

# Visual and oculomotor selection: links, causes and implications for spatial attention

Edward Awh<sup>1</sup>, Katherine M. Armstrong<sup>2</sup> and Tirin Moore<sup>2</sup>

<sup>1</sup>Department of Psychology, University of Oregon, 1227 University of Oregon, Eugene, OR 97403-1227, USA

<sup>2</sup>Department of Neurobiology, Stanford University School of Medicine, Stanford, CA 94305, USA

**Natural scenes contain far more information than can be processed simultaneously. Thus, our visually guided behavior depends crucially on the capacity to attend to relevant stimuli. Past studies have provided compelling evidence of functional overlap of the neural mechanisms that control spatial attention and saccadic eye movements. Recent neurophysiological work demonstrates that the neural circuits involved in the preparation of saccades also play a causal role in directing covert spatial attention. At the same time, other studies have identified separable neural populations that contribute uniquely to visual and oculomotor selection. Taken together, all of the recent work suggests how visual and oculomotor signals are integrated to simultaneously select the visual attributes of targets and the saccades needed to fixate them.**

## Introduction

Visually guided behavior depends first and foremost on the ability to construct an accurate representation of the many objects within the visual environment. In turn, because of the precipitous drop in acuity that occurs with increasing retinal eccentricity, visual perception in foveate animals relies upon the sequential scanning of the items within a scene by way of saccadic eye movements. Thus, the construction of an accurate visual representation depends crucially on the optimal and precise selection of successive fixation locations [1].

Recent evidence suggests that the visuo-oculomotor system of primates has evolved to select the visual parameters of objects concurrently with the specification of oculomotor commands needed to fixate those objects. Further evidence suggests that this system has evolved the capacity to amplify target visual signals *covertly* in the absence of the overt deployment of eye movements. Although the neural mechanisms involved in the triggering of visually guided saccades and those involved in covert attention must diverge at the point where eye movements are either made or withheld, results to date suggest considerable overlap of the circuits mediating both functions (e.g. [2]).

Here we review recent studies of the relationship between visual selection and oculomotor programming. These experiments reveal a causal relationship between the neural circuits controlling saccadic eye movements and shifts of covert spatial attention. Although some studies have identified separable neural populations that contribute uniquely to visual selection or oculomotor programming, recent work suggests how these processes might be integrated during visually guided behavior.

## Links between selective attention and saccadic programming

Psychophysical evidence linking selective attention and oculomotor programming is abundant. A classic demonstration of the influence of directed attention on saccades was provided by Rizzolatti and colleagues [3]. This study examined the influence of covert attention on saccade trajectories in subjects instructed to initiate saccades to a location in one-half of the visual field (e.g. the lower half) according to cues presented in the other half. The cues themselves could be presented in one of several locations in the cued half of the visual field (e.g. left side of upper field). The major finding from this study was that saccade trajectories were systematically deviated according to the location of the covertly attended (cued) location. This and similar observations (e.g. [4]) demonstrate that the deployment of covert attention perturbs oculomotor programming.

In another influential study, Hoffman and Subramaniam [5] instructed subjects to saccade to a specified location while also detecting a visual target presented just before the eye movement. By varying the position of the target for detection they too could measure the interaction of attention and saccade programming. Indeed, they found that target detection was typically best at the location of planned saccades and that essentially subjects were unable to completely dissociate the attended and saccade locations. These results suggest that the preparation of saccades to a location deploys attention to that location. Similar evidence was found by Deubel and Schneider [6] who concluded that a single mechanism drives both the selection of objects for perceptual processing and the information needed to drive the appropriate motor responses.

Corresponding author: Moore, T. (tirin@stanford.edu).

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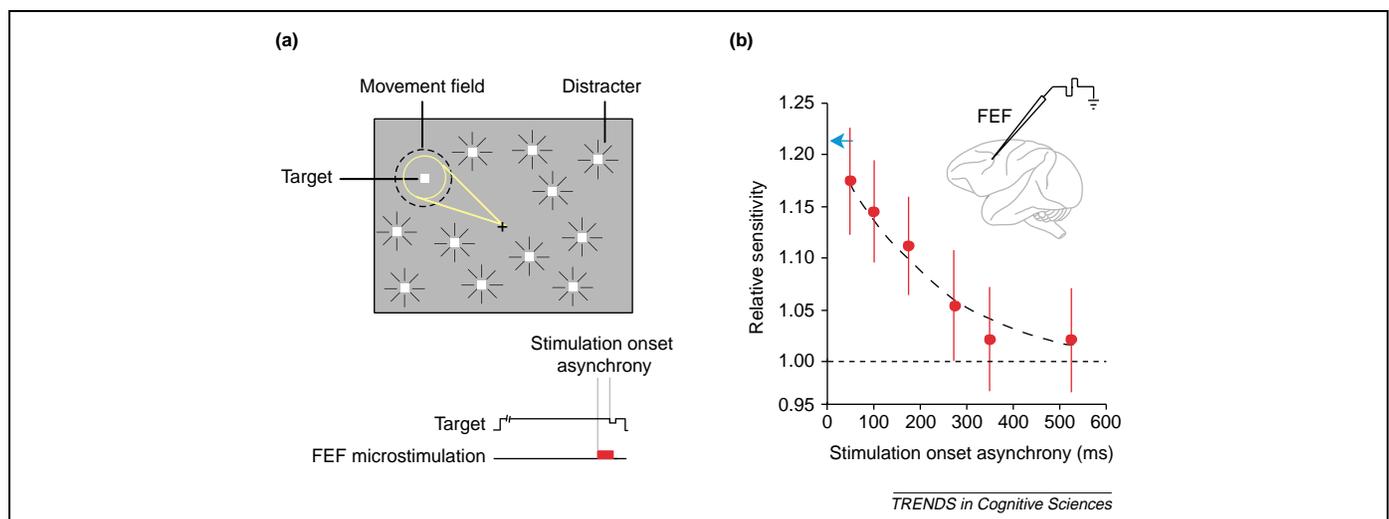
The above observations are generally taken as support for the so-called ‘premotor theory of attention’, which posits that covert attention and saccade programming are driven by overlapping neural mechanisms [3]. Although the provenance of this view dates back to the 19th century and the ideas promulgated by early physiologists and theorists of cognition [7,8], there has been considerably more neurophysiological scrutiny in recent years. What do the psychophysical links between attention and saccade planning suggest about the neural substrates that mediate visual and oculomotor selection? Does the apparent overlap of control of the two functions suggest that attention is a by-product of oculomotor programming? Alternatively, if we consider the idea that visuo-motor processes fall along a continuum from visual to motor operations, then where along this axis should we expect to find the source or sources of attentional filtering?

Although the psychophysical studies provide a solid rationale for the hypothesis that oculomotor and attentional circuits have a common neural substrate, the correlational data from these experiments cannot rule out the alternative view that these are parallel but distinct systems that tend to act in concert. Several recent studies have begun to tackle this problem by perturbing neural signals within oculomotor structures with electrical microstimulation and examining the effects of those perturbations on spatial attention and on visual representations in cortex. These structures include the frontal eye field (FEF) and the superior colliculus (SC), both having a known role in the programming and triggering of saccades. The approach of directly manipulating signals in these areas is particularly valuable in that it addresses the causal relationship between neural activity in oculomotor circuits and shifts of spatial attention.

### Causal mechanisms of spatial selective attention

If you are instructed to continue reading this text while preparing to detect the occurrence of some visual event in one corner of the page (e.g. a change in page number), your ability to detect the event would be heightened in comparison to a situation in which you had not been given those instructions. This is despite the fact that in neither case should your gaze shift to the corner of the page. In the macaque brain, the visual and oculomotor systems are highly interconnected, with cortical and subcortical saccade-related structures having direct output to both the brainstem saccade generator and much of extrastriate visual cortex [9–11]. Recent studies provide evidence that the neural mechanisms implicated in the volitional control of saccades may also contribute to selective attention.

Building on the wealth of psychophysical evidence linking attention and eye movement control, Moore and Fallah [12,13] directly tested the hypothesis that the preparation of saccades to a location brings about improved visual performance at that location (Figure 1). They trained monkeys to detect the dimming of a peripheral visual target while fixating and ignoring flashing distracters. The position of the attended target could be placed at a location to which saccades could be evoked via microstimulation of a site within the frontal eye fields (FEF) (Figure 1a). The authors found that microstimulation of FEF sites with currents that did not evoke saccades to the attended target nonetheless increased the monkeys’ sensitivity to changes in its luminance. This increase was found only when the FEF representation and the target were spatially overlapping. Moreover, the improvement observed was maximized when the temporal asynchrony between the target change



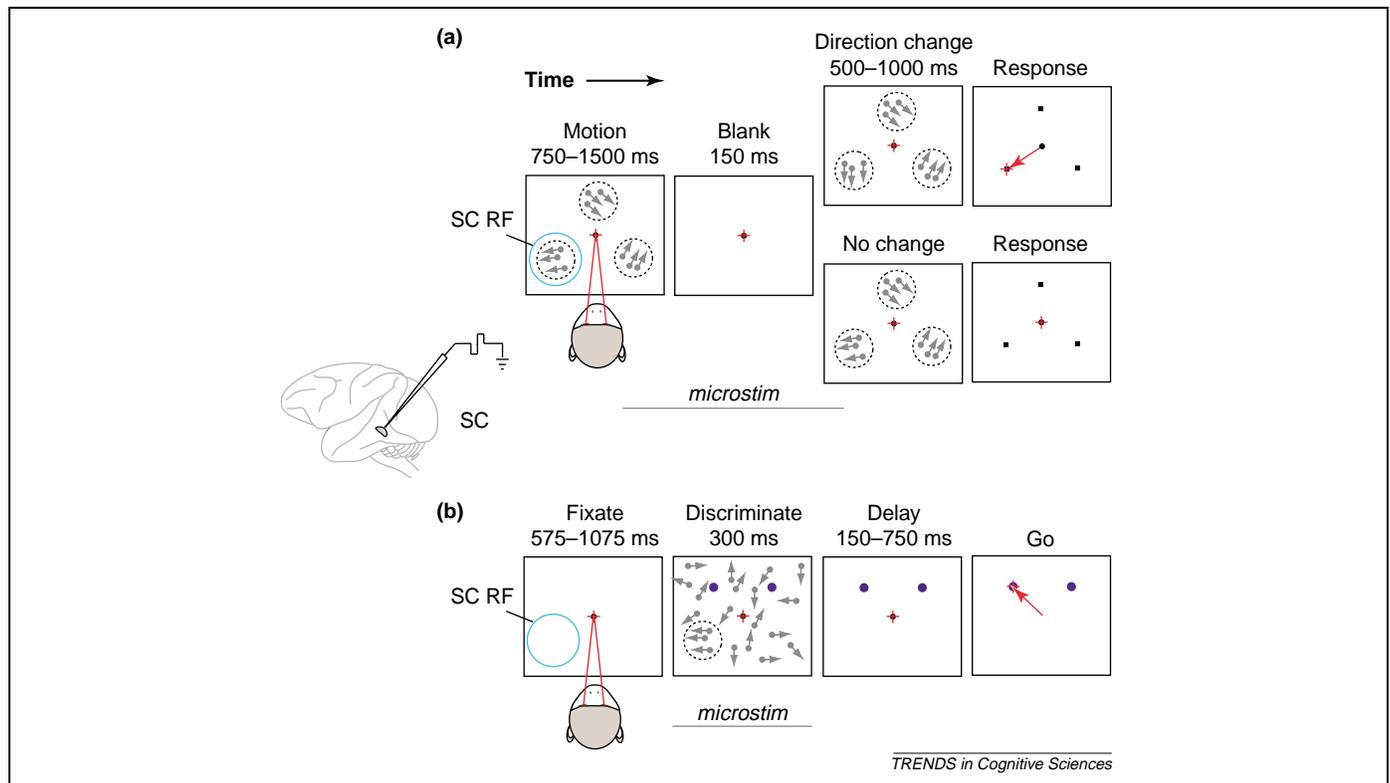
**Figure 1.** Microstimulation of the FEF. (a) Monkeys were trained on an attention task in which they had to detect the transient dimming of a peripheral visual stimulus (target) while ignoring a flashing distracter that appeared sequentially at random locations of the display. The target was placed at the location to which the monkey’s gaze would be shifted with suprathreshold stimulation of the FEF site (Movement field). The attention task was performed with and without subthreshold stimulation of the FEF site on randomly interleaved trials. On stimulation trials, microstimulation occurred at a range of times before the dimming of the target stimulus (stimulation onset asynchrony, SOA). (b) Average relative sensitivity values (microstimulation/control) are shown for each SOA tested (red dots) with red lines indicating the standard error of the mean. The blue arrow indicates the improvement in performance observed when the distracter was removed, with no FEF stimulation. Relative sensitivity values are shifted above 1.0, indicating an improved ability to detect the change following FEF stimulation. This improvement decreases with increasing stimulation-onset asynchrony (dashed curve fit), and is maximal when stimulation is applied concurrently with the target change. Importantly, this effect is only observed when the target was positioned within the movement field (Adapted from [13].)

and FEF microstimulation was near zero (Figure 1b). This observation suggests that microstimulation of FEF sites known to participate in the selection of visual targets for saccades [14–17] has a causal influence on the covert visual selection of the saccade site [13]. Dovetailing with the above observations, are the results of experiments in which transcranial magnetic stimulation has been used to disrupt activity within the FEF, and consequently, to alter the performance of human subjects on covert attention tasks [18–20]. Thus far, these studies have added to the evidence of a causal role of human FEF in the willful deployment of spatial attention (see [21] for review).

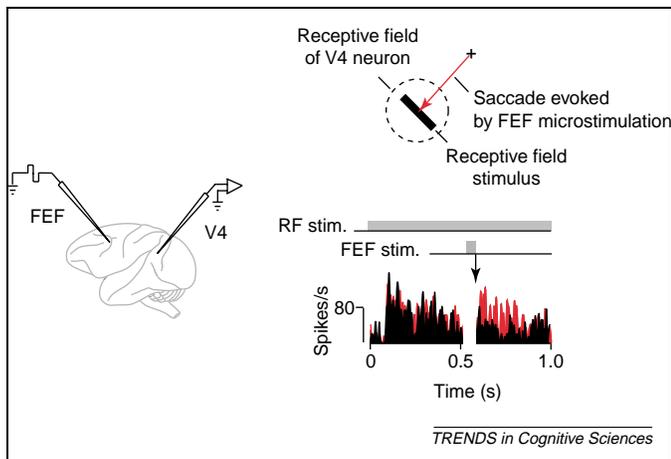
More recently, two studies examined whether microstimulation of the SC could affect covert spatial attention. As with the FEF, evidence has emerged in favor of a role of the SC in the selection of targets for saccades *per se* rather than merely saccade triggering [22,23], which raises the question of SC's role in covert visual selection. Using a change-blindness task (Figure 2a) – a paradigm known for its dependence on attention [24] – Cavanaugh and Wurtz [25] showed that monkeys' ability to detect changes in a visual display during a flashed presentation was improved with subthreshold stimulation of the SC intermediate layers. There was also a 15 ms decrease in reaction time for reporting changes. As in the FEF stimulation study,

this effect depended crucially on the retinotopic correspondence of the saccade represented at the stimulation site and the changing stimulus. Concurrently, Muller *et al.* [26] carried out a set of experiments involving microstimulation of the intermediate layers of the SC. In this study the authors measured how subthreshold SC stimulation affected monkeys' thresholds for discriminating the direction of coherent motion in a spatially restricted aperture, embedded in a larger field of randomly moving dots (Figure 2b). They found that SC stimulation lowered discrimination thresholds when the coherent dot stimulus was presented to the part of the visual field represented at the stimulation site. When the aperture was positioned at other locations, SC stimulation did not affect discrimination thresholds.

The experiments involving the manipulation of neural activity in the FEF and the SC raise the question of how microstimulation of oculomotor areas brings about the observed behavioral enhancements. Recently, Moore and Armstrong addressed this question in an experiment that paired FEF stimulation with single-neuron recordings in extrastriate area V4 [27] (Figure 3). There is considerable evidence demonstrating that V4 responses are enhanced when attention is covertly directed to receptive field stimuli (e.g. [28,29]) or when receptive field stimuli are



**Figure 2.** Microstimulation of the SC. Two recent studies examined the effect of subthreshold SC microstimulation (left) on covert spatial attention. **(a)** One study used a change-blindness task in which monkeys were trained to detect peripheral changes in a visual display. During each trial the animal fixated centrally while moving dot apertures were presented at three locations, including within the response field (RF) of the SC site. After a variable delay there was a full field blanking of the display, followed by the reappearance of the dot apertures. On some trials the direction of movement in one aperture changed direction upon reappearing. The monkey was required to identify which stimulus had changed and indicate his response with a saccade to the appropriate target. If no direction change occurred the animal was required to continue fixating. Monkeys' ability to detect these motion changes within the RF improved with subthreshold stimulation of the SC applied during the initial motion epoch and continuing until the array reappeared (gray line). (Adapted from [25].) **(b)** Another study tested how subthreshold SC stimulation affected performance on a motion discrimination task. Monkeys fixated centrally while a spatially restricted aperture was presented within a full field of randomly moving dots. Monkeys were required to determine the direction of coherent motion and to indicate their judgment with a saccade to the appropriate response target. Microstimulation during the discrimination epoch improved performance when the coherent stimulus aperture was presented within the SC RF. (Adapted from [26].)



**Figure 3.** Effect of FEF microstimulation on the visual response of a V4 neuron. Microstimulation of sites within the FEF was carried out at the same time as recording the responses of single V4 neurons to visual stimuli while monkeys performed a fixation task. For these experiments the FEF microelectrode was positioned so as to align the evoked saccade vector (red arrow) with the RF position of the V4 cell (dotted circle). Histograms show the effect of subthreshold FEF microstimulation on V4 responses to an oriented bar stimulus presented to the RF (RF stim.). Mean response during control trials is shown in black, and the mean response during trials in which a 50-ms microstimulation train (FEF stim.) was applied to the FEF site is shown behind the control, in red. The response of the cell was elevated immediately following the stimulation train. This effect depended on the cell being visually driven, as when there was no RF stimulus present, FEF microstimulation did not change the V4 cell's response. (Adapted from [27].)

used as targets for saccades [30–33]. Moore and Armstrong examined whether similar visual response enhancements would result from FEF stimulation, in monkeys that were *not* performing attention tasks, but merely fixating. They found that very brief (20–50 ms) subthreshold microstimulation of the FEF enhanced visual responses in V4 neurons at retinotopically corresponding locations, whereas responses at other locations were suppressed. Interestingly, both the enhancement and suppression effects depended on the presence of additional ‘distracter’ stimuli outside the V4 neuron receptive field, as has been observed during attention. These findings suggest that the gain of visual responses in extrastriate cortex is directly modulated by the same activity that elicits a saccade to a particular location, and they suggest a mechanism for the voluntary modulation of visual responses when saccades are planned to the attended location but not executed. The results are also consistent with the finding that activity in human visual cortex depends in part on an intact prefrontal cortex [34].

The above stimulation studies provide direct evidence that the FEF and SC – brain regions known to mediate oculomotor programming – also play causal roles in spatially specific shifts of selective attention. One issue that has received considerable attention concerns the neural specificity of these microstimulation-driven effects. Electrical microstimulation affects all neural elements in the region of the electrode tip [35], leading to increased activity within a potentially diverse set of neurons. Thus, the possibility remains that the effects of microstimulation on saccades and visual selection reflect the activation of a heterogeneous neural population containing cells uniquely involved in saccades and visual selection.

Evidence supporting this putative dissociation is discussed in the next section.

### Heterogeneous neural populations and implications for neurophysiological models of spatial attention

Despite evidence of a causal role of oculomotor circuits in the deployment of visual spatial attention, it remains to be seen to what extent particular neurons within those circuits contribute directly to both oculomotor behavior and visual selection. As stated earlier, by definition, covert attention requires at some level the divergence of neural mechanisms controlling visual filtering and the triggering of orienting behaviors. But where in the visuo-oculomotor axis does neural activity have everything to do with the direction and amplitude of the next saccade and little or nothing to do with the filtering of visual signals? Contrary to studies reporting an interdependence of attentional and oculomotor deployment (e.g. [5]), some previous psychophysical studies have actually found that they are nonetheless dissociable [36–38].

Recent physiological evidence suggests that this divergence of function can be observed at the single cell level within oculomotor-related structures such as the FEF and the SC, where a continuum of visual, visuomotor and motor properties can be observed among neurons [39,40]. For example, Sato and Schall examined the activity of single neurons within the FEF during a search task that required saccades either towards (pro-saccades) or in the opposite direction to (anti-saccades) a pop-out target [41]. Some neurons initially selected the location of the singleton target, and then subsequently selected the final endpoint of the saccade. Thus, the activity of these cells was consistent with the predicted movements of visual attention during the trial. By contrast, the activity of other neurons was correlated only with the endpoint of the saccade, consistent with a unique role in oculomotor planning. These data and those from a similar study [42] suggest that visual selection and overt saccade programming involve separable neural populations in the FEF.

One limitation of such studies, however, is that the tasks required saccadic responses to relevant target. The consistent formation of these saccadic plans might have influenced the degree to which the activity of FEF neurons correlated with shifts of visual attention. A recent study by Thompson *et al.* is noteworthy in this regard for examining neural activity in the FEF during a visual search task that required only manual responses [43]. They found that neurons exhibiting visual responses (including cells with purely visual properties and cells with both visual and motor properties) were enhanced during covert attention, whereas neurons with purely motor properties were not enhanced, and often inhibited. This observation is similar to one reported by Ignashchenkova *et al.* [44]. They recorded single unit activity in the superior colliculus and found that both visual and visuomotor neurons were active during covert shifts of attention, but purely motor neurons were not.

These studies demonstrate functional heterogeneity at the level of single units within the FEF and SC. In each case, the activity of ‘purely motor’ neurons was not enhanced by covert shifts of attention. At the same time,

### Box 1. Varieties of attention

This review has focused on the top-down selection of targets at specific locations, but targets can also be selected on the basis of non-spatial dimensions, such as color [52], object file [53], and temporal position [54]. For example, various demonstrations of 'object-based' attention have found improved encoding of information within specific objects in the visual field, relative to unattended objects that occupy precisely the same locations (e.g. [53,55–57]). It has been natural (and indeed productive) to examine the links between oculomotor programs and spatially specific shifts of attention, given the common goal of biasing visual processing towards behaviorally relevant locations. It would be premature, however, to assume that the conclusions reached in these studies will apply uniformly in cases of non-spatial selection.

A similar qualification might be relevant when we consider the temporal locus of attentional selection. We have noted that microstimulation within regions that mediate saccades elicits modulations of processing in extrastriate areas during early stages of visual processing (see Figure 3 in main text). But it is also known that attention can

influence target processing during post-perceptual stages of processing – in some cases without detectable changes in the quality of early perceptual processing. For example, previous work has suggested that temporal selection [58] as well as some instances of object-based selection [59] do not affect the formation of early sensory representations but instead determine the extent to which these representations are granted access to working memory. In fact, even within the domain of spatial selection, substantial variations can be observed in the timing of attentional effects [60]. Thus, attention operates during both early and late stages of target processing [61–64]. Of course, differences in the time course of selection do not *require* multiple mechanisms for spatial selection. A common attentional resource could influence multiple stages of target processing. The most prudent position, therefore, is to acknowledge that this is an unresolved empirical question. Thus, conclusions regarding the relationship between attention and eye movements should bear in mind that 'attention' encompasses a diverse category of selection phenomena, with potentially diverse relationships to oculomotor control.

both studies identified a 'visuomotor' class of cells whose activity suggests a dual role in both visual selection and oculomotor control. Thus, these studies also confirm the hypothesis that the top-down selection of visual targets is intertwined with the preparation of saccades to them [45,46].

#### Top-down versus bottom-up control of attention

Although these electrophysiological studies provide evidence of functional heterogeneity at the single neuron level within the FEF and SC, one common characteristic deserves further comment. In each of the studies, covert shifts of spatial attention were elicited towards locations that had a high bottom-up salience. That is, spatial attention was shifted towards an object that had a unique color or shape [41–43] or towards the abrupt onset of a peripheral cue [44]. Past research has established distinct *goal-driven* and *stimulus-driven* routes for orienting spatial attention [47,48]. In the case of goal-driven orienting, attention is deployed in accordance with the observer's voluntary decision about what is currently most relevant. By contrast, when a specific element in a display has a relatively high salience, attention may be captured by that element in a bottom-up or stimulus-driven fashion. Converging with this view, recent studies have shown that there is simply less need for top-down control over attention when high-salience targets are presented. Pop-out targets suffer less from suppressive interactions with other stimuli [49], and they are detected and localized in a relatively automatic fashion in the posterior parietal cortex [50].

In light of this dichotomy, it is possible that the full role of oculomotor programs in attentional orienting will be most apparent in procedures that emphasize internally generated shifts of attention. In line with this idea, Juan *et al.* [51] stimulated the FEF and found that shifts of attention towards uniquely colored targets were not accompanied by the preparation of a saccade to the target's location. This suggests that covert shifts of attention towards such pop-out targets are not necessarily accompanied by an oculomotor plan. Thus, the degree of

coupling between oculomotor control and spatial attention might depend to some extent on the way in which spatial attention is deployed. Indeed, across decades of research, a wide range of empirical phenomena have been explained via the construct of 'attention', even though this is not likely to be a unitary process. Given the likelihood that there are multiple mechanisms for goal-driven selection, a more fully developed taxonomy of these processes could resolve some of the apparent contradictions in the literature (see Box 1).

#### Concluding remarks

Does the recent neurophysiological evidence confirm or weaken motor-based theories of attention, such as the premotor theory [3]? It can be said that the evidence appears to do both. Increasing the probability that a visual target will be foveated by electrically stimulating oculomotor structures, such as the FEF or the SC, concomitantly increases the probability that visual events at the target location will be detected. Furthermore, the perceptual improvements seen with electrical microstimulation of the FEF are accompanied by enhancements in visual cortical representations of potential target stimuli [27]. These observations provide prima facie evidence that the preparation of saccades to a stimulus necessarily drives the visual selection of that stimulus, and thus provides the best support to date for the view that the circuits controlling saccadic programming and covert spatial attention are one in the same (see also Box 2). However, at the single-neuron level, a division of labor among cells within oculomotor structures exists whereby neurons more involved in the saccade movement command can be dissociated from those more involved in selecting the visual target, at least during exogenously driven attention tasks (e.g. [43]). Thus, any strictly motor-based view of attentional control appears to break down at the level of single cells. Moreover, such a view must break down at some level given that we already know that the locus of attention can be disengaged from the point of fixation and that at the oculomotor periphery there

### Box 2. Questions for future research

- Microstimulation of FEF and SC sites exerts effects on covert spatial orienting. But is the activity of FEF and/or SC neurons necessary for the deployment of covert spatial attention?
- Clear links between oculomotor control and spatial selection have been documented. Will similar links be identified in cases involving post-perceptual or non-spatial selection?
- Does the degree of coupling between attention and oculomotor control depend upon whether attention is oriented in a goal-driven or a stimulus-driven manner?
- Past psychophysical studies have shown that attention tends to be directed towards the endpoint of planned saccades. Similar observations have been made in the case of reaching and grasping movements [65]. What is the role of motor mechanisms (oculomotor or skeleto-motor) in this type of visual selection?

is no anatomical basis by which motor commands can affect visual representations.

So where does this leave us? The controversy concerning the validity of motor-based hypotheses of attention has no doubt played an important role in driving experimental progress. However, we suggest that the need to confirm or refute such hypotheses may not be entirely compatible with the charge of understanding the neural mechanisms of attention *per se*, which might require specifically avoiding any assumptions of strict independence or interdependence of two neural processes, particularly in a system known for its flexibility. We suggest that the evidence instead be considered in a more ethological light: during normal visually guided behavior, oculomotor selection and visual attention are typically, but not always, coincident. It should be no surprise then that their underlying neural substrates are largely, but not inextricably, associated.

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