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# Top-down control of visual attention

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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

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## 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].

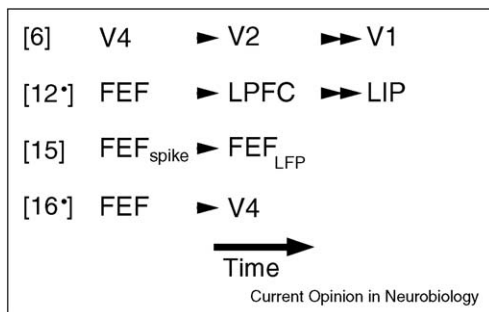
### Sources of attention

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].

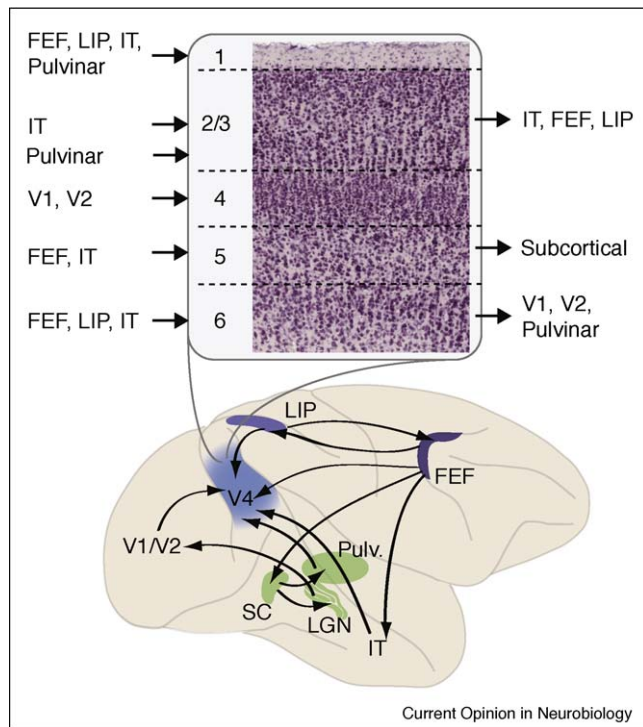
Although there is abundant evidence for a leading role of the fronto-parietal network in driving top-down spatial attention, other evidence suggesting a contribution of the thalamus indicates that the pathways by which the effects of attention are achieved may be more complicated than described above [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  $NA \alpha 2a$  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<sup>\*</sup>] 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

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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.

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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

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