



ELSEVIER

Top-down control of visual attention

Behrad Noudoost¹, Mindy H Chang¹, Nicholas A Steinmetz¹ and Tirin Moore^{1,2}

Top-down visual attention improves perception of selected stimuli and that improvement is reflected in the neural activity at many stages throughout the visual system. Recent studies of top-down attention have elaborated on the signatures of its effects within visual cortex and have begun identifying its causal basis. Evidence from these studies suggests that the correlates of spatial attention exhibited by neurons within the visual system originate from a distributed network of structures involved in the programming of saccadic eye movements. We summarize this evidence and discuss its relationship to the neural mechanisms of spatial working memory.

Addresses

¹ Department of Neurobiology, Stanford University School of Medicine, Stanford, CA 94305, United States

² Howard Hughes Medical Institute, Stanford University School of Medicine, Stanford, CA 94305, United States

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

Current Opinion in Neurobiology 2010, 20:183–190

This review comes from a themed issue on
Cognitive neuroscience
Edited by Earl Miller and Liz Phelps

Available online 19th March 2010

0959-4388/\$ – see front matter

© 2010 Elsevier Ltd. All rights reserved.

DOI 10.1016/j.conb.2010.02.003

Introduction

Selective attention is the basic cognitive faculty that allows us to filter out irrelevant sensory information in favor of the relevant. Disorders of attention are frequently occurring among the symptoms of many neuropsychiatric disorders [33], most notably attention-deficit hyperactivity disorder (ADHD), which afflicts more than 4% of the population [34]. To date, the neural circuits and neural computations underlying normal and abnormal attention are only poorly understood. However, recent experimental work suggests that an understanding of how networks of neurons control the selection of relevant sensory input might be at hand. Much of what is known so far about the neural basis of attention comes from studies of the primate visual system, particularly that of the macaque monkey, which has proven to be a highly valuable model system. In recent years, neurophysiological studies have not only provided a more rigorous description of the correlates and signatures of attention in neural activity,

but they have begun identifying the sources of attentional influences on neural activity and perception. The deployment of attention to a particular location in space (spatial attention) or to a particular feature or object (feature-based or object-based attention) can occur either by virtue of a stimulus' physical salience (exogenous, involuntary or bottom-up attention) or according to internal, behavioral goals (endogenous, voluntary or top-down attention). Most of the studies over the past few years that we discuss, particularly those aimed at identifying neural circuits controlling attention, have focused primarily on top-down, spatial attention. Although it is clear that feature-based attention (e.g. [23,35]) and bottom-up attention (e.g. [12*,36]) both modulate neuronal activity within the visual system, the neurophysiological effects of these forms of attention are less well understood.

Signatures of attention

Attention provides a means of dynamically selecting specific neural representations for further processing, and this filtering involves amplifying behaviorally relevant information at the expense of other information. The objective of attention can be viewed as increasing the signal-to-noise ratio (SNR) of the readout from sub-populations of neurons encoding the selected representation. In theory, this can be accomplished in a number of ways, including strengthening selected signals, improving the efficacy of inputs to the readout stage, and reducing noise. The majority of previous work has demonstrated attention-dependent signal amplification by way of increases in firing rate across multiple stages of the visual system (Table 1), but a growing set of electrophysiological studies report signatures of attention that support complementary ways of improving the SNR of selected signals.

In addition to increases in firing rate, attention can potentially enhance signal efficacy via synchrony among neurons encoding the attended information. In particular, it has been argued that high frequency (gamma-band) synchronization of spiking output from selected groups of neurons can increase the influence of spikes on downstream areas [37–39]. Coherence among spikes and between spikes and local field potentials (LFPs) provides a measure of phase locking within local groups of neurons. Near-zero phase lag synchrony among neurons encoding the attended representation could facilitate the integration of spikes from these populations converging on postsynaptic targets. Studies of selective attention have found increases in local gamma-band [16*,19–21,23,24],

Table 1**Summary of signatures of top-down attention within the visual system.**

Signature	Implications	Area	Effect size	Citation
↑ Spike rate	Increases output signal	LGN	12%	[1*]
		TRN	-4%	
		Pulv		[2]
		SC	21% (visual neurons) 40% (visuomotor neurons)	[3]
		V1	8%	[4,5*,6]
		V2	19%	[6]
		V4	26%	[4,6,7]
		MT	20%	[8]
		IT	70%	[7,9,10]
		LIP	75%'	[11,12*]
		FEF*	100%'	[12*,13,14*,15,16*]
PFC		[12*,17,18]		
↑ Gamma-band LFP power	Increases locally synchronous synaptic activity	FEF	(40–60 Hz)	[16*]
		V4	(40–60 Hz)	
		V4	(30–70 Hz)	[19]
		V4*	43% (45–103 Hz): monkey 1 73% (45–103 Hz): monkey 2	[20*]
↑ Local gamma-band coherence	Potentially increases signal efficacy at post-synaptic targets	FEF	22% (40–60 Hz SFC)	[16*]
		V4	14% (40–60 Hz SFC)	
		V4	(30–70 Hz SSC) (30–70 Hz SFC)	[19]
		V4*	(40–72 Hz SFC)	[21*]
		V4	19% (40–90 Hz SFC)	[22]
		V4	22% (30–60 Hz SFC): feature	[23]
LIP	(25–45 Hz SFC)	[24]		
↑ Cross-areal gamma-band coherence	Potentially facilitates long-range interactions by providing a common temporal reference frame	FEF ↔ V4	13% (40–60 Hz SSC) 24% (40–60 Hz SFC): V4 spikes 37% (40–60 Hz SFC): FEF spikes 63% (40–60 Hz FFC)	[16*]
		PFC/FEF ↔ LIP	(22–55 Hz FFC) (22–34 Hz search > popout) (35–55 Hz popout > search)	[12*]
		LIP ↔ MT	(25–45 Hz SSC) (25–45 Hz FFC)	[24]
↓ Response variability (Fano factor)	Increases reliability of encoded information	V4	-18% (narrow-spiking cells)	[25]
		V4	-9% (broad-spiking cells) -20%	[26]
↓ Low frequency synchrony	Potentially reduces output redundancy by decreasing correlation	V4	(9–11 Hz SSC) (9–11 Hz LFP) (9–11 Hz SFC)	[19]
		V4	-23% (<17 Hz SFC)	[22]
		V4	-23% (<5 Hz SSC)	[27]
↓ Correlated noise at low frequencies	Potentially increases the sensitivity of pooled responses	V4	-40%	[27]
		V4	-52%	[26]
Receptive field modulation	Potentially increases output signal by recruiting neurons	MT	31% shift; -9% size	[28]
		MT	10% shift	[29]
		V4	40% shift	[30–32]

Neural signatures of attention. An overview of reported neural signatures and their implications for increasing the signal to noise ratio of the readout from neurons encoding a selected representation. The included citations highlight recent studies and studies that report effect sizes (listed first in citations). Note that effect sizes and significant frequency ranges are dependent on the different behavioral paradigms as well as recording and analysis methods used in each study. The * denotes studies that have demonstrated that the corresponding signature can be used to predict a behavioral correlate of attention. The ' denotes an effect size value estimated from a figure in the cited article. Abbreviations: LFP, local field potential; SSC, spike-spike coherence; SFC, spike-field coherence; FFC, field-field coherence; RF, receptive field; FEF, frontal eye field; LIP, lateral intraparietal area; IT, inferotemporal cortex; SC, superior colliculus; LGN, lateral geniculate nucleus; Pulv, pulvinar nucleus of the thalamus; PFC, prefrontal cortex.

and beta-band [12°,92] synchrony, which in some cases has also been shown to predict improved behavioral outcomes [20,21] or to track attention shifts [92]. These observations lend support for a functional role of synchrony in attentional selection. However, differences in reported frequency ranges in which significant effects of attention are observed (Table 1) leave open the question of how synchrony might provide a generalized mechanism for attention.

Attention allows for dynamic routing of information to guide decisions and behavior. Recent reports of increased cross-areal interactions during attention suggest that long-range synchrony may play a role in linking distant functional areas by providing a common temporal reference frame for communication [12°,16°,24,40]. In this scheme, incoming spikes could achieve maximal impact when they arrive at an optimal phase of the local oscillations. While gain modulation of the firing rate can allow a selected representation to dominate over others, synchrony presents another potential way to resolve competition during attentional selection by setting narrow windows in time to gate information flow [41].

Recently, attention has also been found to decrease the variability of individual neurons, as quantified by the mean-normalized variance across trials [25]. This finding suggests that attention improves the reliability with which information is represented in neurons encoding the selected stimulus [25,26]. Response variability of individual neurons can arise from independent sources of noise within each neuron and/or correlated fluctuations shared across neurons. While independent variability can easily be averaged away in the population readout by pooling across many neurons, shared variability can potentially place more stringent limits on the sensitivity of the population [42]. Recent studies have found that attention reduces the correlated variability of neurons in area V4, improving the SNR more effectively than increases in firing rate or decreases in independent variability [26,27]. This decorrelation arises mainly from a suppression of low frequency (<5 Hz) rate fluctuations shared across the population and may reflect the attention-dependent low frequency desynchronization observed in area V4 in a separate paradigm [19] as well as EEG studies in humans [43]. Within an area, attention could also potentially amplify and sharpen selected signals by recruiting additional neurons to represent selected information and narrowing their spatial tuning. Studies that show a shift and shrinkage of receptive fields toward attended stimuli provide evidence for adaptive prioritization of visual representations [21,29,30,44].

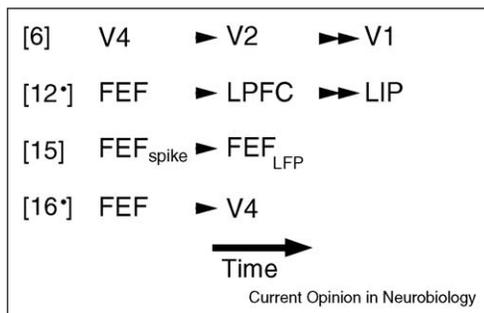
Sources of attention

Experimental evidence of a role of prefrontal and parietal cortex in the control of attention, and particularly of brain structures involved in oculomotor or gaze functions, dates

back to at least the late 19th century [45]. Only in recent years, however, has the relationship between the neural control of gaze and attention been tested directly. Several studies have employed electrical microstimulation to probe the role of saccade-related structures in the deployment of spatial attention. Moore and Fallah [46] 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), they could enhance a monkey's performance on an attention-demanding task. Importantly, the improvements observed with microstimulation were dependent upon the target of attention being positioned at the location to which suprathreshold microstimulation would shift the monkey's gaze. Thus, it appeared that by increasing the likelihood that the monkey would foveate a location in visual space, the experimenters also enhanced the animal's ability to process visual events there. Two other studies reported similar enhancements in visual spatial attention following subthreshold microstimulation of the SC [47,48]. In both cases, the performance enhancing effects of microstimulation were spatially dependent as in the FEF studies. Another study found that subthreshold microstimulation of sites within LIP reduced reaction times in a cued target detection task, albeit in a non-spatially specific manner [49]. In each of the above studies the effects of microstimulation were measured in the absence of any saccadic eye movements, that is, during covert attention. Another study examined the effect of FEF microstimulation on the metrics of saccades made to visual stimuli [50]. In control trials, the endpoints of saccades made to drifting gratings are biased in the direction of grating drift in spite of the fact that the grating aperture is stationary. Subthreshold FEF microstimulation augments 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 not only drives the selection of retinotopically corresponding visual stimuli (i.e. attention), but also the selection of the appropriate saccades needed to fixate those stimuli.

Consistent with the above evidence of 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 visually driven responses of area V4 neurons with receptive fields (RFs) at locations overlapping the stimulated FEF representation [51]. 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 suppressed responses, mimicking the effects observed during endogenous attention. Furthermore, the enhancement of V4 responses is confined only to RF stimuli that

Figure 1



Summary of recent findings from studies comparing the timing of attention effects in different cortical areas. Each row represents a separate study. '►' indicates shorter time difference compared to '►►' for the same study. LPFC, lateral prefrontal cortex.

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 the ones observed when the aligned stimulus is presented alone [52]. Importantly, the above changes in V4 responses are reliable within ~40 ms of the start of stimulation suggesting a direct effect of stimulation on visual representations [53]. More recently, another laboratory used functional magnetic resonance imaging (fMRI) to examine the influence of FEF microstimulation on visual activation throughout cortex [54]. FEF microstimulation enhanced the visual activation of retinotopically corresponding foci within multiple visual areas, most notably within V1 and V2 which receive little or no direct projections from the FEF [55]. FEF microstimulation also increased the contrast sensitivity within multiple visual areas [56]. Taken together, the above studies provide direct evidence of a robust influence of the FEF on the gain of signals within visual cortex.

Studies comparing the onset latencies of attentional modulation across different areas have yielded evidence that is consistent with a fronto-parietal source of that modulation (Figure 1). Paired recordings in the FEF and area V4 not only reveal that FEF neurons exhibit attentional modulation before V4 neurons, but also suggest that the increased gamma-band coherence observed between neural activity in these two areas during attention originates from the FEF [16*]. Within posterior visual cortex, the latency of attention modulation appears to follow a reverse-hierarchical progression, at least for areas V1, V2, and V4 [6]. A comparison of the time required of fronto-parietal area neurons to select targets during top-down attention shows that FEF neurons achieve this first, followed shortly by dIPFC neurons and then by LIP neurons [12*]. Consistent with these findings, Monosov *et al.* [15] reported that signatures of attention emerge in

FEF spiking activity before they appear in the LFPs. Because it has been argued that LFPs largely reflect the inputs to an area rather than its output ([57], but see [93]), the earlier modulation of FEF spiking activity might indicate that FEF is a source of spatial attention control signals.

Circuits of attention

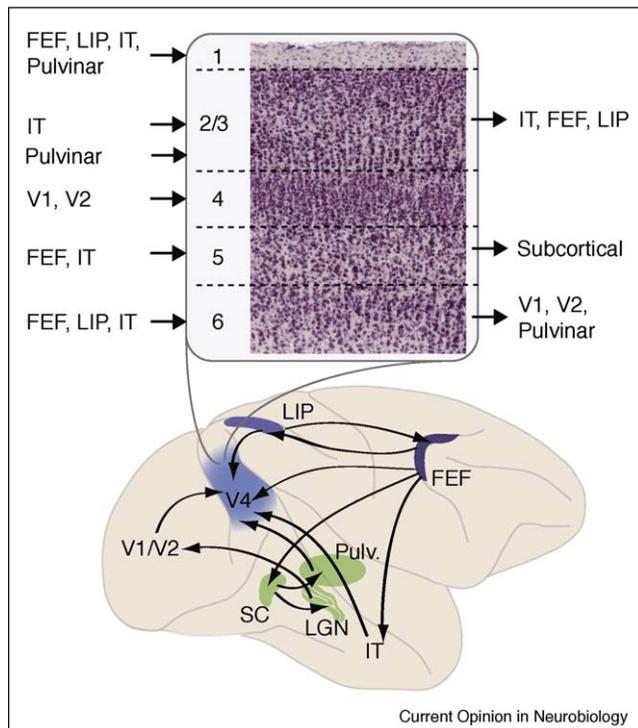
Although recent evidence has begun to identify sources of top-down effects of attention, the particular circuits involved in generating its signatures within visual cortex remain to be identified. The set of known connections between possible sources of attentional control (i.e. the FEF, LIP, and the SC) and visual cortical areas are obvious candidates. Direct corticocortical projections exist from both the FEF and LIP to most extrastriate areas in which signatures of attention have been observed, including well-studied area V4 (Figure 2) [55,58,59]. Moreover, corticocortical feedback projections throughout the visual hierarchy could propagate a modulatory signal from higher (e.g. V4) to lower (e.g. V1) areas. Because the SC does not project directly to visual cortex, any modulatory influence it has there would have to be mediated by the pulvinar nucleus, specifically its lateral and inferior nuclei which project to many areas of extrastriate cortex [60,61].

Although there is abundant evidence for a leading role of the fronto-parietal network in driving top-down spatial attention, other evidence suggesting a contribution of the thalamus indicates that the pathways by which the effects of attention are achieved may be more complicated than described above [62]. Spatial attention modulates visual responses at very short latency in both parvocellular and magnocellular layers of the LGN, and in the thalamic reticular nucleus (TRN) [1*]. This observation raises the possibility of a thalamic origin of attentional control. The pulvinar nucleus has reciprocal connections with most areas within visual cortex [60,61] and pulvinar neurons show modulation of firing rates with attention [2]. Furthermore, pharmacological inactivation of the medial pulvinar impairs performance on a spatial attention task, indicating that it may be necessary for attentional control [2].

The role of neuromodulators

Although the involvement of neuromodulators such as acetylcholine (ACh), noradrenaline (NA), and dopamine (DA) in arousal and attention is widely accepted, it remains to be established how that involvement intersects with known signatures of attention in visual cortex. A recent study however found evidence of a cholinergic contribution to attentional modulation within macaque V1 through muscarinic receptors [5*]. The role of ACh in attention may either be achieved via gating of information within sensory cortical areas [63,64] or via its mediation of PFC functions [65]. Dysfunction in dopaminergic and

Figure 2



Possible routes for attentional signals from frontal and parietal areas (FEF and LIP) to an exemplar visual area (V4). Top, cytoarchitecture of area V4 and laminar patterns of afferent (left) and efferent (right) connections. Corticocortical feedback projections (from FEF, LIP, IT) synapse in superficial and deep layers [55,58]. Specific pulvinar projections synapse primarily in deep layer 3 [83] while nonspecific pulvinar projections synapse in Layer 1 [61]. Feedforward input from visual areas such as V1 and V2 synapses primarily in Layer 4 [84]. Layer 2/3 neurons project to higher cortical areas such as IT [85], Layer 5 neurons project to subcortical structures such as the SC [86] and striatum [87], and Layer 6 neurons project to earlier cortical areas such as V1 and V2 [88] as well as to the pulvinar thalamus [61]. Bottom, selected projections forming paths from FEF and/or LIP to V4. These routes include: direct projections from LIP and FEF to V4 [55,58,59]; indirect projections through higher cortical areas such as IT [59,88]; through SC and pulvinar thalamus [89]; through SC and lower visual areas including LGN, V1, and V2 [90]; or through BF cholinergic nuclei [91]. BF, basal forebrain nuclei.

noradrenergic innervation of the PFC are both thought to contribute to the etiology of ADHD, and the treatment of ADHD typically involves drugs that act on DA and NE [33]. Rodent studies have shown that performance on simple attention tasks is dependent on the optimal activation of dopamine D1 receptors within medial PFC [66]. Both D1 receptors and NA α 2a receptors contribute to the working memory-related, spatial tuning of primate PFC neurons [67], and thus may also contribute to spatial attention (see below). Nevertheless, a direct link between the prefrontal catecholaminergic transmission and the effects of top-down attention within the visual system has yet to be found.

Spatial attention and spatial working memory

Top-down attention is often directed according to information held in working memory [68–70]. Many psychophysical studies have demonstrated a reciprocal relationship between spatial attention, spatial working memory, and oculomotor control, suggesting that the maintenance of visual spatial information may be achieved via some combination of attention-based rehearsal and motor preparation [71–74]. Other studies in humans show enhanced processing of visual targets at locations held in spatial working memory [75–78]. Consistent with this evidence, functional imaging studies in humans have revealed that a fronto-parietal network, including oculomotor structures, appears to underlie both spatial working memory and spatial attention [79].

Early neurophysiological studies demonstrated that persistent neuronal activity within the dIPFC can signal the location of remembered targets and/or the maintenance of a saccade plan during a delay interval [80,81]. A more recent study found that dIPFC neurons can signal the location of remembered targets as well as an attended location in a task that requires both, but that most neurons signal the latter [17]. Like dIPFC neurons, FEF neurons also exhibit persistent activity in memory-guided saccade task [82], raising the question of the relationship of this activity to the FEF's apparent role in spatial attention. Armstrong *et al.* [14^{*}] recently reported that FEF neurons not only signal the location of remembered targets in a task that does not involve saccades, but that the strength of the persistent spatial signal correlates with the selection of the attended target. The results suggest that the ability to behaviorally dissociate the preparation of saccades from their execution may provide a convenient means of achieving both the selection of visual representations and the maintenance of spatial information. Moreover they suggest that persistent saccade-related activity within the FEF may serve an attentional or mnemonic function depending solely on the presence or absence of a visual stimulus at the saccade goal.

Conclusions

Neurophysiological studies have made significant progress both in describing how top-down visual attention alters signals within the visual system as well as in beginning to identifying their causal basis. Nevertheless, our understanding of the neural circuitry of attention remains fairly rudimentary. Evidence to date falls far short of allowing one to identify the specific neurons, synaptic operations, or local and distributed neural computations that are both necessary and sufficient to account for the behavioral effects of attention. Likewise, a neurophysiological account of the relationship between attention and other basic cognitive functions, such as working memory, also awaits future work.

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. McAlonan K, Cavanaugh J, Wurtz RH: **Guarding the gateway • to cortex with attention in visual thalamus.** *Nature* 2008, **456**:391-394.

This study provided evidence for Francis Crick's conjecture that 'if the thalamus is the gateway to the cortex, the reticular complex might be described as the guardian of the gateway'. McAlonan *et al.* found that attention increases visual responses of both magno and parvocellular neurons in lateral geniculate nucleus (LGN) of monkeys while it decreases the response in thalamic reticular nucleus (TRN). Latency of visual response was 21 ms shorter in magnocellular part of LGN compared to TRN whereas attentional modulation appeared 4 ms sooner in TRN. This result shows that attention modulates visual signals in TRN and LGN before they even reach cortex and suggests the LGN-TRN circuit as a gateway for flow of visual information throughout the cortex.

2. Petersen SE, Robinson DL, Morris JD: **Contributions of the pulvinar to visual spatial attention.** *Neuropsychologia* 1987, **25**:97-105.
 3. Ignashchenkova A, Dicke PW, Haarmeier T, Thier P: **Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention.** *Nature Neuroscience* 2004, **7**:56-64.
 4. McAdams CJ, Maunsell JHR: **Effects of attention on orientation-tuning functions of single neurons in macaque cortical area V4.** *Journal of Neuroscience* 1999, **19**:431-441.
 5. Herrero JL, Roberts MJ, Delicato LS, Gieselmann MA, Dayan P, Thiele A: **Acetylcholine contributes through muscarinic receptors to attentional modulation in V1.** *Nature* 2008, **454**:1110-1114.
- This study reported evidence of a selective role of muscarinic acetylcholine (ACh) receptors in attentional modulation of V1 responses. The authors iontophoretically delivered ACh into V1 sites and found increased attentional modulation. They also found that the muscarinic antagonist of ACh reduced the modulation while the nicotinic antagonist did not affect it.
6. Buffalo EA, Fries P, Landman R, Liang H, Desimone R: **A backwards progression of attentional effects in the ventral stream.** In *Proceedings of the National Academy of Sciences* 2009, **107**:361-365.
 7. Moran J, Desimone R: **Selective attention gates visual processing in the extrastriate cortex.** *Science* 1985, **229**:782-784.
 8. Treue S, Trujillo M, Julio C: **Feature-based attention influences motion processing gain in macaque visual cortex.** *Nature* 1999, **399**:575-579.
 9. Chelazzi L, Duncan J, Miller EK, Desimone R: **Responses of neurons in inferior temporal cortex during memory-guided visual search.** *Journal of Neurophysiology* 1998, **80**:2918-2940.
 10. Chelazzi L, Miller EK, Duncan J, Desimone R: **A neural basis for visual search in inferior temporal cortex.** *Nature* 1993, **363**:345-347.
 11. Bisley JW, Goldberg ME: **Neuronal activity in the lateral intraparietal area and spatial attention.** *Science* 2003, **299**:81-86.
 12. Buschman TJ, Miller EK: **Top-down versus bottom-up control of • attention in the prefrontal and posterior parietal cortices.** *Science* 2007, **315**:1860-1862.

In this study, responses of neurons in prefrontal and parietal cortices of monkeys were recorded simultaneously. They found that during top-down attention responses of prefrontal neurons reflected the position of the target stimulus earlier than neurons in parietal cortex whereas in bottom-up attention parietal neurons encode the target position first. They also found that during top down attention the synchrony between neurons in prefrontal and parietal areas was stronger in lower frequencies whereas stronger coherence at higher frequency bands was observed during bottom-up attention. This study provides evidence for sources of top-down and bottom-up attentions and how response coherence

between different sources could be dynamically modulated in various modes of attention.

13. Thompson KG, Biscoe KL, Sato TR: **Neuronal basis of covert spatial attention in the frontal eye field.** *Journal of Neuroscience* 2005, **25**:9479-9487.
 14. Armstrong KM, Chang M, Moore T: **Selection and maintenance • of spatial information by frontal eye field neurons.** *Journal of Neuroscience* 2009, **29**:15621-15629.
- This study examined the relationship between spatial attention and the role of persistent activity in the FEF. The authors demonstrated that FEF neurons maintain spatial information in the absence of saccade preparation and can predict the monkey's performance on an attention-demanding task. Moreover, neurons that exhibited persistent activity were better at selecting the target embedded among distracters than neurons without persistent activity. The results suggest that this maintenance of a spatial signal in the FEF contributes to the selection of relevant visual stimuli.
15. Monosov IE, Trageser JC, Thompson KG: **Measurements of simultaneously recorded spiking activity and local field potentials suggest that spatial selection emerges in the frontal eye field.** *Neuron* 2008, **57**:614-625.
 16. Gregoriou GG, Gotts SJ, Zhou H, Desimone R: **High-frequency, • long-range coupling between prefrontal and visual cortex during attention.** *Science* 2009, **324**:1207-1210.
- This study showed enhanced gamma-band coherence between simultaneously recorded FEF and V4 sites when monkeys directed covert spatial attention to a stimulus in the overlapping response fields of sites in both areas. The authors found that the onset of attentional effects occurred earliest in the firing rates of FEF neurons, followed by short latency coupled oscillations within and between both areas. These results suggest a potential mechanism for top-down control of attention in which neurons in the FEF initiate local and cross-areal communication via synchrony among groups of neurons encoding selected representations.
17. Lebedev MA, Messinger A, Kralik JD, Wise SP: **Representation of attended versus remembered locations in prefrontal cortex.** *PLoS Biology* 2004, **2**:e365.
 18. Everling S, Tinsley CJ, Gaffan D, Duncan J: **Filtering of neural signals by focused attention in the monkey prefrontal cortex.** *Nature Neuroscience* 2002, **5**:671-676.
 19. Fries P, Womelsdorf T, Oostenveld R, Desimone R: **The effects of visual stimulation and selective visual attention on rhythmic neuronal synchronization in macaque area V4.** *Journal of Neuroscience* 2008, **28**:4823.
 20. Taylor K, Mandon S, Freiwald WA, Kreiter AK: **Coherent oscillatory activity in monkey area V4 predicts successful allocation of attention.** *Cerebral Cortex* 2005, **15**:1424-1437.
 21. Womelsdorf T, Fries P, Mitra PP, Desimone R: **Gamma-band synchronization in visual cortex predicts speed of change detection.** *Nature* 2006, **439**:733-736.
 22. Fries P, Reynolds JH, Rorie AE, Desimone R: **Modulation of oscillatory neuronal synchronization by selective visual attention.** *Science* 2001, **291**(5508):1560-1563.
 23. Bichot NP, Rossi AF, Desimone R: **Parallel and serial neural mechanisms for visual search in macaque area V4.** *Science* 2005, **308**:529-534.
 24. Saalman YB, Pigarev IN, Vidyasagar TR: **Neural mechanisms of visual attention: how top-down feedback highlights relevant locations.** *Science* 2007, **316**:1612-1615.
 25. Mitchell JF, Sundberg KA, Reynolds JH: **Differential attention-dependent response modulation across cell classes in macaque visual area V4.** *Neuron* 2007, **55**:131-141.
 26. Cohen MR, Maunsell JHR: **Attention improves performance primarily by reducing interneuronal correlations.** *Nature Neuroscience* 2009, **12**:1594-1600.
 27. Mitchell JF, Sundberg KA, Reynolds JH: **Spatial attention decorrelates intrinsic activity fluctuations in macaque area V4.** *Neuron* 2009, **63**:879-888.
 28. Womelsdorf T, Anton-Erxleben K, Treue S: **Receptive field shift and shrinkage in macaque middle temporal area through attentional gain modulation.** *Journal of Neuroscience* 2008, **28**:8934-8944.

29. Anton-Erxleben K, Stephan VM, Treue S: **Attention reshapes center-surround receptive field structure in macaque cortical area MT.** *Cerebral Cortex* 2009, **19**:2466-2478.
30. Connor CE, Preddie DC, Gallant JL, Van E: **DC spatial attention effects in macaque area V4.** *Journal of Neuroscience* 1997, **17**:3201-3214.
31. Sundberg KA, Mitchell JF, Reynolds JH: **Spatial attention modulates center-surround interactions in macaque visual area v4.** *Neuron* 2009, **61**:952-963.
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. Robbins TW, Arnsten AF: **The neuropsychopharmacology of fronto-executive function: monoaminergic modulation.** *Annual Review of Neuroscience* 2009, **32**:267-287.
34. Biederman J, Faraone SV: **Attention-deficit hyperactivity disorder.** *The Lancet* 2005, **366**:237-248.
35. Mirabella G, Bertini G, Samengo I, Kilavik BE, Frilli D, Della L, Chelazzi CL: **Neurons in area V4 of the macaque translate attended visual features into behaviorally relevant categories.** *Neuron* 2007, **54**:303-318.
36. Burrows BE, Moore T: **Influence and limitations of popout in the selection of salient visual stimuli by area V4 neurons.** *Journal of Neuroscience* 2009, **29**:15169-15177.
37. Salinas E, Sejnowski TJ: **Correlated neuronal activity and the flow of neural information.** *Nature Reviews Neuroscience* 2001, **2**:539-550.
38. Azouz R, Gray CM: **Adaptive coincidence detection and dynamic gain control in visual cortical neurons in vivo.** *Neuron* 2003, **37**:513-523.
39. Tiesinga P, Fellous JM, Sejnowski TJ: **Regulation of spike timing in visual cortical circuits.** *Nature Reviews Neuroscience* 2008, **9**:97-109.
40. Fries P: **Neuronal gamma-band synchronization as a fundamental process in cortical computation.** *Annual Review of Neuroscience* 2009, **32**:209-224.
41. Womelsdorf T, Schoffelen JM, Oostenveld R, Singer W, Desimone R, Engel AK, Fries P: **Modulation of neuronal interactions through neuronal synchronization.** *Science* 2007, **316**:1609-1612.
42. Sompolinsky H, Yoon H, Kang K, Shamir M: **Population coding in neuronal systems with correlated noise.** *Physical Review E* 2001, **64**:051904.
43. Thut GA, Nietzel SA, Brandt A: **Pascual-Leone: alpha-Band electroencephalographic activity over occipital cortex indexes visuospatial attention bias and predicts visual target detection.** *Journal of Neuroscience* 2006, **26**:9494-9502.
44. Connor CE: **Shifting receptive fields.** *Neuron* 2001, **29**:548-549.
45. Moore T: **The neurobiology of visual attention: finding sources.** *Current Opinion in Neurobiology* 2006, **16**:159-165.
46. Moore T, Fallah M: **Control of eye movements and spatial attention.** In *Proceedings of the National Academy of Sciences* 2001, **98**:1273-1276.
47. Cavanaugh J, Alvarez BD, Wurtz RH: **Enhanced performance with brain stimulation: attentional shift or visual cue?** *Journal of Neuroscience* 2006, **26**:11347-11358.
48. Muller JR, Philiastides MG, Newsome WT: **Microstimulation of the superior colliculus focuses attention without moving the eyes.** In *Proceedings of the National Academy of Sciences* 2005, **102**:524-529.
49. Cutrell EB, Marrocco RT: **Electrical microstimulation of primate posterior parietal cortex initiates orienting and alerting components of covert attention.** *Experimental Brain Research* 2002, **144**:103-113.
50. Schafer RJ, Moore T: **Attention governs action in the primate frontal eye field.** *Neuron* 2007, **56**:541-551.
51. Moore T, Armstrong KM: **Selective gating of visual signals by microstimulation of frontal cortex.** *Nature* 2003, **421**:370-373.
52. Armstrong KM, Fitzgerald JK, Moore T: **Changes in visual receptive fields with microstimulation of frontal cortex.** *Neuron* 2006, **50**:791-798.
53. Armstrong KM, Moore T: **Rapid enhancement of visual cortical response discriminability by microstimulation of the frontal eye field.** In *Proceedings of the National Academy of Sciences* 2007, **104**:9499-94504.
54. Ekstrom LB, Roelfsema PR, Arsenault JT, Bonmassar G, Vanduffel W: **Bottom-up dependent gating of frontal signals in early visual cortex.** *Science* 2008, **321**:414-417.
55. Stanton GB, Bruce CJ, Goldberg ME: **Topography of projections to posterior cortical areas from the macaque frontal eye fields.** *Journal of Computational Neurology* 1995, **353**:291-305.
56. Ekstrom LB, Roelfsema PR, Arsenault JT, Kolster H, Vanduffel W: **Modulation of the contrast response function by electrical microstimulation of the macaque frontal eye field.** *Journal of Neuroscience* 2009, **29**:10683-10694.
57. Logothetis NK, Wandell BA: **Interpreting the BOLD signal.** *Annual Review of Physiology* 2004, **66**:735-769.
58. Andersen RA, Asanuma C, Essick G, Siegel RM: **Corticocortical connections of anatomically and physiologically defined subdivisions within the inferior parietal lobule.** *The Journal of Comparative Neurology* 1990, **296**:65-113.
59. Ungerleider LG, Galkin TW, Desimone R, Gattass R: **Cortical connections of area V4 in the macaque.** *Cerebral Cortex* 2007, **60** Shipp, S: **The functional logic of cortico-pulvinar connections.** *Philosophical Transactions: Biological Sciences* 2007, 477-499.
60. Shipp S: **The functional logic of cortico-pulvinar connections.** *Philosophical Transactions: Biological Sciences* 2003, **358**:1605-1624.
61. Jones EG: *The Thalamus.* Cambridge University Press; 2007.
62. Saalmann YB, Kastner S: **Gain control in the visual thalamus during perception and cognition.** *Current Opinion in Neurobiology* 2009, **19**:408-414.
63. Munk MHJ, Roelfsema PR, Knig P, Engel AK, Singer W: **Role of reticular activation in the modulation of intracortical synchronization.** *Science* 1996, **272**:271-274.
64. Xiang Z, Huguenard JR, Prince DA: **Cholinergic switching within neocortical inhibitory networks.** *Science* 1998, **281**:985-988.
65. Parikh V, Sarter M: **Cholinergic mediation of attention: contributions of phasic and tonic increases in prefrontal cholinergic activity.** *Annals of the New York Academy of Sciences* 2008, **1129**:225-235.
66. Chudasama Y, Robbins TW: **Psychopharmacological approaches to modulating attention in the five-choice serial reaction time task: implications for schizophrenia.** *Psychopharmacology* 2004, **174**:86-98.
67. Vijayraghavan S, Wang M, Birnbaum SG, Williams GV, Arnsten AFT: **Inverted-U dopamine D1 receptor actions on prefrontal neurons engaged in working memory.** *Nature Neuroscience* 2007, **10**:376-384.
68. Desimone R, Duncan J: **Neural mechanisms of selective visual attention.** *Annual Review of Neuroscience* 1995, **18**:193-222.
69. Knudsen EI: **Fundamental components of attention.** *Annual Review of Neuroscience* 2007, **30**:57-78.
70. Soto D, Hodsoll J, Rotshtein P, Humphreys GW: **Automatic guidance of attention from working memory.** *Trends in Cognitive Sciences* 2008, 342-348.
71. Postle BR: **Working memory as an emergent property of the mind and brain.** *Neuroscience* 2006, **139**:23-38.

72. Belopolsky AV, Theeuwes J: **Inhibition of saccadic eye movements to locations in spatial working memory.** *Attention, Perception & Psychophysics* 2009, **71**:620-631.
73. Nobre AC, Griffin IC, Rao A: **Spatial attention can bias search in visual short-term memory.** *Frontiers in Human Neuroscience* 2007, **1**:4.
74. Lavie N: **Distracted and confused? Selective attention under load.** *Trends in Cognitive Sciences* 2005, **9**:75-82.
75. Awh E, Jonides J, Smith EE, Buxton RB, Frank LR, Love T, Wong EC, Gmeindl L: **Rehearsal in spatial working memory: Evidence from neuroimaging.** *Psychological Science* 1999, **10**:433-437.
76. Postle BR, Awh E, Jonides J, Smith EE, D'Esposito M: **The where and how of attention-based rehearsal in spatial working memory.** *Cognitive Brain Research* 2004, **20**:194-205.
77. Awh E, Anllo-Vento L, Hillyard SA: **The role of spatial selective attention in working memory for locations: Evidence from event-related potentials.** *Journal of Cognitive Neuroscience* 2000, **12**:840-847.
78. Jha AP: **Tracking the time-course of attentional involvement in spatial working memory: an event-related potential investigation.** *Cognitive Brain Research* 2002, **15**:61-69.
79. Corbetta M, Shulman GL: **Control of goal-directed and stimulus-driven attention in the brain.** *Nature Reviews Neuroscience* 2002, **3**:201-215.
80. Fuster JM, Alexander GE: **Neuron activity related to short-term memory.** *Science* 1971, **173**:652-654.
81. Funahashi S, Bruce CJ, Goldman-Rakic PS: **Mnemonic coding of visual space in the monkey's dorsolateral prefrontal cortex.** *Journal of Neurophysiology* 1989, **61**:331-349.
82. Sommer MA, Wurtz RH: **Composition and topographic organization of signals sent from the frontal eye field to the superior colliculus.** *Journal of Neurophysiology* 2000, **83**:1979-2001.
83. Trojanowski JQ, Jacobson S: **Areal and laminar distribution of some pulvinar cortical efferents in rhesus monkey.** *The Journal of Comparative Neurology* 1976, **169**:371-392.
84. Gattas R, Sousa AP, Mishkin M, Ungerleider LG: **Cortical projections of area V2 in the macaque.** *Cerebral Cortex* 1997, **7**:110-129.
85. Desimone R, Fleming J, Gross CG: **Prestriate afferents to inferior temporal cortex: an HRP study.** *Brain Research* 1980, **184**:41-55.
86. Lock TM, Baizer JS, Bender DB: **Distribution of corticotectal cells in macaque.** *Experimental Brain Research* 2003, **151**:455-470.
87. Saint-Cyr JA, Ungerleider LG, Desimone R: **Organization of visual cortical inputs to the striatum and subsequent outputs to the pallido-nigral complex in the monkey.** *The Journal of Comparative Neurology* 1990, **298**:129-156.
88. Felleman DJ, Van Essen DC: **Distributed hierarchical processing in the primate cerebral cortex.** *Cerebral Cortex* 1991, **1**:1-47.
89. Benevento LA, Fallon JH: **The ascending projections of the superior colliculus in the rhesus monkey (Macaca mulatta).** *The Journal of Comparative Neurology* 1975, **160**:339-361.
90. Stepniewska I, Qi H, Kaas J: **Projections of the superior colliculus to subdivisions of the inferior pulvinar in New World and Old World monkeys.** *Visual Neuroscience* 2000, **17**:529-549.
91. Mesulam MM, Mufson EJ, Levey AI, Wainer BH: **Cholinergic innervation of cortex by the basal forebrain: cytochemistry and cortical connections of the septal area, diagonal band nuclei, nucleus basalis (Substantia innominata), and hypothalamus in the rhesus monkey.** *The Journal of Comparative Neurology* 1983, **214**:170-197.
92. Buschman TJ, Miller EK: **Serial, covert shifts of attention during visual search are reflected by the frontal eye fields and correlated with population oscillations.** *Neuron* 2009, **63**:386-396.
93. Ray S, Hsiao SS, Crone NE, Franaszczuk PJ, Niebur E: **Effect of stimulus intensity on the spike-local field potential relationship in the secondary somatosensory cortex.** *Journal of Neuroscience* 2008, **28**:7334-7343.