeth & Yantis 1997). Such targets are said to pop out from background stimuli, as they can be located more rapidly, even in the presence of many distracters (Treisman & Gelade 1980, Treisman & Sato 1990). Popout stimuli are thus believed to draw attention in an automatic, bottom-up fashion, with search being largely driven via parallel (Treisman & Sato 1990) or preattentive mechanisms (Wolfe 1994). In comparison, targets made up of a unique conjunction of nontarget features are more difficult to locate during search and thus require longer search times as the number of distracters increases (Treisman & Gelade 1980). One report appeared to establish that neurons within V1 exhibit enhanced responses to popout RF stimuli (Knierim & Van Essen 1992). However, a subsequent study showed that V1 responses to popout stimuli
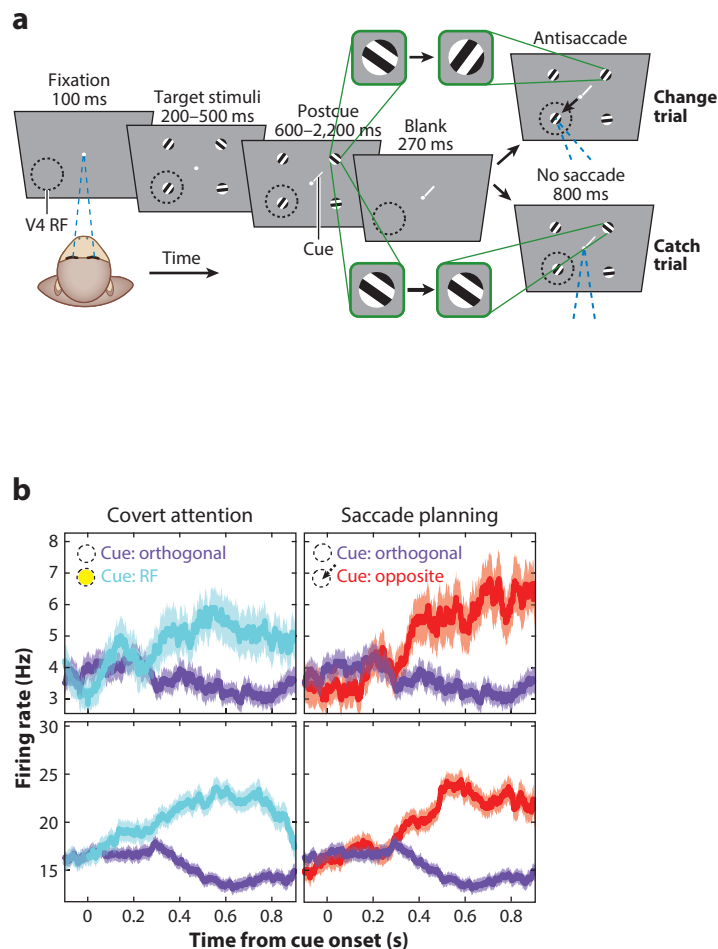
Figure 1

Dissociation of the effects of covert attention and saccade planning on visual area 4 (V4) activity.
(*a*) Antisaccade detection task design and trial sequence (Steinmetz & Moore 2014). Monkeys fixated on a
white dot while four peripheral oriented-grating stimuli were presented. After a variable delay, stimuli
disappeared then reappeared, either with or without one of the four stimuli rotating (i.e., either change trial
or catch trial). Monkeys could earn a reward by making a saccade to the diametrically opposite stimulus from
the change in change trials or by maintaining fixation in catch trials. A small, central cue (*white line*) indicated
which stimulus, if any, was most likely to change. The panels outlined in green show the change in
orientation, or lack of change, across the blank period. The dashed circle indicates V4 receptive field (RF)
locations, and the arrow indicates saccade direction. (*b*) Responses of two example neurons in the antisaccade
detection task. The left subpanels show a peristimulus time histogram of spiking activity around the time of
cue onset for trials in which the monkey was cued to attend to the RF stimulus (*cyan*) and prepare a saccadic
response to a distracter stimulus in the opposite direction. Activity is compared to control trials in which the
monkey attended to a stimulus orthogonal to the RF (*purple*). The shaded region indicates ±1 standard
error of the mean. The right panels show data from the same neuron for trials in which the monkey was cued
to attend to a location opposite the RF but had to prepare an antisaccade to a distracter stimulus in the RF.
Activity increased under both conditions, indicating that saccade planning modulated V4 responses even
when dissociated from covert attention. Figure adapted with permission from Steinmetz & Moore (2014).

do not actually differ substantially from responses to conjunction stimuli (Hegdé & Felleman 2003), whereas neurons within V4 do (Burrows & Moore 2009). Even so, selectivity to popout stimuli is not the sole test of bottom-up modulation. Abrupt onset stimuli also produce transient, involuntary shifts of attention toward the location of the onset (Posner 1980, Carrasco 2011). A recent study reported correlating enhancements in the activity of V1 neurons following such abrupt onsets (Wang et al. 2015). Thus, the way in which bottom-up salience early in the visual system contributes to visual processing may depend critically on the stimulus.

When assessing the influence of bottom-up salience on visual responses, one must also consider the extent to which those influences interact with top-down (endogenous) factors. Although the top-down/bottom-up dichotomy is frequently assumed to reflect independent mechanisms (Corbetta & Shulman 2002), confirmations of that independence tend to yield evidence to the contrary. Numerous neurophysiological and human neuroimaging studies have used passive fixation tasks to probe bottom-up attention (Knierim & Van Essen 1992, Lamme 1995, Nothdurft et al. 1999, Hegdé & Felleman 2003, Beck & Kastner 2005, Constantinidis & Steinmetz 2005). However, other studies, particularly those examining activity in higher order cortical areas, have employed visual search tasks (Chelazzi et al. 1998, Bichot et al. 2005, Thompson et al. 2005, Ogawa & Komatsu 2006, Buschman & Miller 2007, Bichot et al. 2015), and thus the measured activity necessarily included some component of top-down modulation. In fact, popout and conjunction stimuli are most often used in the context of visual search tasks. Some have argued that this task may not be the optimal way to measure purely bottom-up effects (e.g., Prinzmetal & Taylor 2006), as bottom-up and top-down effects clearly interact under these conditions (Einhäuser et al. 2008, Müller et al. 2009). Both psychophysical (e.g., Joseph et al. 1997) and neurophysiological (e.g., Ipata et al. 2006, Burrows & Moore 2009) evidence indicate that the interaction of bottom-up and top-down attention during visual search can lead to a diminution of bottom-up salience and its neural correlates when that salience is not behaviorally relevant (Hamker 2005a).

Major models of visual attention typically involve separate stages for the computation of differences in local features (feature maps) and global salience (salience maps) (Treisman & Sato 1990, Wolfe 1994, Itti & Koch 2001). Recent neurophysiological studies have provided persuasive evidence that global salience is computed, or at least amplified, within the parietal cortex (Balan & Gottlieb 2006, Goldberg et al. 2006, Soltani & Koch 2010) or prefrontal cortex (PFC) (Moore et al. 2003, Thompson & Bichot 2005). Although there is some evidence that neurons in parietal (Constantinidis & Steinmetz 2005, Ipata et al. 2006, Buschman & Miller 2007) and prefrontal (Bichot & Schall 2002, Buschman & Miller 2007) structures are uniquely modulated by popout stimuli, whether this modulation arises de novo in these proposed salience maps, converges there from more feature-selective (feature map) areas, or perhaps does both (Soltani & Koch 2010), remains unknown. The relative contributions of the parietal cortex, the PFC, the feature-selective cortex, and the superior colliculus (SC) (Fecteau & Munoz 2006) to the salience computation persist as one of the more fundamental open questions in attention (see the section Future Issues).

Feature-Based Versus Spatial Attention

The variety of attention whose adaptive significance is perhaps easiest to appreciate is feature-based (or object-based) attention, in which objects are selected on the basis of the degree to which their component features match a behaviorally relevant object. The adaptive significance of feature-based attention is easy to envision because many organisms frequently need to locate important objects within their environment, such as ripe fruit or easy prey. Note also that the selection of such objects is adaptive not only during active search for them, e.g., when hungry, but also under more passive, involuntary circumstances. In classical studies of feature-based attention

using visual search tasks, subjects are instructed to localize objects based on their similarity to one that was previously cued (Wolfe 1994). Several classic neurophysiological studies have identified neurons that exhibit correlates of feature-based attention within the primate visual system, beginning, at the latest, within the middle temporal visual area and V4 (Motter 1994a,b; Maunsell and Treue 2006; Bichot et al. 2005) and continuing in later cortical areas (Chelazzi et al. 1993, Bichot & Schall 1999, Sheinberg & Logothetis 2001). Unlike the case of spatial attention, in which the modulation of visually driven activity depends critically on the relationship between a given RF stimulus and the attended location, the modulation of visual activity during feature-based attention specifically depends on the relationship between the RF stimulus and the searched-for (attended) feature. For example, neurons in area V4 respond more vigorously to RF stimuli that more closely match the features that an animal is searching for, and this effect occurs whether or not the stimulus is located at a currently attended location (Bichot et al. 2005). The observation of this effect indicates that representations of stimuli are biased in a spatially invariant manner; that is, the selection of features and objects is spatially global (Treue & Martínez-Trujillo 1999, Sàenz et al. 2002, Martínez-Trujillo & Treue 2004, Cohen & Maunsell 2011). In contrast to the case of spatial attention, few studies have examined the neurophysiological effects of feature-based attention beyond changes in firing rates, the exception being a study finding that the effects of feature-based attention on γ-band LFP power and spike-LFP synchrony in the γ-band are similar to those of spatial attention (Bichot et al. 2005). However, although it is easy to envision how spatial attention should influence perception (e.g., increased detection of all stimuli at relevant locations), it is less straightforward to envision how feature-based attention should affect visual perception. Does feature-based attention simply facilitate the processing of stimuli sharing an attended feature (e.g., Sàenz et al. 2003), or can it cause more complex perceptual biases reflecting task-dependent changes in the encoding or decoding of visual features (Jazayeri & Movshon 2007, Navalpakkam & Itti 2007, Scolari & Serences 2009, Zirnsak & Hamker 2010)?

Covert and Overt Attention

More often than not, the direction of our gaze and the focus of our attention are spatially aligned. This makes it possible to resolve the fine details of fixated stimuli via the fovea, where visual acuity is greatest. Nonetheless, it is also possible to attend to objects of interest in the visual scene without shifting our gaze to them. This covert attention is the form of spatial attention most often studied by visual neuroscientists, as described in the previous sections. The importance of covert spatial attention has been appreciated since at least the nineteenth century, when Hermann von Helmholtz [1867 (1925)] conducted his research. In a classic experiment, von Helmholtz briefly illuminated an array of letters with an electric spark while holding his gaze steady. Von Helmholtz found that he was able to remember only the letters appearing in the area of the screen where his attention was directed, despite his gaze fixating elsewhere. His experiment thus showed that attention and gaze can be dissociated and that the perceptual benefits of attention (in this case, facilitation of memory) can be achieved both at the fovea and in the visual periphery. Since von Helmholtz's time, many psychophysical experiments have demonstrated that covert spatial attention improves the detection (e.g., Bashinski & Bacharach 1980, Hawkins et al. 1990, Müller & Humphreys 1991, Handy et al. 1996, Herrmann et al. 2010), as well as the discrimination (e.g., Downing 1988), of stimulus features at an attended location.

Before the discovery that the effects of covert attention are widespread within the primate visual system, researchers knew that visual activity in a number of brain regions is enhanced when an animal targets a RF stimulus with a saccadic eye movement. This effect was first observed by Goldberg & Wurtz (1972) among neurons within the superficial layers of the SC and subsequently

by Mountcastle and colleagues (1981) in the posterior parietal cortex. Later studies demonstrated that the presaccadic visual enhancement is also observed among neurons in V4 (Fischer & Boch 1981) and the inferior temporal cortex (Chelazzi et al. 1993). Moore and colleagues (Moore et al. 1998, Moore & Chang 2009) followed up on the study of Fischer & Boch (1981) and found that, as is observed during covert attention, the presaccadic enhancement of V4 visual responses consists of a reemergence of stimulus selectivity to targeted RF stimuli. When saccades are prepared to non-RF locations, the presaccadic activity and selectivity of V4 neurons are reduced (Moore 1999, Moore & Chang 2009). Thus, the presaccadic response reliably and selectively encodes the stimulus features of the target stimulus. Moreover, the stimulus selectivity present in the presaccadic response correlates significantly with the degree to which saccadic landing points are influenced by the orientation of the RF stimulus (Moore 1999), suggesting that, rather than merely providing a passive perceptual representation of visual attributes (Goodale & Milner 1992), neurons in this ventral stream visual area are instead actively involved in guiding oculomotor commands according to those attributes. In the next section, we describe further studies of the relationship between gaze control mechanisms and visual spatial attention, a relationship that appears to be causal.

GAZE CONTROL MECHANISMS AND THEIR ROLE IN VISUAL SPATIAL ATTENTION

Interdependence of Saccade Planning and Spatial Attention

Perhaps the first evidence of an interdependence of gaze control and attention came from a psychophysical study in which subjects made discriminations about peripherally flashed digits (Crovitz & Daves 1962). This study reported a positive correlation between discrimination performance and the direction of the first saccade subjects made after the stimulus was presented, suggesting that eye movements might facilitate attention. In the 1980s, Rizzolatti and colleagues proposed a premotor theory of attention, which hypothesized that the mechanisms responsible for spatial attention and the mechanisms involved in programming saccades are accomplished by the same neurons, but that in the covert case "the eyes are blocked at a certain peripheral stage" (Rizzolatti et al. 1987, p. 27). Later studies demonstrated that visual detection and discrimination are facilitated at the endpoints of saccades, even when the subject is given a cue to attend elsewhere (Shepherd et al. 1986, Hoffman & Subramaniam 1995, Deubel & Schneider 1996). Thus, it was apparent that planning a saccade is sufficient to facilitate visual perception at targeted locations. These results led to the proposal that a single mechanism drives both the selection of objects for perceptual processing and the preparation needed to produce an appropriate motor response (Schneider 1995).

The Frontal Eye Field in the Prefrontal Cortex

The earliest evidence of a causal role of gaze-control mechanisms in the perceptual benefits of attention comes from Sir David Ferrier (1886), a Scottish physiologist working in the late nineteenth century. Ferrier found that after removal of part of the PFC in a single hemisphere, monkeys were unable to direct their gaze into the affected hemifield and that this movement deficit was accompanied by a "loss of the faculty of attention"; he hypothesized that the "power of attention is intimately related to volitional movements of the head and eyes" (Ferrier 1886, p. 151). Ferrier's approach was subsequently refined by twentieth-century investigators who found that similar deficits in attention resulted from PFC lesions that were restricted to a small band of

tissue lying anterior to the arcuate sulcus, which is known as the frontal eye field (FEF) (Welch & Stuteville 1958, Latto & Cowey 1971).

Anatomically, the FEF is appropriately situated for a role in visually guided saccades. FEF neurons receive projections from most of the functionally defined areas within the visual cortex (Schall et al. 1995), and FEF neurons project to both the brainstem saccade generator and the SC, which is a midbrain structure with a known involvement in saccade production (Fries 1984, Stanton et al. 1988, Lynch et al. 1994). However, the FEF also sends feedback projections to much of the visual cortex (Schall et al. 1995, Stanton et al. 1995), suggesting a pathway by which saccade-related signals can influence visual representations. The visually driven responses of some classes of FEF neurons (visual and visuomovement) are enhanced when the RF stimulus is used as a saccade target compared to when no saccade is made to the stimulus (Wurtz & Mohler 1976, Goldberg & Bushnell 1981, Bruce & Goldberg 1985). In addition, neural correlates of visual selection have been observed in the FEF during a search task in which monkeys were required to make a saccade to a singleton embedded among distracters (Bichot & Schall 1999). Although early studies suggested that FEF neuron response enhancement was specifically related to the execution of a saccade (e.g., Goldberg & Bushnell 1981), more recent studies demonstrate that FEF visual responses are enhanced even in the absence of saccades and during purely covert attention (Thompson et al. 2005, Armstrong et al. 2009). Perhaps most compelling is the observation that operantly induced increases in FEF neuronal activity result in both perceptual benefits at spatially specific locations and corresponding enhancements in target selectivity in the visual responses of FEF neurons (Schafer & Moore 2011).

Several studies have employed electrical microstimulation to probe the role of gaze-control structures in the deployment of spatial attention. Moore & Fallah (2001) were the first to examine the effect of intracortical microstimulation on visual attention. They found that when sites within the FEF were stimulated using currents that were too low to evoke saccades (subthreshold), these currents could enhance attentional deployment in a spatially specific manner. Two subsequent studies reported similar enhancements in visual spatial attention following subthreshold microstimulation of the SC (Cavanaugh & Wurtz 2004, Müller et al. 2005). In both cases, the performance-enhancing effects of microstimulation were spatially dependent, as in the FEF studies. In each of the above studies, the effects of microstimulation were measured in the absence of any saccadic eye movements, i.e., during covert attention. Another study examined the effect of FEF microstimulation on the metrics of saccades made to visual stimuli (Schafer & Moore 2007). In control trials, the endpoints of saccades made to drifting gratings were biased in the direction of grating drift even though the grating aperture was stationary. Subthreshold FEF microstimulation augmented this motion-induced saccadic bias for gratings positioned at locations represented at the stimulation site, in addition to increasing the likelihood of saccades to those locations. This result suggests that activation of FEF sites with microstimulation drives the selection of not only retinotopically corresponding visual stimuli (i.e., attention) but also the appropriate saccades needed to fixate those stimuli.

Consistent with the above evidence of the attention-related effects of FEF microstimulation, a number of subsequent studies have observed modulation of visual cortical responses during subthreshold microstimulation of the FEF. FEF microstimulation elicits a brief enhancement of the visually driven responses of V4 neurons with RFs at locations overlapping the stimulated FEF representation (Moore & Armstrong 2003). The magnitude of the enhancement is greater for more effective RF stimuli and when a non-RF (distracter) stimulus is present. Microstimulation of FEF sites that do not overlap the V4 RF suppresses responses, mimicking the effects observed during endogenous attention. Furthermore, the enhancement of V4 responses is confined only to RF stimuli that align with the endpoint of the saccade vector represented at the FEF site. As a

result, when two competing stimuli are present within the V4 RF, FEF microstimulation drives the visual responses toward those observed when the aligned stimulus is presented alone (Armstrong et al. 2006, Armstrong & Moore 2007). A subsequent study using functional magnetic resonance imaging (fMRI) examined the influence of FEF microstimulation on visual activation throughout the visual cortex (Ekstrom et al. 2008). FEF microstimulation enhanced the visual activation of retinotopically corresponding foci within multiple visual areas, including V1. Taken together, the above studies provide direct evidence of a robust influence of the FEF on gain of signals within the visual cortex.

OVERT ATTENTION AND PERISACCADIC PERCEPTION

In humans and other primates, the perception of fine detail is limited to a small fraction of the retina, the fovea. To overcome this limitation, we redirect our gaze about three times per second, typically with saccades. These gaze shifts ultimately lead to foveation of important or salient stimuli, yet even before our eyes begin to move, profound changes in perception and neural representations within the visual cortex can be observed. As mentioned above, psychophysical and neurophysiological studies have demonstrated a strong bias in the visual processing of saccadic targets around the time of the movement, and it is now widely believed that shifts of spatial attention precede the actual movement. In psychophysical studies, this belief is supported by observations of enhanced perceptual performance for saccadic targets compared to perceptual performance for nontarget stimuli (Hoffman & Subramaniam 1995, Kowler et al. 1995, Rolfs & Carrasco 2012; for a review, see Zhao et al. 2012).

Psychophysical studies arguing in favor of a presaccadic shift of spatial attention toward saccadic targets in humans are supported by neurophysiological studies in nonhuman primates demonstrating robust enhancements in visually driven neuronal responses prior to saccades to RF stimuli (see the section Covert and Overt Attention). In addition to these enhancements, other studies have reported changes in the RFs of visual cortical neurons. The RFs of V4 neurons, for example, shift closer to the saccadic target when measured around the time of saccades (Tolias et al. 2001). In other words, V4 neurons become more responsive to stimuli appearing closer to the target when an animal is about to make an eye movement as compared to when fixation is stable. This presaccadic convergence of V4 RFs resembles the modulations of V4 RFs measured during covert attention tasks resulting in RF shifts toward the attended target (Connor et al. 1996, 1997). Similar observations of convergent RF shifts around the time of saccades have been reported for FEF neurons as well (Zirnsak et al. 2014). As a result of these convergent RF shifts (**Figure 2**), visual activity within the FEF population is heavily biased toward the saccadic target at the time of the eye movement. This effect leads to a threefold increase in the proportion of RFs near the target region. These observations appear to be at odds with earlier studies reporting a presaccadic shift of FEF RFs toward their postmovement location (Umeno & Goldberg 1997, Sommer & Wurtz 2006, Shin & Sommer 2012). However, similar to studies reporting related RF shifts within other structures (Duhamel et al. 1992, Walker et al. 1995, Nakamura & Colby 2002, Churan et al. 2012), previous reports of FEF RF shifts relied on coarse spatial measurements of presaccadic RFs, making them difficult to distinguish from convergent shifts (Zirnsak et al. 2010, Zirnsak & Moore 2014).

The seemingly biased spatial representations in favor of the movement target within V4 (Tolias et al. 2001) and the FEF (Zirnsak et al. 2014) are reminiscent of the perceptual distortions of space around the time of saccadic eye movements. The ability of human observers to localize briefly presented stimuli at the time of saccades is largely impaired. Typically, human observers perceive such stimuli as if they were presented much closer to the saccadic target than they actually are, resembling a compression of visual space (Ross et al. 1997, Kaiser & Lappe 2004). Hamker et al.
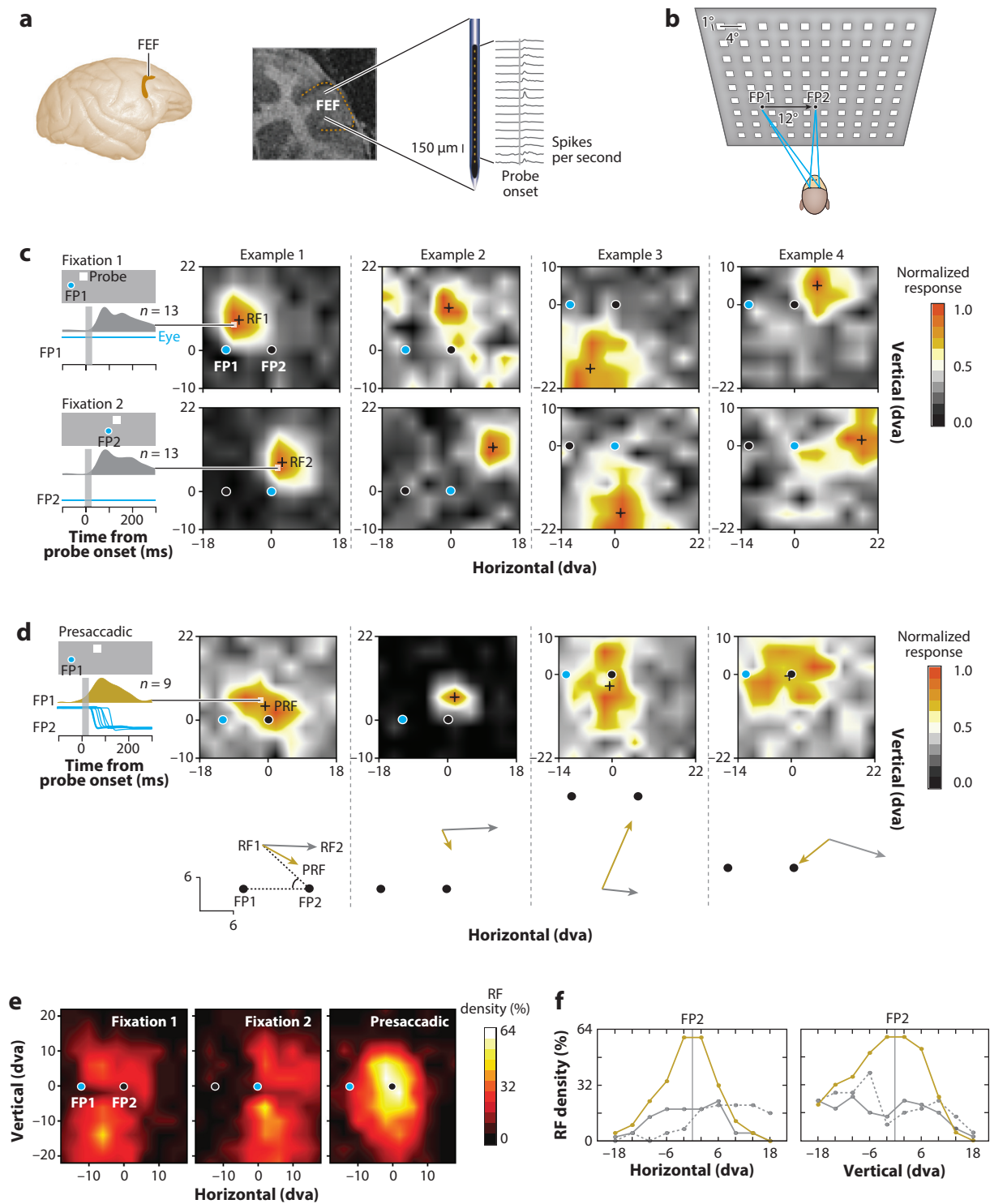
(2008) unified the changes in spatial representations within visual structures and the perceptual distortions at the time of saccades in a computational model. The proposed mechanism is based on the modulation of visual signals around the time of the eye movement. Consistent with the reports of enhanced responses of neurons within extrastriate areas to targets of eye movements, it is assumed that the modulation is strongest for neurons with RFs close to the saccadic target and levels off gradually for neurons with more distant RFs (Armstrong et al. 2006, Hamker & Zirnsak 2006). This gain modulation leads to severe distortions of the neuronal population response to nontarget stimuli, resulting in their mislocalization toward the saccadic target. Moreover, these distorted population responses cause changes in model RFs further downstream. Overall, model RFs converge toward the saccadic target (Zirnsak et al. 2010), leading to an increase in the number of model neurons effectively processing the target region.

Whereas a large body of evidence suggests an interdependence of spatial attention and eye movement preparation, a similar link between eye movement preparation and feature-based attention seems less clear (Born et al. 2012, Jonikaitis & Theeuwes 2013, White et al. 2013). During visual search, feature-based selection is thought to guide subsequent spatial selection both covertly and overtly (Bichot et al. 2005), but effects in the other direction have been given much less consideration. However, in a recent study, Burrows et al. (2014) tested whether spatially directed, overt attention, specifically the preparation of saccades, can produce feature-based-like effects on the responses of neurons in V4 (**Figure 3**). Monkeys made saccades to gratings presented at different orientations at one location while gratings were briefly flashed at another location and in the RF of V4 neurons. Importantly, there was no other task requirement in this paradigm; the orientation of the grating target was unrelated and not important for the completion of the task and the reward. Nonetheless, similar to the classic effects of feature-based attention, V4 responses at the nontarget locations depended reliably on the orientation of the targeted grating. Specifically, responses were greater when the orientation of the targeted grating was the orientation preferred by the recorded neuron. This apparent default initiation of feature-based effects from spatially directed attention is consistent with a computational model of gaze-control influences on visual representations (Hamker 2005b).

In summary, it appears that around the time of gaze shifts, visual representations are largely dominated by the target, in terms of both their spatial and their featural composition. That is, even before a stimulus is foveated, our perception is already biased by it (Pollatsek et al. 1990, Jüttner & Röhler 1993, Ganmor et al. 2015, Herwig et al. 2015).

Figure 2

Presaccadic changes of frontal eye field (FEF) neuronal receptive fields (RFs). (*a*) The FEF in the macaque cortex (*left*) and in a coronal magnetic resonance image from one macaque (*middle*) are shown (Zirnsak et al. 2014). (*Right*) Linear array microelectrode and traces of FEF visual responses were recorded simultaneously across 16 electrode contacts. (*b*) FEF RFs were mapped with a 10 × 9 array [36 × 32 degrees visual angle (dva)] of probe stimuli (*squares*) flashed during fixation at fixation point (FP) 1 and FP2 and immediately before saccades from FP1 to FP2. (*c*) Four example neuronal RF maps. The far left shows the mean peristimulus response histogram for the most effective probe location during fixation at FP1 (*top*) and FP2 (*bottom*). Blue lines and circles indicate eye position and fixation location, respectively. The black circles represent the FP, which is not fixated. Black crosses indicate RF centers during fixation at FP1 (RF1) and FP2 (RF2). (*d*) Presaccadic RF maps of the same neurons measured immediately before saccades from FP1 to FP2. The far left shows the mean peristimulus response histogram for the most effective probe location. Probe presentation (*vertical gray shading*) was completed before saccade onset in all trials. Black crosses indicate the presaccadic RF (PRF) centers. Below each RF map is the measurement of the changes in RF centers during fixation (RF1 to RF2; *gray vectors*) and saccade preparation (RF1 to PRF; *gold vectors*). (*e*) Subpanels plot the percentage of population RFs (*N* = 179) responsive for a given probe location. Blue circles denote the location of fixation. (*f*) Subpanels show horizontal and vertical cross sections through RF density plots centered on the saccade target (FP2) for fixation 1 (*solid gray*), fixation 2 (*dotted gray*), and presaccadic (*gold*) conditions. Figure adapted with permission from Zirnsak et al. (2014).
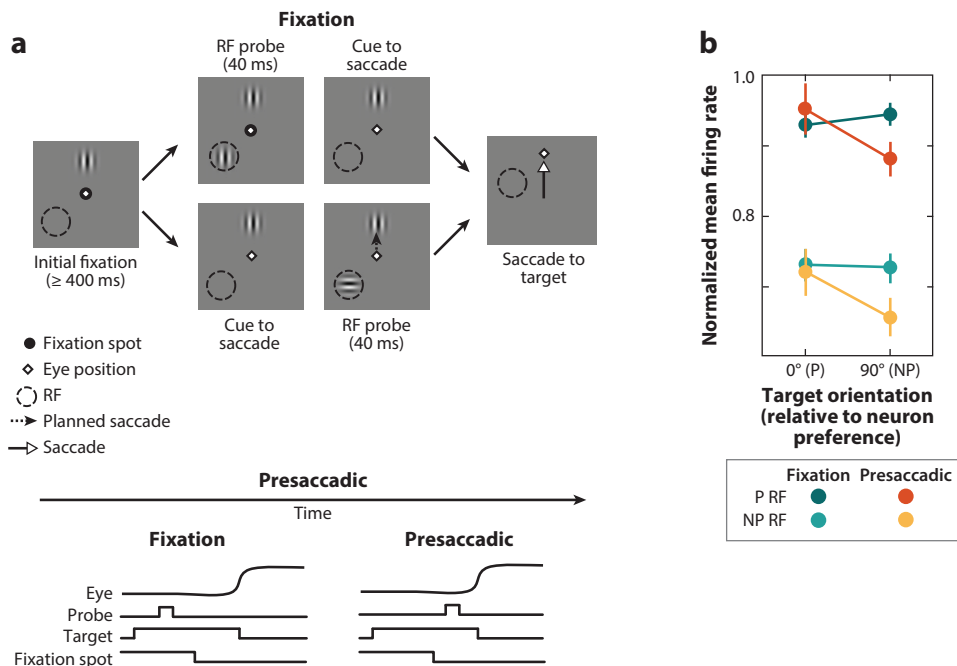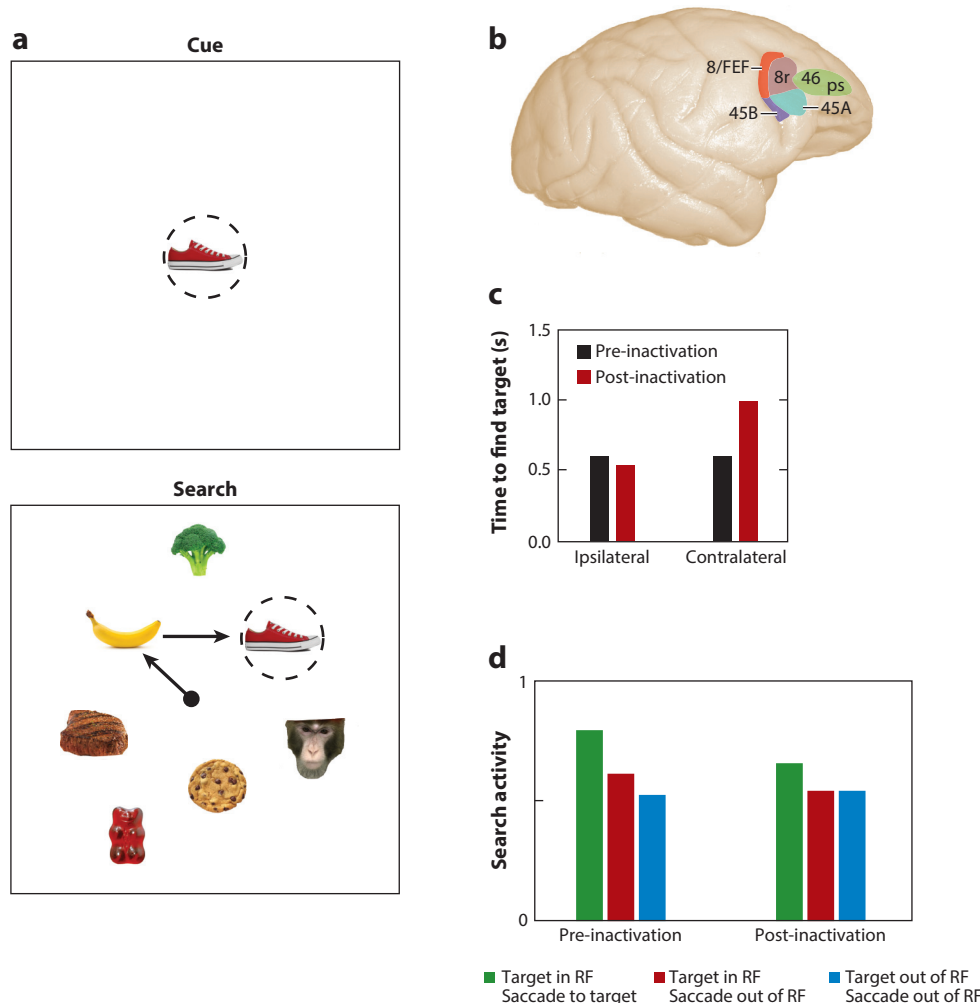
Figure 3

Global selection of saccadic target features by V4 neurons. (*a*) Measurement of target feature-dependent modulation in a delayed saccade task (Burrows et al. 2014). In each trial, the monkey fixated (*diamond*) on a central fixation spot (*black circle*) on the display and was then presented with a saccade target. In the fixation condition (*top*), a probe stimulus appeared briefly in the receptive field (RF) while the monkey continued to fixate, followed by the cue to saccade (the removal of the fixation spot). In the presaccadic condition (*bottom*), the cue to saccade occurred before the probe, and the probe appeared just before saccade initiation. The saccadic target and the RF probe were both gratings, presented at either a neuron's preferred (P) or nonpreferred (NP) orientation. Event traces depict the timelines of the trial events in the two conditions. (*b*) Normalized mean firing rates for all neurons ($N = 128$) during the fixation and presaccadic conditions plotted as a function of target feature (orientation) relative to each neuron's preference. Error bars denote the standard area of the mean. Figure adapted with permission from Burrows et al. (2014).

MECHANISMS OF FEATURE-BASED ATTENTION

As described in the section Feature-Based Versus Spatial Attention, it is relatively easy to appreciate the adaptive significance of feature-based attention. Yet despite the obvious significance of this type of attention to visually guided behavior, remarkably little is understood about its underlying neural basis. In particular, the origin of the clear neural correlates of feature-based attention and the causal basis for its impact on behavior remain elusive. Perhaps one reason for the relative lack of progress in understanding feature-based attention compared to spatial attention is that it is more difficult to envision the type and source of neural signals capable of biasing sensory input in favor of those matching the searched-for object. That is, it has remained unclear where in the brain one should expect the search templates of feature-based attention to reside. By contrast, motor systems, particularly the oculomotor system, have long been considered possible sources of the spatial template employed during spatial attention (for a review, see Moore et al. 2003). It could be that feature- or object-based templates exist somewhere within the visual system (Baldauf & Desimone 2014), yet to date it has remained difficult to identify them.

Figure 4

Influence of VPA neurons on visual search and feature selection within the FEF. (*a*) Visual search task (Bichot et al. 2015). The monkey was cued to find a specific object among distracters. The dashed circle represents the current point of fixation, and the arrows represent the monkey's scan path. (*b*) Lateral view of the macaque brain. VPA neurons are likely located within cytoarchitectonic areas 45A and ventral 46. (*c*) Following VPA inactivation, the search times of the animals almost doubled if the target object was presented in the contralateral hemifield but were unaffected if it was presented in the ipsilateral hemifield relative to the inactivated sites. (*d*) Following inactivation of the ventral bank of the principal sulcus, feature selection of target objects by FEF neurons was abolished (compare *red bar* and *blue bar*). Figure adapted with permission from Bichot et al. (2015). Abbreviations: FEF, frontal eye field; ps, principal sulcus; RF, receptive field; VPA, ventral prearcuate.

A recent study by Bichot et al. (2015), however, makes a compelling case for the existence of such a template within the monkey ventral PFC (**Figure 4**). Their data provide evidence that the representation of searched-for object features and the source of feature-based templates reside among neurons within a region of the PFC anterior and ventral to the arcuate sulcus [ventral prearcuate (VPA)], likely within cytoarchitectonic areas 45A and ventral 46. In this study, monkeys

performed a standard visual search task in which they were rewarded for localizing, via eye movements, a memorized visual image presented among multiple distracters. On average, monkeys located the remembered target within only approximately three eye movements among eight total images in each behavioral trial, indicating that their search was guided by a memory of the cued stimulus. The authors recorded the responses of neurons within the VPA, as well as the FEF, inferior temporal cortex, and another region of the PFC within the ventral bank of the principal sulcus. Among neurons from these four areas, only neurons in the VPA were selective for the memorized object throughout the entire search period. Neurons in the VPA and the FEF exhibited both feature-based and spatially based attentional modulation. However, the observed feature-based modulation emerged earlier for VPA neurons than it did among neighboring FEF neurons, suggesting that the modulation among VPA neurons was the source of the activity within the other structures, particularly the FEF. To test this hypothesis directly, the authors locally inactivated sites within the VPA. Following local inactivation of the VPA, monkeys exhibited a clear reduction in search performance when the target object appeared within the contralateral (inactivated) visual hemifield. In particular, the average number of saccades required to locate the target object among distracters increased significantly. In addition, following inactivation of the VPA, the feature-based modulation previously observed among neurons within the FEF was no longer present. These results provide compelling evidence that activity within the VPA is necessary for feature-based search behavior as well as the neural correlates of search within other areas of the PFC. The results also raise important questions that may be addressed in future studies. For example, does inactivation of the VPA lead to a loss of feature-based modulation throughout the visual cortex, as it does within the FEF?

NEUROMODULATORS AND ATTENTION

Neuromodulators compose a class of neurotransmitters that influence synaptic transmission broadly within neural circuits, often altering the postsynaptic effects of other transmitters (e.g., glutamate) as well as one another. Generally, researchers have considered, to varying degrees, the roles of three neuromodulators, acetylcholine (Ach), dopamine (DA), and norepinephrine (NE), in attention (Noudoost & Moore 2011a,b). Each of these neuromodulators has a discrete origin from localized brainstem or midbrain nuclei and is released widely throughout other subcortical and cortical structures. Ach is synthesized and released by the nucleus basalis of Meynert, the substantia innominata, and the diagonal band of the basal forebrain. DA is synthesized and released from a set of midbrain nuclei, including the substantia nigra pars compacta and the ventral tegmental area, the latter of which projects broadly to cortical areas. NE is synthesized centrally by neurons within the locus coeruleus (LC) and, like Ach and DA, is released widely throughout subcortical and cortical structures. Importantly, when considering the effects of neuromodulators on specific circuits, like those controlling selective attention, it is necessary to bear in mind the relative breadth of the neuromodulatory projection patterns. In contrast to global arousal and vigilance, selective attention necessarily involves the amplification of highly specific signals, often nested within multiple sensory dimensions, as when vision is amplified over other senses or color is amplified over motion. Although, on the one hand, it seems likely that each of these neuromodulators interacts with multiple forms of selective attention, on the other hand, it seems less likely that they are uniquely involved in the selective component of selective attention (see the section Future Issues).

Acetylcholine

Systemic increases in Ach activity are known to enhance selective visual attention in normal human subjects (Warburton & Rusted 1993, Furey et al. 2008). Within cortical areas, basal forebrain

stimulation enhances sensory signals within the somatosensory (Tremblay et al. 1990), auditory (Metherate & Ashe 1993), and visual cortices (Goard & Dan 2009), thus providing a means by which Ach release can increase perceptual performance globally and perhaps augment attention selection by other circuit mechanisms. Although these effects appear to be achieved largely via metabotropic muscarinic receptors (mAchRs), the extent to which Ach's role in attention is achieved via mAchRs, ionotropic nicotinic receptors (nAchRs), or both, remains unclear. Studies in rodents suggest that the processing of sensory signals within posterior areas might be influenced by the interaction of the PFC with ascending cholinergic projections, and this interaction appears to depend on nAchRs (Guillem et al. 2011). Indeed, within the primary visual cortex (area V1), gain control appears to be achieved largely by nAchRs (Disney et al. 2007). However, Thiele and colleagues (Herrero et al. 2008) found evidence that mAchRs play a specific role in the modulation of visual cortical responses during selective attention. They recorded visual responses of V1 neurons in monkeys performing a covert attention task and found that iontophoretic application of Ach augmented the attentional modulation of V1 responses. In addition, they found that application of scopolamine, a mAchR antagonist, reduced the attentional modulation, but application of the nAchR antagonist, mecamylamine, had no effect. More recent neurophysiological evidence in monkeys suggests that basal forebrain Ach interacts with the amygdala to direct spatial attention according to motivational factors (Peck & Salzman 2014). Combined, the above evidence demonstrates the important role of Ach-mediated activity, operating via mAchRs, nAchRs, or both, in the control of sensory activity during selective attention.

Dopamine

The effect of DA on selective attention appears to be achieved via its effects on the PFC (Noudoost & Moore 2011a,b). DA can alter the strength and reliability of converging glutamatergic synapses (Seamans & Yang 2004). However, this modulatory influence can exhibit an inverted U–shaped property wherein optimal DA levels lead to peak effects on synaptic efficacy and reduced effects at levels above or below optimal (Vijayraghavan et al. 2007). This complex property of DA neuromodulation appears consistent with hypotheses about a dopaminergic dysfunction in attentional disorders such as attention deficit hyperactivity disorder (ADHD) (Arnsten 2011). ADHD patients not only exhibit perceptual deficits (Mason et al. 2003) but also show evidence of abnormal PFC DA (Ernst et al. 1998).

Several rodent studies have implicated PFC DA in the control of attention (e.g., Chudasama & Robbins 2004). However, many of the behavioral paradigms utilized in rodents do not clearly involve a selective processing component in their task design (e.g., Kim et al. 2016), and thus they do not clearly distinguish between behavioral vigilance and selective attention. Recent work in primates suggests a basis by which changes in PFC DA can alter selective attention. Noudoost & Moore (2011a,b) studied the impact of manipulating DA-mediated activity within the FEF by injecting sub-microliter volumes of D1 and D2 receptor agonists and antagonists into discrete FEF sites. Following injections of a D1 receptor antagonist, visual targets presented within the affected part of space were more likely to be chosen by the monkey as targets for saccades than during control trials. Manipulation of D2 receptor activity had no effect. Thus, the manipulation increased saccadic target selection. In addition, the manipulation produced an enhancement in the gain of visually driven responses in V4 during passive fixation. D1 manipulation effectively elicited correlates of covert attention within the extrastriate cortex in the absence of a behavioral task. Importantly, similar injections of a D2 agonist into FEF sites resulted in target selection effects equivalent to those of the D1 antagonist. However, only the latter produced attention-like

effects within V4. Thus, the control of attention and target selection by the FEF appears to be dissociable at the level of DA receptors.

Norepinephrine

In contrast to the extensive range of studies on the roles of Ach and DA in selective attention, less is understood about the role of NE. Past work has generally associated NE with behavioral arousal rather than selective attention (Berridge & Waterhouse 2003). Noradrenergic neurons within the LC respond selectively to salient sensory stimuli (Foote et al. 1980, Grant et al. 1988), and stimulation of the LC can modulate sensory responses in awake animals (Devilbiss et al. 2006). However, other studies indicate that LC activity does not simply reflect stimulus-driven salience but rather depends heavily on the task relevance of stimuli. For example, LC neurons respond with robust phasic bursts to the presentation of learned targets, but they respond only weakly when nontargets are presented (Aston-Jones & Cohen 2005). Thus, noradrenergic modulation may contribute to more than mediation of the influence of arousal state on sensory responses. This view may be consistent with the known benefits of noradrenergic drugs in ADHD (Arnsten et al. 2007) and the finding that blockade of α2A NE receptors impairs response inhibition (Ma et al. 2003) and increases hyperactivity (Ma et al. 2005) in monkeys. Nonetheless, as with Ach and DA, further studies are needed to determine the degree to which noradrenergic modulation is necessary and sufficient for attentional selection.

ASSESSING ATTENTIONAL DYSFUNCTIONS

A fundamental issue facing the study of neural mechanisms of attention is how to define and quantify dysfunctions in selective attention. For future studies aimed at identifying the neural mechanisms causally related to the filtering of behaviorally relevant visual information, the need to answer this question will only grow in importance. Subsequent attempts to pinpoint the neurons, neural circuits, and neural computations that uniquely confer on the nervous system the capacity to distinguish a target from distracters will need to determine more definitively the behavioral phenotypes that reflect a loss in that capacity rather than a loss in some other function. Because attention appears to be defined most specifically by the benefits observed in the processing of relevant sensory information, it is reasonable to posit that one should expect the loss of those benefits, rather than a deficit in some aspect of sensory processing, when attentional mechanisms are absent.

Several models have been proposed to account for the effects of attention on visual signals (Desimone & Duncan 1995, Reynolds et al. 2000, Lee & Maunsell 2009, Reynolds & Heeger 2009). These models provide a framework for understanding the interaction between attentional control and the encoding of visual information, thus allowing one to potentially distinguish between deficits in either process. Each model involves an interaction between attentional gain control and the competition inherent in visual processing. For example, although a representation with higher stimulus drive will tend to exert greater suppression on its competitors than one with lower stimulus drive, attention to one stimulus or the other is expected to mitigate (or exacerbate) that effect. But crucially, when attention is held constant, decreases in the strength of a representation can be brought about not only by reduced competitiveness with the representations of other stimuli but also by reduced stimulus drive, including reduced drive due to brain damage. This loss in stimulus drive should result in a competitive disadvantage at locations within intact maps. As a result, because stimulus drive and attention both interact competitively, the above models suggest that altering stimulus drive in such a way should affect the magnitude of neural responses in a manner that is consistent with a loss of attention, even when attention is functioning

normally. Thus, even when attentional gain remains intact, a diminution in the strength of visual input could be sufficient to produce a distracter-dependent deficit (Squire et al. 2013). Unfortunately, distracter dependency is often used to define a loss in attentional function (e.g., De Weerd et al. 1999, Wardak et al. 2006, Lovejoy & Krauzlis 2010). Such a definition may thus be overly broad in many cases (Desimone & Duncan 1995) and may lead to a difficulty in distinguishing between the role of brain structures in visual attention and their role in visual processing, as in the case of V4 (e.g., Schiller & Lee 1991, De Weerd et al. 1999), and their possible role in response selection, as in the case of the SC (Zénon & Krauzlis 2012). Thus, rather than assessing the effect of distracters on perceptual performance as a means of probing attentional dysfunctions, it may be best for future studies to instead assess the potential of attentional cues to produce benefits in the perception of particular stimuli, whether such cues are top-down or bottom-up.

CONCLUDING REMARKS

In this review, we have discussed the aspects and types of visual selective attention, how they alter processing of stimuli by neurons within the visual system, what is currently known about the causal basis of selective attention, and how to assess attentional dysfunctions. We hope it will be apparent to the reader how incomplete current knowledge is about the neural circuitry underlying the selective processing of visual information, particularly when considering the variety of ways in which visual information can be selectively processed. Our goal has been to highlight the comparison between aspects of attention for which much progress has been made (e.g., spatial attention) and aspects for which little progress has been made (e.g., feature-based and bottom-up attention). Although it would certainly be convenient if different aspects of attention were controlled by common, or even homologous, mechanisms, this clearly is not the case, at least in the primate visual system. Thus, as we highlight in the section Future Issues, future studies need to focus on identifying the specific neural mechanisms that underlie each unique aspect of visual selective attention. However, we suspect that such progress is forthcoming.

FUTURE ISSUES

1. What are the relative contributions of the parietal and prefrontal cortices to bottom-up and top-down attention?

2. Is the modulation of visual responses during attentional deployment necessary and sufficient for the perceptual benefits observed in behavior?

3. What is the precise role of particular neuromodulators in selective attention?

4. Aside from gaze-control mechanisms, what is the role, if any, of other effector systems (e.g., reaching) in selective visual attention?

5. What is the precise relationship between mechanisms signaling reward and motivation and (other) mechanisms controlling selective visual attention?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

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Errata

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