



ELSEVIER

The neurobiology of visual attention: finding sources

Tirin Moore

The profusion of progress during the past twenty years in identifying neural correlates of selective attention within the visual system has left open the question of how visual representations are biased to favor target stimuli. Studies aimed at specifying the mechanisms that can be causally implicated in the control of visual selective attention have only recently begun in earnest. Employing both the psychophysical and the neuroanatomical data, recent neurophysiological experiments in monkeys and neuroimaging studies in humans are converging on the neural circuits that provide the source of at least some forms of attentional control signals.

Addresses

Department of Neurobiology, Stanford University School of Medicine, Stanford, CA 94305, USA

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

Current Opinion in Neurobiology 2006, **16**:159–165

This review comes from a themed issue on
Cognitive neuroscience
Edited by Paul W Glimcher and Nancy Kanwisher

Available online 24th March 2006

0959-4388/\$ – see front matter

© 2006 Elsevier Ltd. All rights reserved.

DOI [10.1016/j.conb.2006.03.009](https://doi.org/10.1016/j.conb.2006.03.009)

Introduction: varieties of attention

Although it is generally true that, as William James [1] put it more than a century ago, “everyone knows what attention is”, it has become crucial in the intervening years to distinguish between the various ways by which “. . . one out of what seem several simultaneously possible objects or trains of thought” are selected by the nervous system. James himself made a distinction between instances in which attention is brought to an object either by virtue of its physical salience, that is, involuntary attention, or when such objects are willfully selected by the subject, that is, voluntary attention. Respectively, the two types are also referred to as the ‘bottom-up’ and ‘top-down’ (e.g. [2]), or ‘stimulus-driven’ and ‘goal-directed’ (e.g. [3]) forms of attention. Independent of that dichotomy is one in which attention is directed either to a location in space (e.g. [4]) (spatial attention) or to a particular feature or object regardless of its position in space (feature-based attention; e.g. [5]). Recent neurophysiological work on the neural basis of visual attention has involved all four varieties in one combination or another, and the results suggest that they have different underlying mechanisms. In addition,

whether or not attention is deployed in conjunction with a motor response (overt attention), for example, acquisition of fixation by way of an eye and/or head movement, can be distinguished from instances in which perceptual enhancements are accomplished wholly in the absence of orienting motor behavior (covert attention). Most of the neurophysiological studies of selective attention concern the influence of covert attention on visual representations. However, it appears that the similarities between overt attention and covert attention are more revealing than their differences. Current evidence suggests a common mechanism for both types of attention.

Here, I discuss this evidence and the recent progress in finding sources of visual attentive selection.

Mechanisms of involuntary attention

Involuntarily directed attention is driven by the target itself, by virtue of its relative salience, such as an inhomogeneity with surrounding stimuli, or by having any feature that makes it ‘pop-out’ from an array of other stimuli [6]. Already in primary visual cortex (V1), responses to arrays of multiple visual stimuli are enhanced when the receptive field (RF) of a neuron contains a single stimulus that differs from all others [7,8]. This and similar results have often been interpreted as evidence of early visual selection of ‘pop-out’ stimuli [7–10], and thus as a basis for an involuntary bias in visual selection. However, a recent study challenges this interpretation. Hedge and Felleman [11] found that V1 neurons were enhanced by all types of RF surround discontinuities, even when those discontinuities do not result in perceptual ‘pop-out’. Nevertheless, other evidence from behaving subjects, both human [12*] and monkey [13], demonstrates that in the absence of voluntary attention the activity within many visual areas is dominated by ‘pop-out’ stimuli. These observations contribute to the notion that separate neural mechanisms underlie involuntary and voluntary attention [14], and suggest that involuntary attention originates in earlier visual areas. However, the finding that visually responsive neurons within parietal area LIP [15] and within the frontal eye field (FEF) [16,17] have very short latencies leaves open the possibility that these areas are important for involuntary attention. Such short latencies in these two areas suggest a means by which frontal and parietal cortex might contribute to the immediate effect that stimulus salience has on attentional deployment.

Mechanisms of voluntary attention

One issue that has received increased focus lately is how perceptual biases might be brought about when attention

is voluntarily directed to one of multiple stimuli, regardless of their physical saliency. Where do control signals responsible for top-down filtering of sensory representations originate? Recent work suggests that, at least when attention is directly spatially, top-down selection is in part driven by neurons involved in oculomotor preparation. Despite the fact that attention can be dissociated from the direction of gaze (i.e. during covert attention), a large body of psychophysical evidence suggests that the same mechanisms of visual selection are involved whether or not the eyes move. A now classic study by Rizzolatti and co-workers [18] demonstrated that spatially directed attention can influence the trajectory of saccades, albeit modestly. This and other similar observations (e.g. [19]) inspired and spurred along the influential premotor theory of attention, which suggests that there is an equivalence of mechanisms for saccadic programming and covert spatial attention. Other psychophysical evidence has lent support to this view, in addition to suggesting a direction of causality in which saccade programming drives visual selection. For example, some studies have found that detection of visual events is improved at the location of an intended saccade [20]. Deubel and Schneider [21] concluded from such studies that a single mechanism drives both the selection of objects for perceptual processing and the information needed to drive the appropriate motor responses. Although the realization that oculomotor mechanisms might underlie voluntary spatial attention has been around at least since the time of Ferrier's lesion studies in the 19th century [22], the possibility has only recently been put to scrutiny in neurophysiological studies.

Visual representations during covert and overt attention

It is well established that the responses of cortical neurons to visual stimuli are modulated by covert attention [23]. Compelling evidence for attentional modulation started with observations of robust enhancement of visually driven activity in 'higher' visual areas in the parietal [24] and temporal lobes [25]. This evidence has accumulated to include that from earlier visual areas [26,27], and attentional effects both on V1 simple cells [28[•]] and within the dorsal lateral geniculate nucleus [29]. In parallel with these observations is the less well established or understood finding that at least in areas V4 and inferior temporal cortex, visually driven activity depends on whether or not a monkey will use a RF stimulus as a saccade target [30]. Employing either single saccade tasks [31–33] or tasks with naturalistic free-viewing [34,35,36[•]] of the type pioneered by Gallant *et al.* [37], several studies have found that neuronal responses to visual stimuli are enhanced presaccadically when the RF stimulus becomes the target. Thus, consistent with the fact that shifts of attention tend to accompany shifts in gaze [20], visual cortical representations are modulated during overt and covert attention. Whether the attention-related modulation reflects an influence of oculomotor planning on visual

representations [32], vice versa [35] or both [30,38] remains to be determined. However, some recent studies have begun to address this question.

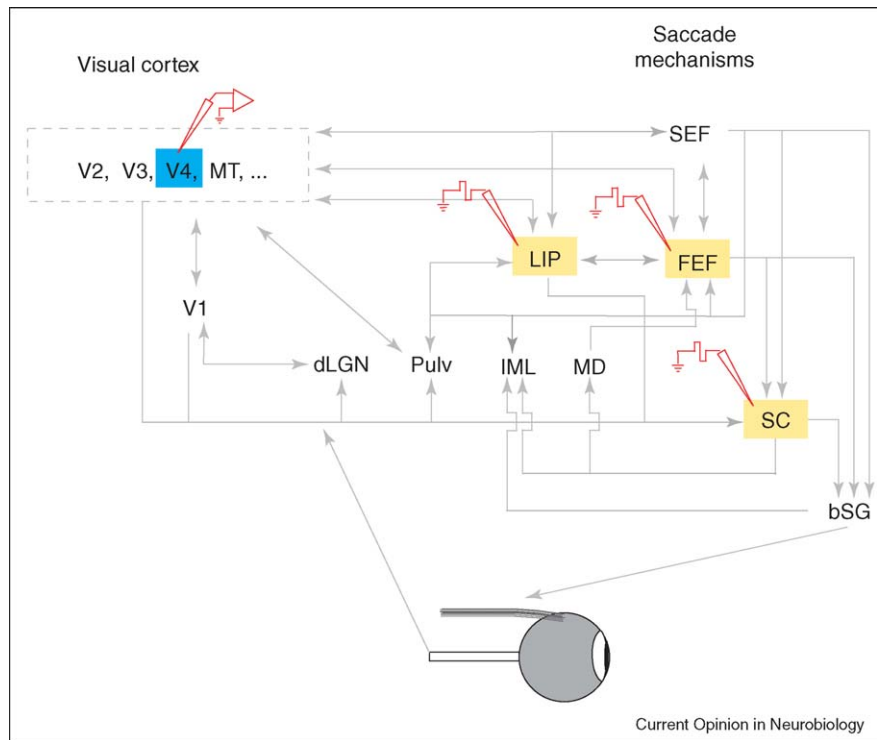
Focusing covert spatial attention with microstimulation

Given that saccadic eye movements are the primary way by which visual resources, namely the foveas, are brought to bear on relevant stimuli, it is not surprising that the visual and saccadic systems of the primate brain are highly interconnected (Figure 1). Moreover, these connections include pathways by which saccade-related signals can influence visual cortical representations via cortical [39] or subcortical routes [40]. Several recent studies have begun to assess the influence of oculomotor signals on vision by perturbing neural signals within oculomotor-related structures with electrical microstimulation (Figure 1). These oculomotor-related structures include the frontal eye field (FEF), the superior colliculus (SC), and the lateral intraparietal area (LIP), each of which has a known role in the programming and triggering of saccades, in particular the FEF and the SC. Experimenters employing reversible inactivation of these structures have found selective deficits in the ability of monkeys to choose visual targets when they are among distractors, as opposed to low-level visual or motor impairments [41–43]. Such results suggest an additional role of these structures, either individually or collectively, in voluntary attention, perhaps as a result of their involvement in saccade programming.

Moore and Fallah [44[•]] directly tested the hypothesis that the preparation of saccades to a location improves visual detection at that location. They trained monkeys to report the change in luminance of a peripheral visual target while fixating centrally and ignoring distractors. It was possible in the experiment to place the attended target in a position to which saccades could be evoked by microstimulation of sites within the frontal eye fields (FEF). Microstimulation of FEF sites that spatially overlapped the target position increased the monkeys' sensitivity to the target changes. The increased sensitivity resulted from performance improvements both on change trials (more 'hits') and on no-change trials (fewer 'false alarms'). Consistent with these observations are the results of recent studies in which transcranial magnetic stimulation has been used to disrupt activity within the FEF and consequently the performance of human subjects on covert attention tasks [45].

Two recent studies have examined the influence of microstimulation of the SC on covert visual attention. Using a change-blindness task, Cavanaugh and Wurtz [46] found that monkeys' ability to detect a brief change in the visual display was improved with subthreshold microstimulation of the intermediate layers of the SC where, like the FEF, saccades can be evoked. Similar to the situation in the FEF stimulation study, this effect was

Figure 1



Studies of the effects of microstimulation of oculomotor structures in the macaque brain on attention and its correlates in visual cortex.

A schematic depiction of the major neural pathways beginning with the output of the retina and returning to the eye muscles. Several oculomotor structures involved in planning and triggering visually guided eye movements, and their connections (gray arrows), are shown. Structures such as LIP, the FEF and the SC (yellow boxes) are each involved in transforming visual information into saccade commands. These areas are connected to each other, and to visual cortex (dashed line box with sample visual areas and V1), and the SC, SEF and FEF also have projections directly to the BSG. Recent experiments have examined the effects of microstimulation of the FEF [44*], LIP [48] and the SC [46,47] on the allocation of spatial attention. In all cases, evidence of improvement in spatial attention with microstimulation was obtained. In another study, microstimulation of the FEF was combined with single cell recordings in extrastriate area V4 (blue box). This study found that FEF stimulation produces transient increases in the gain of V4 visual responses. All of these results suggest that common neural circuits underlie the planning of visually guided saccades and the covert selection of visual stimuli. Abbreviations: BSG, brainstem saccade generator; FEF, frontal eye field; IML, internal medullary lamina of the thalamus; dLGN, dorsal lateral geniculate nucleus; LIP, lateral intraparietal area; MD, medial dorsal nucleus of the thalamus; MT, middle temporal area; Pulv, pulvinar nucleus; SC, superior colliculus; SEF, supplemental eye field.

crucially dependent on the retinotopic correspondence of the saccade represented at the stimulation site and the changing stimulus. When the stimulus change occurred at another location, SC stimulation did not improve performance and reaction times for reporting changes were increased. Concurrently, Muller *et al.* [47] also observed that intermediate layer SC microstimulation could reduce the perceptual thresholds of monkeys performing a direction of motion discrimination. They also found that the microstimulation effects depended on the spatial overlap of the stimulated representation and the discriminanda.

In another study, Cutrell and Marrocco [48] measured the influence of LIP microstimulation on the effects of visual cueing on reaction time to detect targets. When LIP microstimulation was delivered following the appearance of the cue, the authors observed a general decrease in reaction time for all conditions. That is, microstimulation appeared to alert the monkey to the impending target

appearance independent of cue presence or whether the cue correctly indicated the location of the subsequently appearing target. Thus, in contrast to the effects of FEF or SC microstimulation, the effects in LIP do not appear to be spatially specific. The effects of microstimulation of LIP on attention are not easy to reconcile with the compelling evidence of an involvement of LIP neurons in mapping the salience of visual targets [49]. However, the finding that LIP neurons appear able to signal multiple target items [50] might be consistent with the spatial non-specificity of the microstimulation effects.

Driving correlates of attention with microstimulation

The spatially selective effects of microstimulation of the FEF and the SC suggest that increasing the probability that a stimulus will be the target of a saccade increases the visual representation of that stimulus. Moore and Armstrong [51] directly tested this possibility in an experiment that paired FEF stimulation with single-cell

recording in extrastriate area V4. In this study the authors examined whether attention-like modulation would result from FEF stimulation, using monkeys that were not performing attention tasks but merely fixating. They found that 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. Similar to what has been observed during voluntary covert attention [26], the magnitude of the enhancement (and the suppression) depended on the presence of additional ‘distracter’ stimuli outside the V4 neuron receptive field. This facilitatory effect of microstimulation on visual responses suggests that the gain of visual signals is modulated according to the likelihood that a saccade will be made to a particular location in space.

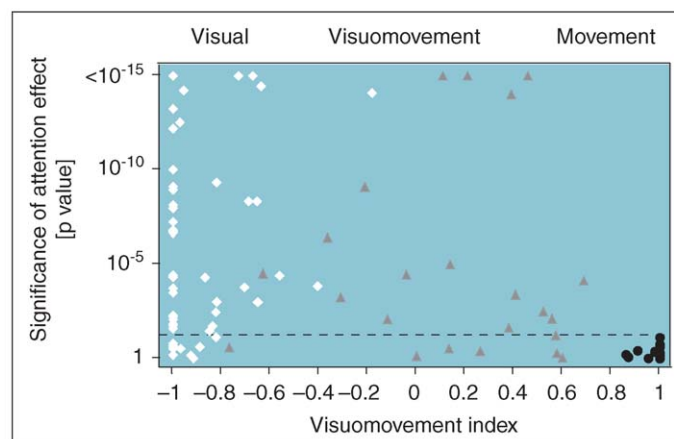
How might the above observations generalize to other types of top-down sensorimotor interactions? Could it be that biasing spatially directed movements facilitates other types of sensory processing at the intended location of action? A recent study of midbrain auditory neurons provides some support for this notion. Neurons within the optic tectum of the barn owl comprise a map of auditory space [52]. The owl’s gaze direction is controlled in part by neurons within the arcopallial gaze field (AGF), in the forebrain, and is considered homologous with the FEF in primates. Microstimulation of sites within the AGF evokes short latency head and eye movements of a given direction [53]. Winkowski and Knudsen [54] examined the influence of subthreshold microstimulation of AGF on auditory responses of tectal neurons and found

that responses to stimuli in the space represented by the stimulated AGF site were enhanced. By contrast, the same microstimulation suppressed auditory responses to stimuli presented at other locations in space. Thus, the mounting evidence that signals associated with motor preparation can provide spatial attention-like biases in sensory processing extends to the auditory domain, and to non-primate species.

‘Premotor theory’ and the overlap question

The flurry of recent efforts to pin down the origin of visual attention signals has also reinvigorated a debate long maintained among psychophysicists. Are the mechanisms that drive oculomotor preparation the same ones that drive visual selection during covert spatial attention? At present, this issue appears to remain hotly debated [55]. Moreover, this debate has spread to the single neuron level at which one can assess directly the involvement of motor-related neural activity in attention. For example, a recent study by Thompson *et al.* [56*] examined the incidence of attentional modulation among the different classes of neurons within the FEF (Figure 2). They first classified neurons as visual, visuomotor, or motor according to a standard memory-guided saccade task in which one can disentangle the visual and motor-related responses. They then measured the attention-related enhancement of those neurons in a task that did not involve a saccade response. They found that both visual and visuomotor neurons 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.* [57].

Figure 2



Statistical significance of attentional modulation of FEF neurons with visual, visuomotor or motor properties. The plot shows the distribution of visuomotor indices and the corresponding significance of attentional effects for a population of FEF neurons. The visuomovement index measures the contrast ratio of the visual and saccade related responses recorded during the memory guided saccade task. Neurons with values approaching -1 (white diamonds) are dominated by a visual response and neurons approaching $+1$ (black circles) are dominated by saccade related activity. Neurons with values near 0 (gray triangles) indicate approximately equivalent visual and saccade related activation. The abscissa shows the statistical probability that target and distractor activity is the same for each of the functionally categorized neurons. The dotted line denotes the $p < 0.05$ α level. Both visual and visuomovement neurons are modulated by the attentional manipulation, whereas the movement neurons are not. Adapted from Thompson *et al.* [56*].

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. Both results are noteworthy in that they provide evidence that the functional divergence of spatial attention and saccade command signals occurs at the single neuron level within the FEF and the SC. That is, they demonstrate that attentional modulation is both separable from and associated with the preparation of saccades. As it is apparent that the mechanisms involved in the triggering of saccades and those involved in covert attention must diverge at least at the point at which the eye must either be moved or be held in place, hence the covert–overt distinction, these results appear to make considerable sense. Together with other recent studies, they suggest that the visuo–oculomotor system of primates has evolved the capacity to amplify target visual signals in the absence of the overt deployment of eye movements [30], and that the covert and overt mechanisms do not diverge until a point in the neuronal circuitry close to the neurons that trigger the saccade [58].

Mechanisms of object-based attention

Although recent microstimulation work lends support for a role of oculomotor mechanisms in spatially directed visual attention, it says nothing about the source of feature-based selection. Objects or features can be selectively attended independent of their location in space [5], and the influence of feature-based attention on vision is pervasive enough even to determine which of two spatially coextensive binocular rivalry stimuli is perceived [59]. In addition to the well-documented effects of covert spatial attention on visual cortical responses, there is good evidence that attention to particular objects or their features results in similar effects in visual cortex [23,60]. However, converging data from human and monkey studies indicates that the influence of feature-based attention on visual cortical representations precedes that of spatial attention [61,62]. In contrast to the probable sources of spatial attention signals, in which it appears that saccade representations function as salience maps [30,63], it appears thus far that the source of object and feature-based salience is within the visual areas that represent those objects and features. Human imaging experiments reveal that attention to features (e.g. color or motion) results in selective modulation within areas that are sensitive to that feature [64]. Likewise, monkey neurophysiology experiments suggest that visual cortical neurons sensitive to a particular feature are selectively enhanced when that feature is the target of attention [36,60]. These observations suggest that initial biases in object or featural representations form a salience map with which matching items can be preferentially selected during visual search [31]. Thus, one assumes that the relevant feature-based bias signals must persist during search as a form of working memory [6]. Indeed, recent neurophysiological studies suggest a difficulty in

distinguishing between attention-related and working-memory related activity within prefrontal cortex [65*].

Conclusions

Convergent evidence of a causal role for oculomotor signals in the deployment of attention from both neurophysiological experiments in monkeys and imaging and TMS studies in humans have supplied a foothold on the problem of identifying the sources of attention-driving signals. They suggest, for example, that perhaps all types of pre-existing neural states, be they persisting representations of a visual stimulus, moment-to-moment fluctuations in oculomotor preparation, or even learned sensitivity to featural discontinuities, might constructively interfere with feed-forward visual input and bias visual selection. Thus, the source of visual attention bias could be any signal capable of interacting with the representation of incoming stimuli.

Acknowledgements

This work was supported by NIH Grant EY14924, the Pew Charitable trusts, and the Sloan Foundation.

References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. James W: *Principles of Psychology*. H. Holt; 1890.
 2. Miller BT, D'Esposito M: **Searching for 'the Top' in top-down control**. *Neuron* 2005, **48**:535-538.
 3. Kincade JM, Abrams RA, Astafiev SV, Shulman GL, Corbetta M: **An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention**. *J Neurosci* 2005, **25**:4593-4604.
 4. Silver MA, Ress D, Heeger DJ: **Topographic maps of visual spatial attention in human parietal cortex**. *J Neurophysiol* 2005, **94**:1358-1371.
 5. Hopf JM, Boelmans K, Schoenfeld MA, Luck SJ, Heinze HJ: **Attention to features precedes attention to locations in visual search: evidence from electromagnetic brain responses in humans**. *J Neurosci* 2004, **24**:1822-1832.
 6. Desimone R, Duncan J: **Neural mechanisms of selective visual attention**. *Annu Rev Neurosci* 1995, **18**:193-222.
 7. Knierim JJ, van Essen DC: **Neuronal responses to static texture patterns in area V1 of the alert macaque monkey**. *J Neurophysiol* 1992, **67**:961-980.
 8. Kastner S, Nothdurft HC, Pigarev IN: **Neuronal correlates of pop-out in cat striate cortex**. *Vision Res* 1997, **37**:371-376.
 9. Hopf JM, Noesselt T, Tempelmann C, Braun J, Schoenfeld MA, Heinze HJ: **Popout modulates focal attention in the primary visual cortex**. *Neuroimage* 2004, **22**:574-582.
 10. Zhaoping L: **The primary visual cortex creates a bottom-up saliency map**. In *Neurobiology of Attention*. Edited by Itti L, Rees G, Tsotsos JK. Elsevier; 2005:570-575.
 11. Hegde J, Felleman DJ: **How selective are V1 cells for pop-out stimuli?** *J Neurosci* 2003, **23**:9968-9980.
 12. Beck DM, Kastner S: **Stimulus context modulates competition in human extrastriate cortex**. *Nat Neurosci* 2005, **8**:1110-1116.
- This human functional imaging study examines competitive interactions of multiple visual stimulus representations in extrastriate cortex. The activity driven by single stimuli is suppressed by the addition of others, but top-down attention can bias competitive interactions in favor of the attended item, thus removing some of the distractor-driven suppression.

This study finds that when items are presented in a pop-out display, in which the item is involuntarily selected, the suppressive interactions are eliminated.

13. Constantinidis C, Steinmetz MA: **Posterior parietal cortex automatically encodes the location of salient stimuli.** *J Neurosci* 2005, **25**:233-238.
 14. Corbetta M, Shulman GL: **Control of goal-directed and stimulus-driven attention in the brain.** *Nat Rev Neurosci* 2002, **3**:201-215.
 15. Bissley JW, Krishna BS, Goldberg ME: **A rapid and precise on-response in posterior parietal cortex.** *J Neurosci* 2004, **24**:1833-1838.
 16. Thompson KG, Hanes DP, Bichot NP, Schall JD: **Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search.** *J Neurophysiol* 1996, **76**:4040-4055.
 17. Thompson KG, Bichot NP, Sato TR: **Frontal eye field activity before visual search errors reveals the integration of bottom-up and top-down salience.** *J Neurophysiol* 2005, **93**:337-351.
 18. Rizzolatti G, Riggio L, Dascola I, Umiltà C: **Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention.** *Neuropsychologia* 1987, **25**:31-40.
 19. Kowler E, Anderson E, Doshier B, Blaser E: **The role of attention in the programming of saccades.** *Vision Res* 1995, **35**:1897-1916.
 20. Hoffman JE, Subramaniam B: **The role of visual attention in saccadic eye movements.** *Percept Psychophys* 1995, **57**:787-795.
 21. Deubel H, Schneider WX: **Saccade target selection and object recognition: evidence for a common attentional mechanism.** *Vision Res* 1996, **36**:1827-1837.
 22. Ferrier D: *Cerebral Localisation.* Smith, Elder and co.; 1890.
 23. Reynolds JH, Chelazzi L: **Attentional modulation of visual processing.** *Annu Rev Neurosci* 2004, **27**:611-647.
 24. Bushnell MC, Goldberg ME, Robinson DL: **Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention.** *J Neurophysiol* 1981, **46**:755-772.
 25. Moran J, Desimone R: **Selective attention gates visual processing in the extrastriate cortex.** *Science* 1985, **229**:782-784.
 26. Motter BC: **Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli.** *J Neurophysiol* 1993, **70**:909-919.
 27. Li W, Piech V, Gilbert CD: **Perceptual learning and top-down influences in primary visual cortex.** *Nat Neurosci* 2004, **7**:651-657.
 28. McAdams CJ, Reid RC: **Attention modulates the responses of simple cells in monkey primary visual cortex.** *J Neurosci* 2005, **25**:11023-11033.
- An impressive and carefully conducted test of the influence of attention on the V1 simple cells. Remarkably, the authors find that attention effects are present within both the primary and secondary subfields of simple cells, which sit at the first stage of visual cortical processing.
29. Kastner S, O'Connor DH, Fukui MM, Fehd HM, Herwig U, Pinsk MA: **Functional imaging of the human lateral geniculate nucleus and pulvinar.** *J Neurophysiol* 2004, **91**:438-448.
 30. Moore T, Armstrong KM, Fallah M: **Visuomotor origins of covert spatial attention.** *Neuron* 2003, **40**:671-683.
 31. Chelazzi L, Miller EK, Duncan J, Desimone R: **A neural basis for visual search in inferior temporal cortex.** *Nature* 1993, **363**:345-347.
 32. Tolias AS, Moore T, Smirnakis SM, Tehovnik EJ, Siapas AG, Schiller PH: **Eye movements modulate visual receptive fields of V4 neurons.** *Neuron* 2001, **29**:757-767.
 33. Ogawa T, Komatsu H: **Target selection in area V4 during a multidimensional visual search task.** *J Neurosci* 2004, **24**:6371-6382.
 34. Sheinberg DL, Logothetis NK: **Noticing familiar objects in real world scenes: the role of temporal cortical neurons in natural vision.** *J Neurosci* 2001, **21**:1340-1350.
 35. Mazer JA, Gallant JL: **Goal-related activity in V4 during free viewing visual search. Evidence for a ventral stream visual salience map.** *Neuron* 2003, **40**:1241-1250.
 36. Bichot NP, Rossi AF, Desimone R: **Parallel and serial neural mechanisms for visual search in macaque area V4.** *Science* 2005, **308**:529-533.
- This elegant study looks for evidence of parallel and serial search correlates in the responses of single neurons, and the synchrony between the neuronal responses and the local field potential at sites within area V4 of monkeys performing a freely scanning visual search task. The authors find evidence of parallel selection by V4 neurons: distractor items with similar features as the target item yielded enhanced responses and synchrony in the gamma frequency range. The authors also found evidence of serial selection: enhanced neural activity when the RF stimulus was ultimately selected as the target for a saccade.
37. Gallant JL, Connor CE, Van Essen DC: **Neural activity in areas V1, V2 and V4 during free viewing of natural scenes compared to controlled viewing.** *Neuroreport* 1998, **9**:2153-2158.
 38. Moore T: **Shape representations and visual guidance of saccadic eye movements.** *Science* 1999, **285**:1914-1917.
 39. Stanton GB, Bruce CJ, Goldberg ME: **Topography of projections to posterior cortical areas from the macaque frontal eye fields.** *J Comp Neurol* 1995, **353**:291-305.
 40. Shipp S: **The brain circuitry of attention.** *Trends Cogn Sci* 2004, **8**:223-230.
 41. Schiller PH, Tehovnik EJ: **Neural mechanisms underlying target selection with saccadic eye movements.** *Prog Brain Res* 2005, **149**:157-171.
 42. McPeck RM, Keller EL: **Deficits in saccade target selection after inactivation of superior colliculus.** *Nat Neurosci* 2004, **7**:757-763.
 43. Wardak C, Olivier E, Duhamel JR: **A deficit in covert attention after parietal cortex inactivation in the monkey.** *Neuron* 2004, **42**:501-508.
 44. Moore T, Fallah M: **Microstimulation of the frontal eye field and its effects on covert spatial attention.** *J Neurophysiol* 2004, **91**:152-162.
- This study tests the hypothesis that saccade preparation biases visual detection at the location to which the saccade is prepared. The authors found that when they stimulated sites within the FEF (using currents too weak to evoke a movement) it led to improved detection of visual events at the location represented by neurons at the stimulation site. Importantly, the authors also find that the psychophysical improvement is best when the microstimulation temporally coincides with the time of the target event.
45. Chambers CD, Mattingley JB: **Neurodisruption of selective attention: insights and implications.** *Trends Cogn Sci* 2005, **9**:542-550.
 46. Cavanaugh J, Wurtz RH: **Subcortical modulation of attention counters change blindness.** *J Neurosci* 2004, **24**:11236-11243.
 47. Muller JR, Philiastides MG, Newsome WT: **Microstimulation of the superior colliculus focuses attention without moving the eyes.** *Proc Natl Acad Sci USA* 2005, **102**:524-529.
 48. Cutrell EB, Marrocco RT: **Electrical microstimulation of primate posterior parietal cortex initiates orienting and alerting components of covert attention.** *Exp Brain Res* 2002, **144**:103-113.
 49. Gottlieb J: **Parietal mechanisms of target representation.** *Curr Opin Neurobiol* 2002, **12**:134-140.
 50. Gottlieb J, Kusunoki M, Goldberg ME: **Simultaneous representation of saccade targets and visual onsets in monkey lateral intraparietal area.** *Cereb Cortex* 2005, **15**:1198-1206.

51. Moore T, Armstrong KM: **Selective gating of visual signals by microstimulation of frontal cortex.** *Nature* 2003, **421**:370-373.
52. Cohen YE, Knudsen EI: **Maps versus clusters: different representations of auditory space in the midbrain and forebrain.** *Trends Neurosci* 1999, **22**:128-135.
53. Knudsen EI, Cohen YE, Masino T: **Characterization of a forebrain gaze field in the archistriatum of the barn owl: microstimulation and anatomical connections.** *J Neurosci* 1995, **15**:5139-5151.
54. Winkowski J, Knudsen EI: **Top-down gain control of the auditory space map by gaze control circuitry in the barn owl.** *Nature* 2006, **439**:336-339.
55. Awh E, Armstrong KM, Moore T: **Visual and oculomotor selection: links, causes and implications for spatial attention.** *Trends Cogn Sci* 2006, **10**:124-130.
56. Thompson KG, Biscoe KL, Sato TR: **Neuronal basis of covert**
 - **spatial attention in the frontal eye field.** *J Neurosci* 2005, **25**:9479-9487.

The first demonstration of attentional modulation of FEF neurons in a task that does not involve a saccadic eye movement. The authors find that of the three major classes of neurons, visual, visuomovement, and movement, defined in a standard memory-guided saccade task, it is the visual and visuomovement neurons that are modulated by attention. The movement neurons appeared to be suppressed, thus demonstrating that the functional divergence of covert and overt attention signals occurs within the FEF.
57. Ignashchenkova A, Dicke PW, Haarmeier T, Thier P: **Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention.** *Nat Neurosci* 2004, **7**:56-64.
58. Schall JD: **On the role of frontal eye field in guiding attention and saccades.** *Vision Res* 2004, **44**:1453-1467.
59. Mitchell JF, Stoner GR, Reynolds JH: **Object-based attention determines dominance in binocular rivalry.** *Nature* 2004, **429**:410-413.
60. Martinez-Trujillo JC, Treue S: **Feature-based attention increases the selectivity of population responses in primate visual cortex.** *Curr Biol* 2004, **14**:744-751.
61. Hayden BY, Gallant JL: **Time course of attention reveals different mechanisms for spatial and feature-based attention in area V4.** *Neuron* 2005, **47**:637-643.
62. Hopf JM, Boelmans K, Schoenfeld MA, Luck SJ, Heinze HJ: **Attention to features precedes attention to locations in visual search: evidence from electromagnetic brain responses in humans.** *J Neurosci* 2004, **24**:1822-1832.
63. Thompson KG, Bichot NP: **A visual salience map in the primate frontal eye field.** *Prog Brain Res* 2005, **147**:251-262.
64. Chawla D, Rees G, Friston KJ: **The physiological basis of attentional modulation in extrastriate visual areas.** *Nat Neurosci* 1999, **2**:671-676.
65. Lebedev MA, Messinger A, Kralik JD, Wise SP: **Representation of**
 - **attended versus remembered locations in prefrontal cortex.** *PLoS Biol* 2004, **2**:e365.

This timely study compares the influence of working memory and attention on the activity of neurons in prefrontal cortex. Monkeys performed a task in which they had to attend simultaneously to one location while remembering another. The authors found that the largest proportion of neurons signaled the attended location and not the remembered one, thus calling into question long-held assumptions of a role of prefrontal cortex principally in working memory.