The Neuroscientist
201X, Vol XX(X) 1–13

DOI: 10.1177/1073858413514136
nro.sagepub.com
SAGE

Bottom-Up and Top-Down Attention: Different Processes and Overlapping Neural Systems

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Abstract

The brain is limited in its capacity to process all sensory stimuli present in the physical world at any point in time and relies instead on the cognitive process of attention to focus neural resources according to the contingencies of the moment. Attention can be categorized into two distinct functions: bottom-up attention, referring to attentional guidance purely by externally driven factors to stimuli that are salient because of their inherent properties relative to the background; and top-down attention, referring to internal guidance of attention based on prior knowledge, willful plans, and current goals. Over the past few years, insights on the neural circuits and mechanisms of bottom-up and top-down attention have been gained through neurophysiological experiments. Attention affects the mean neuronal firing rate as well as its variability and correlation across neurons. Although distinct processes mediate the guidance of attention based on bottom-up and top-down factors, a common neural apparatus, the frontoparietal network, is essential in both types of attentional processes.

Keywords

prefrontal, posterior parietal, neurophysiology, intraparietal sulcus, monkey

Our surroundings give rise to a vast amount of sensory information that is more than our brain can process simultaneously. Selecting the most relevant stimuli in the physical world for processing while filtering out less relevant information allows us to respond quickly to critical environmental changes and achieve behavioral goals more efficiently. This process of information selection is referred to as attention. Attention is commonly categorized into two distinct functions: bottom-up (or exogenous) attention, an externally induced process in which information to be processed is selected automatically because of highly noticeable features of stimuli; and top-down (or endogenous) attention, an internally induced process in which information is actively sought out in the environment based on voluntarily chosen factors (Connor and others 2004; Corbetta and Shulman 2002; Itti and Koch 2001). Although any type of sensory modality could be attended based on bottom-up or top-down factors, attention in the visual system has been most extensively studied over the past decades and will be the focus of this review.

Early psychophysical research showed that when searching for a stimulus defined by bottom-up factors, target stimuli "pop out" if they differ sufficiently from their background in terms of features such as color or orientation and can be processed in parallel without the need to examine every element in view (Duncan and Humphreys 1989; Treisman and Gelade 1980). On the other hand, in a search in which the target is defined by top-down factors in the absence of substantial differences between target and background stimuli, the target needs to be identified through an intentional examination of elements in the field of view, stimulus by stimulus (Wolfe and Horowitz 2004). The two attentional processes are often described separately and are thought to involve distinct neural mechanisms and anatomic substrates. It is important to note, however, that in everyday experience, bottom-up and top-down factors constantly influence each other to orient attention; this mutual interaction is reflected in models of visual search (Wolfe 2010). Studies in patients with cortical lesions suggest that different subregions of the parietal cortex could be segregated for their distinct roles in bottom-up and top-down attentional systems; however, these two systems and associated brain

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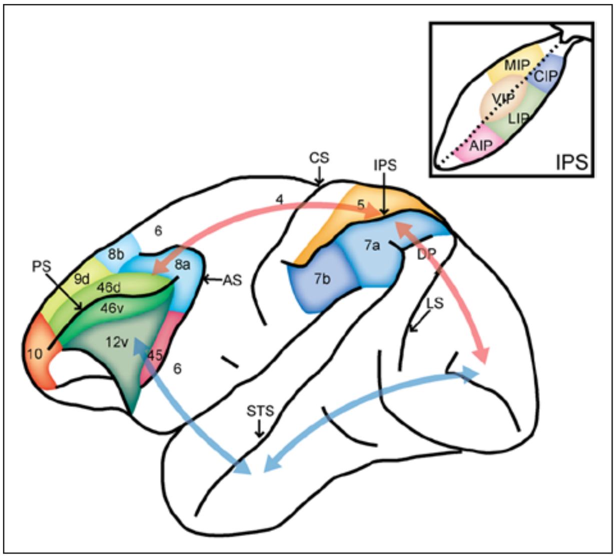

Figure 1. Schematic diagram of a monkey brain. Lateral view of the monkey brain indicating the areas making up the prefrontal cortex and the posterior parietal cortex. Inset illustrates an unfolded view of the intraparietal sulcus (IPS). Arrows indicate dorsal (red arrows) and ventral (blue arrows) visual pathways. AIP = anterior intraparietal area; AS = arcuate sulcus; CIP = caudal intraparietal area; CS = central sulcus; DP = dorsal prelunate area; LIP = lateral intraparietal area; LS = lunate sulcus; MIP = medial intraparietal area; PS = principal sulcus; STS = superior temporal sulcus; VIP = ventral intraparietal area.

regions also closely interact with each other (Shomstein 2012; Shomstein and others 2010).

A common idea among theoretical models developed to account for attentional processes is that attention is allocated to the most salient stimulus, location, or feature that evokes the stronger neural activation than others in the visual field (Desimone and Duncan 1995; Koch and Ullman 1985; Wolfe 1994). Along the lines of this idea, attention is often described in terms of a global map, where incoming bottom-up visual information is processed according to its separate features. Each stimulus is represented in a separate feature map (e.g., orientation or color), which is then incorporated to a global "saliency map," representing the overall most salient stimulus in the field of view. Through a winner-take-all mechanism, attention is thought to be oriented to the spot on the map with the most prominent activation (Koch and Ullman 1985).

The ability of stimuli to attract attention is determined not only by their inherent saliency but also by their relevance to current goals, an idea captured by early models of visual search (Wolfe 1994). This idea has been increasingly emphasized in recent years and led to proposals of a "priority map," simultaneously integrating bottom-up and top-down factors (Bisley and Goldberg 2010; Serences and Yantis 2006). In fact, it has been argued that distinguishing between top-down and bottom-up attentional control may be a false dichotomy (Awh and others 2012). Even if the two processes are clearly distinct, neural correlates of bottom-up and top-down attention reveal coactivation of the same network of parietal and prefrontal cortical areas, giving credence to the idea of a priority map simultaneously modulated by both types of factors (Katsuki and Constantinidis 2012b). These processes have been studied extensively in nonhuman primates, providing neurophysiological evidence that will be the emphasis of this review.

Bottom-Up Attention

Bottom-up visual attention starts with basic visual processing along the visual cortical pathways. From the primary visual cortex (V1), feed-forward signals ascend to multiple cortical areas and branch into two major visual pathways: a ventral pathway (Fig. 1, blue arrows) dealing with object- and feature-based visual processes, and a dorsal pathway (Fig. 1, red arrows) dealing with spatial- and movement-related visual processes (Ungerleider and Haxby 1994; Ungerleider and Mishkin 1982). Areas that are part of the ventral pathway include V1, V2, V3, V4, as well as inferior temporal (IT) cortex, which project to the ventral part of the lateral prefrontal cortex (PFC). The dorsal pathway comprises areas V1, V2, V3, middle temporal (MT), and medial superior temporal (MST) and areas in the posterior parietal cortex (PPC), which project to the dorsolateral part of the PFC (dlPFC). The two cortical pathways are organized across a cortical hierarchy in which receptive fields grow bigger and functional properties become more complex as inputs ascend from the earlier stages to the later stages of the pathways (Felleman and Van Essen 1991). Bottom-up information that can guide attention propagates thus from the visual cortex to the PFC.

Visual Competition

Stimuli that stand out from their background are selectively represented by neuronal activity throughout the visual system. Neurons are activated to a greater extent when salient stimuli appear in their receptive fields compared to activation elicited by background elements alone, and this phenomenon occurs from the earliest stages of visual cortical processing, including V1 (Knierim and van Essen 1992). This differential processing of salient stimuli suggests a competitive process in the selection of stimuli (Bichot and others 2005; Desimone and Duncan 1995). As a result of competition, the most salient stimulus is represented predominantly at all stages of the visual system and leads to bottom-up orienting of attention (Desimone and Duncan 1995; Hegde and Felleman 2003; Knierim and van Essen 1992; Lamme 1995). However, local competition between elements at early stages of the visual system is not sufficient for the guidance of attention; it is critical to be able to access information in the visual field as broadly as possible to capture the most salient stimulus. Thus, visual cortical areas whose neuronal receptive field covers only a small portion of the visual field do not seem to be adequate for detecting the most salient stimulus in the entire visual scene (Burrows and Moore 2009; Hegde and Felleman 2003). To be able to orient attention including to the peripheral areas of the visual field, areas with spatial selectivity and large, often bilateral, receptive fields such as the PPC or PFC are thought to be critical for stimulus selection (Constantinidis 2006).

Saliency Map

A related concept regarding the allocation of attention is that of a saliency map in which all types of feature information (e.g., shape, color, and orientation) in the visual field are pooled together (Koch and Ullman 1985; Niebur and Koch 1996), and attention is allocated to the location with the highest activity in this global map. Where could such a map be present in the brain? Suitable brain regions should have access to a wide array of visual information, therefore most likely being areas found at the later stages of visual cortical pathways. Considering that the generation of eye movements is intricately intertwined with the allocation of attention, the neural site of the saliency map is also likely to be closely related to eye movement preparation. Studies have suggested multiple brain areas that could serve as maps of saliency, including the frontal eye field (FEF) and area 46 of the PFC (Katsuki and Constantinidis 2012a; Schall and Hanes 1993; Thompson and others 1996), area 7a and the lateral intraparietal area (LIP) in the PPC (Constantinidis and Steinmetz 2001; Gottlieb and others 1998), the superior colliculus (McPeek and Keller 2002), and the substantia nigra (Basso and Wurtz 2002).

Anatomically, areas in the PFC and PPC such as the FEF and LIP have reciprocal projections to each other and direct connections with many other extrastriate areas in the dorsal and ventral pathways (Felleman and Van Essen 1991). The FEF and LIP also send output signals and receive indirect inputs from the superior colliculus (Schall and others 2011). They seem well suited, therefore, to process diverse streams of information and to influence downstream effectors.

It has been well recognized that prefrontal areas such as the dlPFC and FEF represent salient stimuli in "oddball" stimulus tasks (Fig. 2A), requiring detection or a response towards a stimulus differing in color or shape from background elements (Sato and others 2003; Schall

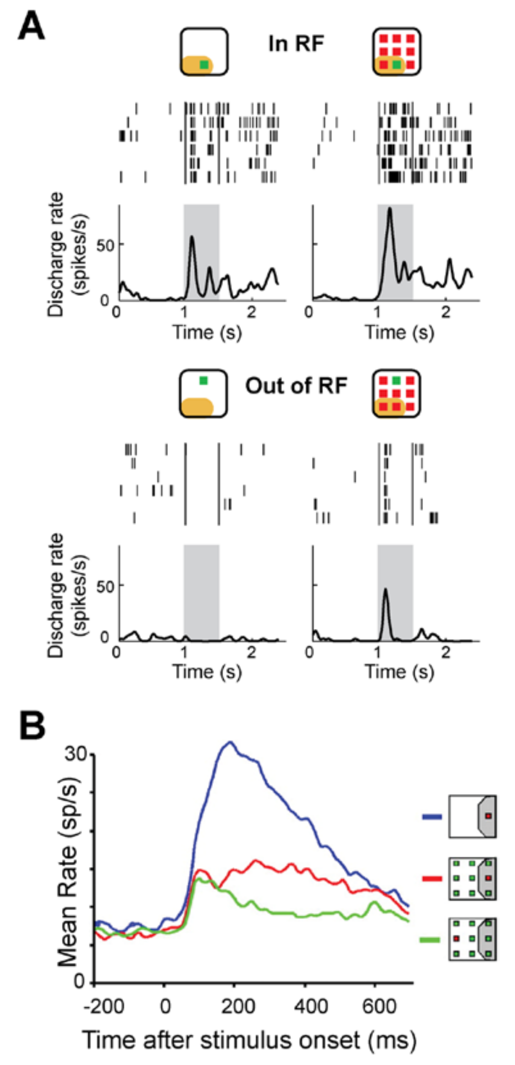

Figure 2. Activity of neurons in the prefrontal cortex (PFC) and area 7a of the posterior parietal cortex (PPC), representing a bottom-up salient stimulus. (A) Raster plots and histograms of a PFC neuron for single-stimulus and multiple-stimuli presentations. Orange areas in insets indicate the receptive field (RF) of the neuron. Gray shaded areas in histograms represent the stimulus presentation period. The activity of the neuron increased when a single stimulus appeared in the RF (left top), while there was no change in activity when the stimulus appeared out of the RF (left bottom). Neuronal activity significantly increased with the presentation of a salient stimulus in the RF among distractors (right top). The neuron responded briefly when only distractors were in the RF (right bottom), but this initial phasic response diminished quickly (Katsuki and Constantinidis 2012b). (B) The time course of the population discharge rate in area 7a during the presentation of single and multiple stimuli in monkeys naïve to training, requiring the detection of a target stimulus and only required to passively view visual displays. The RF of the neuron is depicted as a gray shaded area in insets. When a salient stimulus was in the RF either appearing by itself (blue) or among distractors (red), an increased neuronal discharge rate was observed throughout the stimulus presentation. When the salient stimulus was outside of the RF (green), an initial phasic response quickly decreased (Constantinidis and Steinmetz 2005).

and Hanes 1993; Schall and others 1995; Thompson and others 1996). Similar to the PFC, neurons in the PPC including area 7a and the LIP represent salient stimuli. Neurons in area 7a display selective responses to salient stimuli regardless of color and represent the spatial location of the stimulus (Fig. 2B). Importantly, studies in which animals were not trained to locate the target stimulus but were only required to fixate still revealed a selective response to the salient stimulus in area 7a and the LIP of the PPC, indicating that this response pattern observed in the PPC was not the effect of volitional allocation of attention required to execute behavioral tasks but rather automatic processing of bottom-up information (Arcizet and others 2011; Constantinidis and Steinmetz 2005). Demonstrations of bottom-up saliency reflected in the activity of PFC and PPC neurons are not limited to oddball stimulus paradigms. Other studies reported that LIP neurons represented a visual stimulus more strongly when the stimulus was made salient by being flashed as surrounding stimuli were kept stable, compared to the condition in which the same stimulus was not flashed (Gottlieb and others 1998; Kusunoki and others 2000). Taken together, the studies indicate that the PFC and PPC are actively engaged in the processing of information essential for the allocation of bottom-up attention.

Neuronal Time Course of Bottom-Up Attention

Whether a further specialization exists between parietal and prefrontal areas in terms of the guidance of bottom-up (and top-down) attention has been a matter of debate. In accordance with information transmission along the visual cortical pathways, it has been traditionally thought that bottom-up information of salient stimuli is represented first in the areas of the PPC and then in the PFC. One way to directly test this idea is to compare the time course of the neural representation of salient stimuli between the areas. A study performed neurophysiological recording in the PFC (including the lateral PFC and FEF) and the PPC (LIP) during a search task and compared the time course of neuronal activity (Buschman and Miller 2007). The authors reported that latencies in PPC neurons representing stimuli that pop-out were shorter than in PFC neurons, suggesting that the PPC is the primary area that represents visual saliency, and that the PFC receives the saliency information from the PPC. Other studies, however, report that neurons in the FEF showed latencies as fast as neurons in the LIP using the similar pop-out tasks (Schall and others 2007; Thomas and Pare 2007; Thompson and others 1996). A recent neurophysiological study compared the time course of bottom-up salient representation between the dlPFC (including areas 8 and 46) and PPC (LIP and area 7a) in the same animals using tasks in which top-down and eye movement planning factors were minimized (Katsuki and Constantinidis 2012a). In these experiments, tasks were designed to allocate attention through bottom-up factors relying on color difference, and the animals' decision was indicated by a lever movement instead of an eye movement. The results revealed that latencies to detect salient stimuli were virtually identical in the dlPFC and PPC, even though initial visual response latencies occurred later in the dlPFC than the PPC (Fig. 3). One possible explanation for this discrepancy was the difference in task designs. The task used in the Buschman and Miller (2007) study informed subjects about the identity of the target before the pop-out search phase. Once such a top-down influence has been established, however, it is possible for lower cortical areas to filter the properties of incoming stimuli, allowing for faster representation of the target stimulus; this is the essence of top-down control (Chelazzi and others 2001; Herrington and Assad 2009; Luck and others 1997).

Another recent series of experiments compared the timing of salient stimulus representation in FEF spiking and the local field potential (LFP) with the event-related potential, indicative of salient target selection in the visual cortex (Cohen and others 2009; Purcell and others 2013). Results showed that stimulus selection was observed first in spiking activity of the FEF, then in FEF LFPs, and only later in the visual cortex both in pop-out and serial searches. The results indicate that a frontal area such as the FEF represents stimulus saliency earlier than the visual cortex. In addition to the neurophysiological studies, deficits in a pop-out visual search were observed after inactivation of the dlPFC with muscimol injection (Iba and Sawaguchi 2003; Wardak and others 2006). In summary, evidence suggests that the dlPFC (including area 46 and FEF) does not simply reflect bottom-up salient information extracted in earlier stages of cortical pathways, but saliency representation in the dlPFC itself is critical for bottom-up search tasks. How saliency information represented in these multiple areas interacts with each other and ultimately directs attention to a particular point in the visual field from moment to moment is not yet known.

Bottom-Up Effects beyond Firing Rate

In recent years, it has been recognized that stimuli that attract attention by bottom-up factors influence neuronal activity in more ways than simply by increasing the mean firing rate of neurons. An abrupt onset of a stimulus (which is a powerful bottom-up factor likely to capture attention) has been shown to reduce the variability of neuronal firing (Fig. 4A and 4B) across multiple brain areas (Churchland and others 2010). The variability of the firing rate across trials is often computed as a noise-to-signal ratio, called the Fano factor (the variance of

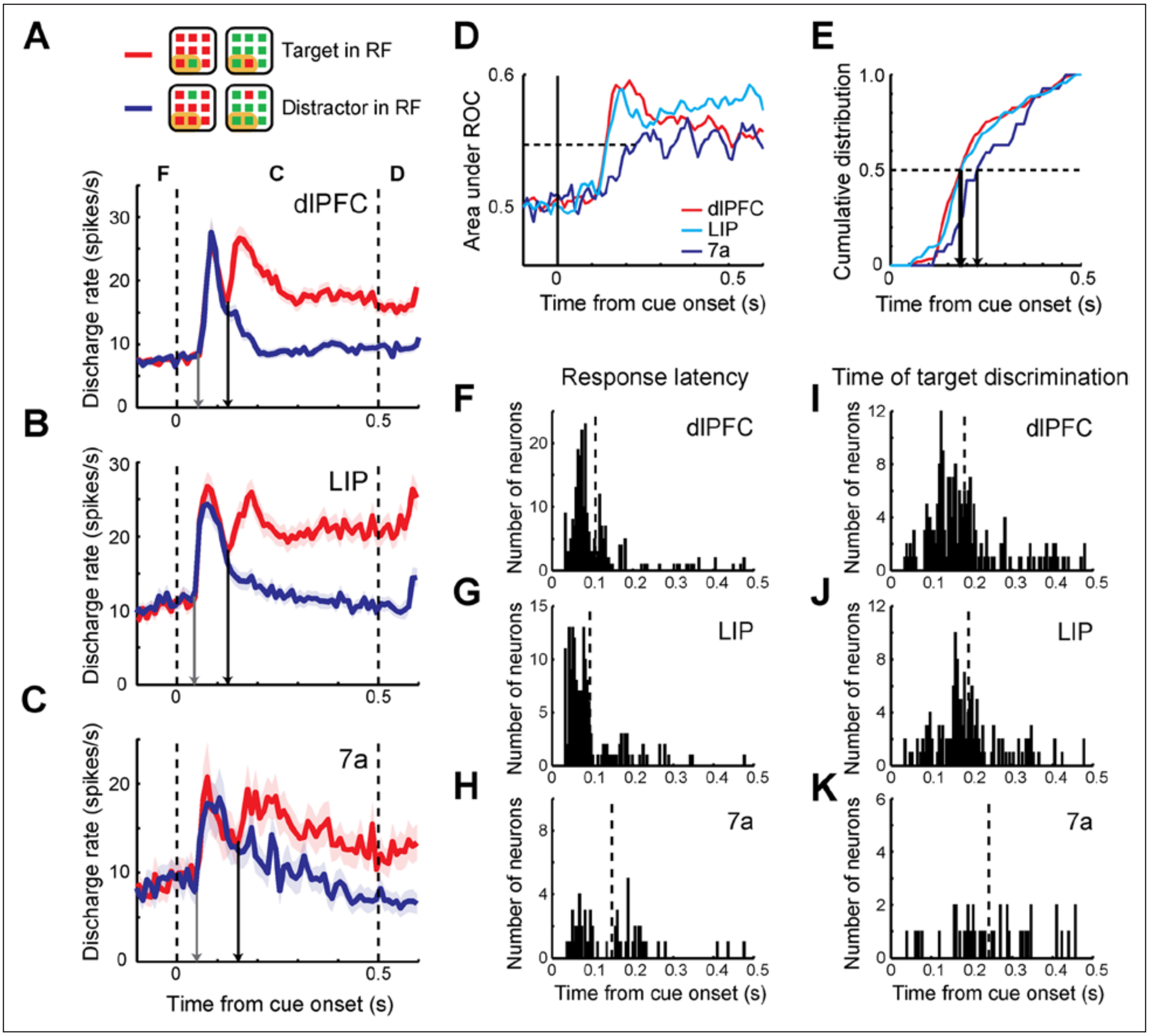

Figure 3. Neuronal responses of the dorsolateral part of the prefrontal cortex (dlPFC), lateral intraparietal area (LIP), and area 7a during a bottom-up visual attention task. (A-C) Population peristimulus time histograms of neurons in the dlPFC, LIP, and area 7a, respectively. Mean discharge rates of the salient stimulus in the receptive field (red) and the distractor in the receptive field (blue) are plotted for the fixation (F), cue (C), and delay (D) period. The dotted vertical lines represent the time of cue onset and offset. The initial visual response latency and the time of salient stimulus discrimination are indicated by the gray arrow and black arrow, respectively, in each panel. The receptive field location is schematically illustrated as an orange area in insets (receptive field location differed across neurons). Although the initial visual response latency (gray arrows) occurred earlier in the LIP than the dlPFC, there was no significant difference between the dlPFC and LIP in the time of salient stimulus discrimination (black arrows). (D) Receiver operating characteristic (ROC) analysis. The area under the ROC curve was computed based on the firing rates of the salient stimulus in the receptive field and the distractor in the receptive field and plotted as a function of time. The curves of the dlPFC (red) and LIP (cyan) reach the mean midpoint between the peak and baseline (dotted line) essentially simultaneously. (E) Cumulative distribution of neurons with a significant area under the ROC curve. The times when 50% of the neurons of the dlPFC and LIP reached significance were very similar (black arrows). (F-K) Neuron-by-neuron analysis. Distribution of the initial visual response latency (F-H) and the time of salient stimulus discrimination (I-K). The dotted lines represent the means of each distribution (Katsuki and Constantinidis 2012b).

spike counts divided by the mean). A decrease in the Fano factor in the interval of stimulus presentation may therefore be a signature of attentional capture. On the other hand, a recent study reported no decrease in the variability for an oddball stimulus in the FEF (Purcell and others 2012).

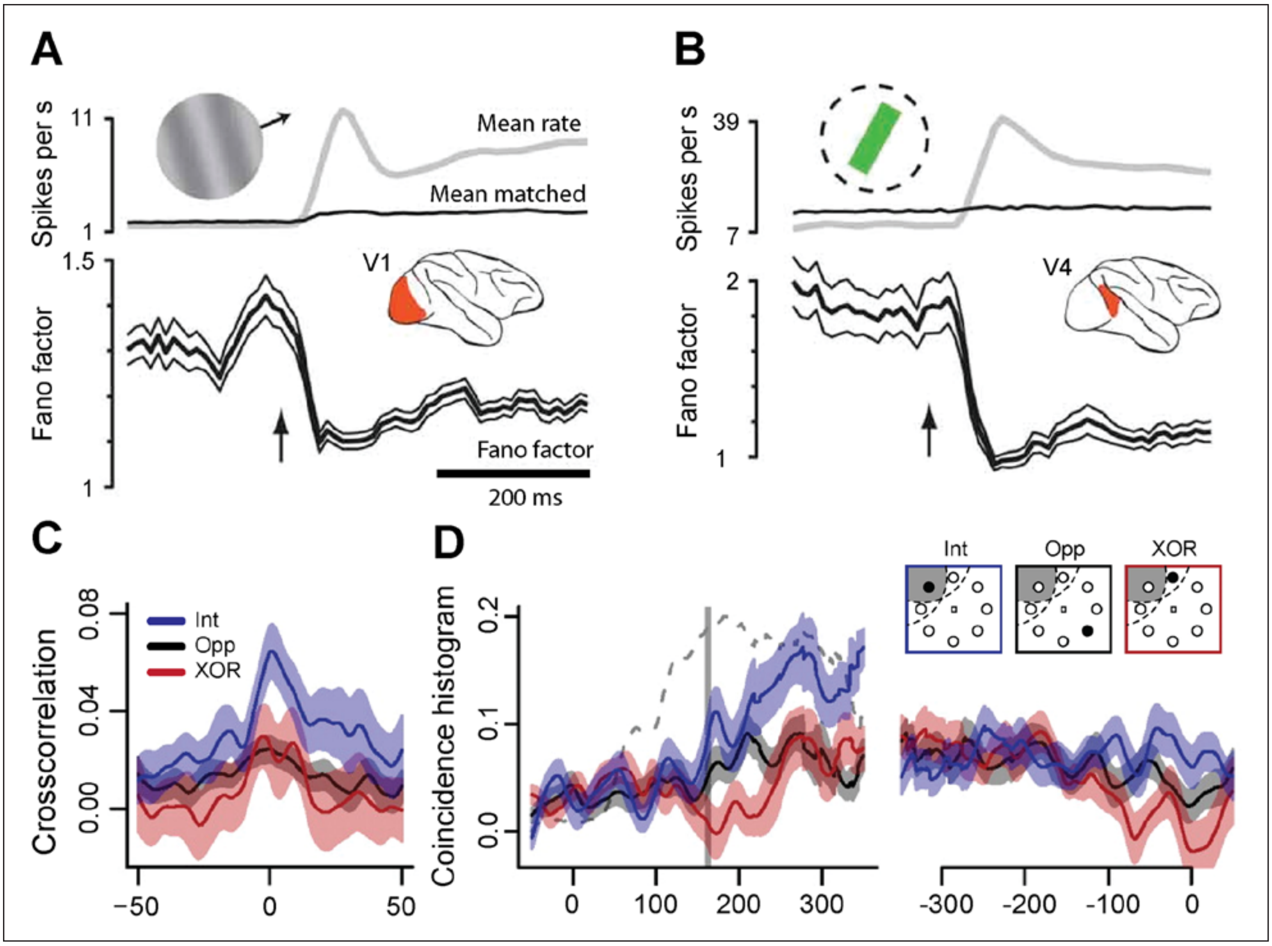

Figure 4. Effects of bottom-up attention beyond the firing rate. (A, B) The mean firing rate (top panel, gray line) and Fano factor (bottom panel) in V1 and V4. Arrows indicate stimulus onset. The variability in the firing rate (Fano factor) decreased at the onset of stimulus presentation in both areas (Churchland and others 2010). (C, D) Increase in neuronal synchronization when salient stimuli activate a pair of neurons. (C) Mean cross-correlograms of pairs of frontal eye field neurons with significant target selectivity for three experimental conditions: the target was located within the intersection of the receptive fields (blue line), opposite the intersection of the receptive fields (black line), and within one receptive field but not the other (red line). An increase in synchronized firing was observed (blue line v. red line) when pairs of neurons were simultaneously activated by an oddball stimulus. (D) Time course of mean coincidence of the pairs with significant target selectivity. Histograms are plotted for three stimulus presentation conditions as described in panel C, aligned to stimuli onset (left panel) and saccade onset (right panel). The mean target selection time is shown by the gray vertical line. The dashed plot in the left panel represents the mean firing rate of individual neurons when the target was inside receptive fields (Cohen and others 2010). Figures reproduced with permission.

The correlation of neuronal discharges recorded simultaneously has also been shown to be influenced by bottom-up factors. An increase in synchronized firing, based on cross-correlation analysis (Fig. 4C and 4D), has been reported for two neurons simultaneously activated by an oddball stimulus (Cohen and others 2010). These findings suggest that multiple mechanisms of neuronal modulation are affected by bottom-up attention and can affect information transmission for a stimulus that attracts attention. Neural changes beyond modulation of the firing rate have been implicated in top-down attention as well (discussed below).

Top-Down Attention

Neurophysiology of Top-Down Attention

Top-down visual attention is a voluntary process in which a particular location, feature, or object relevant to current behavioral goals is selected internally and focused upon

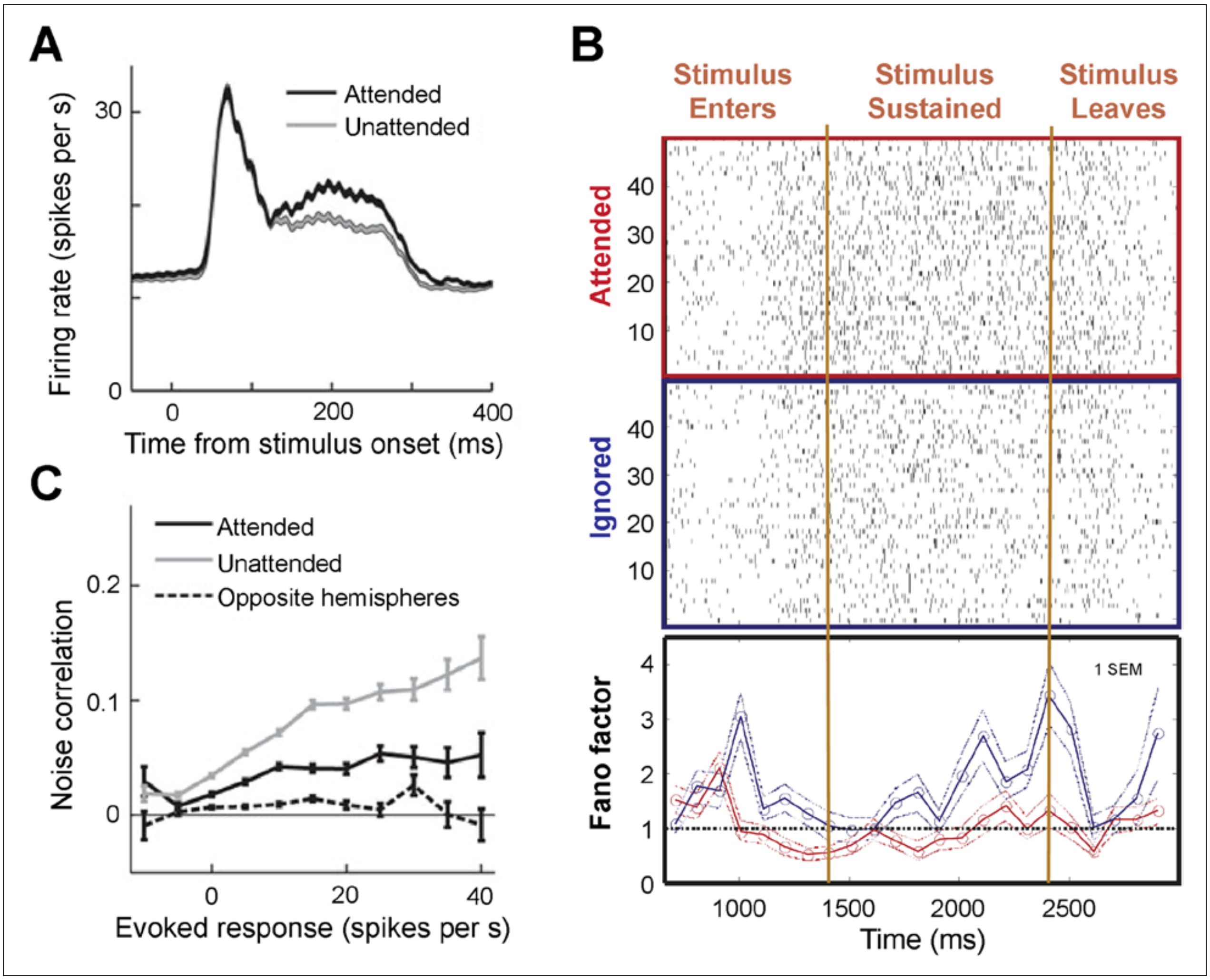

Figure 5. Effects of top-down attention beyond the firing rate. (A) Top-down modulation of the firing rate. The mean firing rate of V4 neurons was plotted for when the stimulus was attended (black line) and unattended (gray line). The firing rate was enhanced with attention (Cohen and Maunsell 2009). (B) Top-down influence on response variability. The top two panels show spike raster plots for attended and ignored conditions. The variability in the neuronal response (shown as the Fano factor in the bottom panel) decreased for the attended (red line) stimulus compared to the unattended (blue line) stimulus (Mitchell and others 2009). (C) Top-down influence on spike count correlation. The mean correlation for the pairs of neurons is plotted as a function of the mean response modulation by the stimulus. The noise correlation was reduced for the attended (black solid line) stimulus than for the unattended (gray solid line) stimulus (Cohen and Maunsell 2009). Figures reproduced with permission.

or examined (Connor and others 2004; Corbetta and Shulman 2002; Itti and Koch 2001). The main effect of top-down attention is that neural activity is enhanced for the particular location/feature/object of interest compared to behaviorally irrelevant stimuli (Fig. 5A), while suppression of neuronal responses is observed for irrelevant stimuli. These types of response modulation have been observed in areas of both ventral and dorsal visual pathways, such as V1, V2, V4, IT , MT, the PPC, and the PFC (Noudoost and others 2010). The magnitude of top-down modulation on neuronal firing tends to increase across the cortical hierarchy (Cook and Maunsell 2002; Luck and others 1997).

Connections between cortical areas are generally reciprocal; thus, feedback signals can descend from the higher stages to the lower stages of the pathways (Douglas and Martin 2004; Douglas and Martin 2007; Felleman and Van Essen 1991). Microstimulation of the FEF has been shown to enhance stimulus responses in visual cortical area V4, particularly when the stimulus contrast is low or distracting stimuli are present in the field of view, providing direct evidence for top-down modulation (Ekstrom and others 2009; Moore and Fallah 2004).

The appearance of a stimulus at an attended location may not always enhance neuronal responses. Suppression of responses has been reported in the PPC for stimuli appearing at locations already in the focus of attention (Steinmetz and Constantinidis 1995). The phenomenon is analogous to the repetition suppression described for repeated presentation of the same object for areas of the ventral pathway (Grill-Spector and others 2006). This mechanism that emphasizes responses to unattended stimuli might play a role in filtering out already attended stimuli and facilitating the shift of attention to new stimuli during visual search (Constantinidis 2006).

Origin of Top-Down Signals

Where do top-down signals originate? Higher cortical areas such as the PFC and PPC have been thought of as a source of top-down influences. One way to directly investigate the causal effect of top-down signals is modulating the activity in a source region and observing its influence in other visual areas and behavioral performance. Studies applying microstimulation to the FEF showed enhancement in both the firing rate in visual areas and in behavioral performance, indicating the involvement of the PFC in attentional control (Moore and Armstrong 2003; Moore and Fallah 2001; Moore and Fallah 2004). More recent neurophysiological studies have also indicated that the selection of a target location or feature among distractors emerges in the FEF during spatial- and object-based attention tasks (Monosov and others 2008; Zhou and Desimone 2011). Additionally, inactivation of the FEF by applying muscimol impairs behavioral performance in visual attention tasks (Wardak and others 2006). The feedback projections from the frontal cortex to areas in the dorsal and ventral pathways appear to be anatomically separated, allowing the transmission of diverse top-down signals to specific areas depending on stimulus properties and task demands (Ninomiya and others 2012).

Similarly, a causal effect of PPC signals in orienting attention has been studied by activating and inactivating the region. Microstimulation of PPC regions during a covert attention task also evoked shifts of attention and shortened reaction times to detect a target (Cutrell and Marrocco 2002). Inactivation of the LIP in the PPC with muscimol produces deficits in performance of overt and covert attention tasks (Liu and others 2010; Wardak and others 2002; Wardak and others 2004).

The results reviewed above suggest that both PFC areas and PPC areas can provide top-down signals to control attention to some degree (Katsuki and Constantinidis 2012b). Is one of the areas more dominant or definitive in top-down attention control than the other? A study comparing the time course of PFC and PPC activity reported that the activity of PFC neurons represents a target earlier than the PPC in a top-down–oriented visual search task (Buschman and Miller 2007). Another recent study suggested that FEF neurons responded faster than LIP neurons when stimulus selection relied more on top-down information (Ibos and others 2013). These results support the idea that top-down signals appear earlier in PFC activity in comparison to the PPC.

In addition to the timing of the signals, the two areas demonstrated distinct characteristics in terms of behavioral performance (Wardak and others 2006; Wardak and others 2004). Inactivation of the FEF impaired psychophysical performance in a visual search task regardless of the difficulty (either conjunction or feature detection) of the tasks (Wardak and others 2006). On the other hand, inactivation of the LIP only impaired performance in a difficult visual search (Wardak and others 2004). A recent neurophysiological study showed that dlPFC neurons displayed weaker responses to distractors compared to LIP neurons during a working memory task (Suzuki and Gottlieb 2013). These distractor-related responses of the dlPFC were more tightly linked to behavioral performance than those of the LIP. Additionally, reversible inactivation experiments demonstrated that inactivation of the dlPFC led to more severe impairment in distractor suppression and a higher behavioral error rate than LIP inactivation (Suzuki and Gottlieb 2013). These results suggest that although both the PFC and PPC are involved in target selection, the PFC may have a more direct influence on behavioral response than the PPC in top-down tasks.

Top-Down Modulation beyond Firing Rate

In addition to modulation of the firing rate, other mechanisms that may mediate the effects of top-down attention have been described in the form of decreased variability (Fig. 5B) and neuronal correlations (Fig. 5C) as well as increased spike field coherence. Variability in trial-to-trial responses in individual neurons is a critical parameter of neuronal firing as high levels of random fluctuations representing irrelevant noise that can dilute the impact of a stimulus representation during the attentional process. Thus, decreasing the internal noise can help improve representation of an attended stimulus. Studies in V4 neurons reported that the Fano factor of neuronal responses decreased for attended stimuli (Fig. 5B) in addition to changes in the mean firing rate (Cohen and Maunsell 2009; Mitchell and others 2009). On the other hand, a recent study reported no decrease in variability for a cued

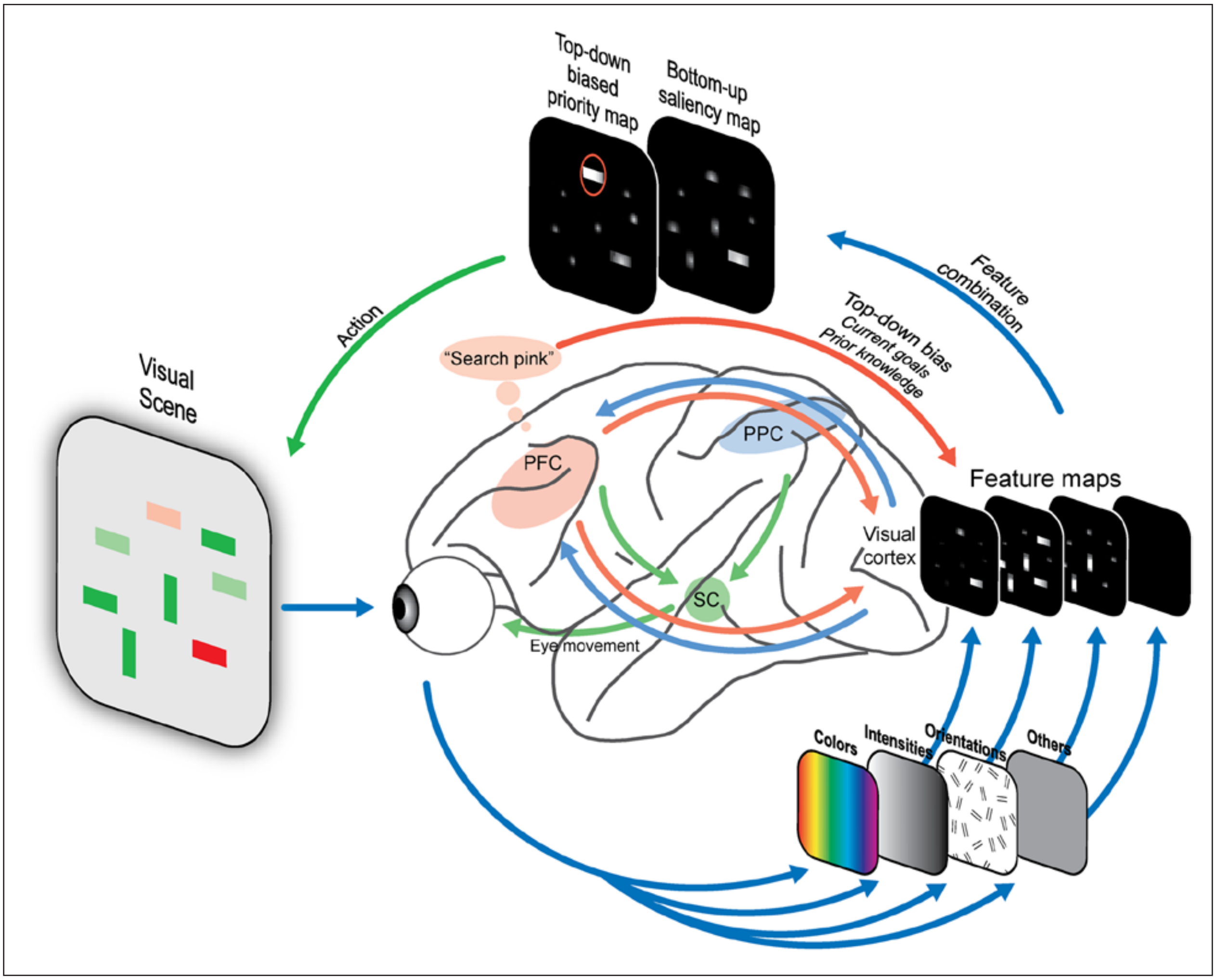

Figure 6. Schematic diagram of bottom-up and top-down attentional processes. The outer flow diagram illustrates the theoretical stages involving representation of bottom-up saliency and integration with top-down influences into a priority map. A diagram within the brain illustrates the cortical pathways involved in visual attention. Blue, red, and green arrows represent bottom-up signal processing, top-down signal processing, and eye movement–related signal processing, respectively. Visual input entering through the eyes is processed separately for its features (e.g., colors, intensities, or orientations). Separate feature maps represent components of each stimulus, which are then integrated into a saliency map, representing the physical saliency of stimuli in the visual field and orienting attention to the overall most salient stimulus. Salience is represented simultaneously in the prefrontal cortex (PFC) and posterior parietal cortex (PPC). This bottom-up–based process could be modulated by top-down factors, such as current behavioral goals and prior knowledge. Signals incorporating bottom-up and top-down factors are reflected in the priority map. Top-down signals originating from the PFC are thought to modulate the representation of stimuli across the cortical pathways. Attention is oriented to the location with the most prominent activity in the map, and signals to generate an eye movement are delivered accordingly through the superior colliculus (SC).

stimulus in the FEF, despite a change in the firing rate (Chang and others 2012).

Modulation of correlated activity in neuronal populations within and across visual cortical areas could also be a way to provide more information and improve representation of the attended stimulus. If response variability on a trial-by-trial basis is positively correlated between neurons (spike count correlation or noise correlation), the benefit of pooling responses from multiple neurons quickly saturates (Shadlen and Newsome 1998; Zohary and others 1994). Top-down attention has been shown to reduce this spike count correlation between neurons (Fig. 5C) and improve the signal-to-noise ratio of responses and amount of information carried by the population of neurons in area V4 (Cohen and Maunsell 2009; Mitchell and others 2009). Furthermore, spike count correlation between pairs of neurons in area MT changed depending on the context, even though identical visual stimuli were presented, indicating a top-down effect (Cohen and Newsome 2008). These changes in correlated firing by top-down attention appear to affect differentially specific cell types. In V4, strong modulation was observed especially in fast spiking interneurons during attention (Mitchell and others 2007). The firing rate of bursty yramidal cells was also shown to be increased by attention, whereas nonbursty pyramidal cells were less likely to show attentional modulation (Anderson and others 2011).

Neurophysiological studies have also implicated neuronal synchronization in attentional processes (Bichot and others 2005; Fries and others 2001; Saalmann and others 2007). An increase in synchronization, especially in the 35- to 70-Hz (γ) band among neurons that selectively respond to the attended stimulus, has been observed both in spatial- and object-based attention tasks (Bichot and others 2005; Fries and others 2001; Taylor and others 2005). γ-band synchronization has been proposed as a mechanism to label information about an attended stimulus and distinguish it from unattended stimuli. For example, γ-band synchronization was observed more often, as attended stimuli were located in the receptive field during an object-based attention task (Bichot and others 2005; Buschman and Miller 2007; Siegel and others 2009). Simultaneous recordings of multiunit spikes and LFPs from the FEF and V4 reveal that the FEF is a source of the enhanced γ synchrony observed in V4 (Gregoriou and others 2009). Whether and how this neuronal synchrony is the neural substrate of attention are still a matter of investigation, although it has been shown on theoretical grounds that enhanced synchrony and increased firing rates may jointly improve the selectivity toward behaviorally relevant stimuli with high precision (Borgers and others 2008; Tiesinga and others 2008).

Conclusion

With a limited capacity to process information in the brain, attention is an indispensable cognitive process that has evolved in higher organisms. Being able to ignore unnecessary information when one needs to engage in a behavior but also being able to detect possibly life-threatening changes in the environment at the same time require quick yet precise neural responses. Here, we reviewed studies of visual-based bottom-up attention and willful, voluntary top-down attention separately. The two processes are defined by the origin of information, from the sensory periphery and higher cortical areas, respectively, and are associated with quite distinct neural processes and needs. Nonetheless, both attention modes act upon visual cortical areas in the dorsal and ventral pathways, and their simultaneous influence is often integrated in processes such as visual search, illustrated schematically in Figure 6. In recent years, this interplay between top-down and bottom-up attention has come to the forefront, as it has become apparent that the same set of brain areas, particularly in the PPC and PFC, is engaged in both top-down and bottom-up attention. These areas can be thought as providing a priority map for the selection of stimuli based on both bottom-up and top-down factors (Fig. 6). Therefore, rather than the two attentional systems being separated processes, they should be better thought as intricately intertwined. In the extreme form of this view, the distinction between bottom-up and top-down attention is arbitrary. Regardless of the origin of information, studies have indicated that attention is allocated to an object or location that evokes the highest activity at the moment. Another recent realization is that both modes of attention may affect more subtle characteristics of neural firing, beyond the mean firing rate, such as the variability of discharges, their correlation across neurons, and the synchrony between spikes and LFPs. Further research will be necessary to understand the details of the specific roles of distinct cortical areas in the guidance of attention and how the different mechanisms contribute to the overall attentional system.

Acknowledgments

The authors thank Kathini Palaninathan for valuable technical support and Anthony Elworthy for editorial assistance.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received the following financial support for the research, authorship, and/or publication of this article: This work was supported by National Institutes of Health grants R01 EY016773 and T32 NS073553 and by the Tab Williams Family Endowment.

References

Anderson EB, Mitchell JF, Reynolds JH. 2011. Attentional modulation of firing rate varies with burstiness across putative pyramidal neurons in macaque visual area V4. J Neurosci 31(30):10983–92.

Arcizet F, Mirpour K, Bisley JW. 2011. A pure salience response in posterior parietal cortex. Cereb Cortex 21(11):2498–506.

Awh E, Belopolsky AV, Theeuwes J. 2012. Top-down versus bottom-up attentional control: a failed theoretical dichotomy. Trends Cogn Sci 16(8):437–43.

Basso MA, Wurtz RH. 2002. Neuronal activity in substantia nigra pars reticulata during target selection. J Neurosci 22(5):1883–94.

Bichot NP, Rossi AF, Desimone R. 2005. Parallel and serial neural mechanisms for visual search in macaque area V4. Science 308(5721):529–34.

Bisley JW, Goldberg ME. 2010. Attention, intention, and priority in the parietal lobe. Annu Rev Neurosci 33:1–21.

Borgers C, Epstein S, Kopell NJ. 2008. Gamma oscillations mediate stimulus competition and attentional selection in a cortical network model. Proc Natl Acad Sci U S A 105(46):18023–8.

Burrows BE, Moore T. 2009. Influence and limitations of popout in the selection of salient visual stimuli by area V4 neurons. J Neurosci 29(48):15169–77.

Buschman TJ, Miller EK. 2007. Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. Science 315(5820):1860–2.

Chang MH, Armstrong KM, Moore T. 2012. Dissociation of response variability from firing rate effects in frontal eye field neurons during visual stimulation, working memory, and attention. J Neurosci 32(6):2204–16.

Chelazzi L, Miller EK, Duncan J, Desimone R. 2001. Responses of neurons in macaque area V4 during memory-guided visual search. Cereb Cortex 11(8):761–72.

Churchland MM, Yu BM, Cunningham JP, Sugrue LP, Cohen MR, Corrado GS, and others. 2010. Stimulus onset quenches neural variability: a widespread cortical phenomenon. Nat Neurosci 13(3):369–78.

Cohen JY, Crowder EA, Heitz RP, Subraveti CR, Thompson KG, Woodman GF, and others. 2010. Cooperation and competition among frontal eye field neurons during visual target selection. J Neurosci 30(9):3227–38.

Cohen JY, Heitz RP, Schall JD, Woodman GF. 2009. On the origin of event-related potentials indexing covert attentional selection during visual search. J Neurophysiol 102(4):2375–86.

Cohen MR, Maunsell JH. 2009. Attention improves performance primarily by reducing interneuronal correlations. Nat Neurosci 12(12):1594–600.

Cohen MR, Newsome WT. 2008. Context-dependent changes in functional circuitry in visual area MT. Neuron 60(1): 162–73.

Connor CE, Egeth HE, Yantis S. 2004. Visual attention: bottom-up versus top-down. Curr Biol 14(19):R850–2.

Constantinidis C. 2006. Posterior parietal mechanisms of visual attention. Rev Neurosci 17(4):415–27.

Constantinidis C, Steinmetz MA. 2001. Neuronal responses in area 7a to multiple stimulus displays, I: neurons encode the location of the salient stimulus. Cereb Cortex 11:581–91.

Constantinidis C, Steinmetz MA. 2005. Posterior parietal cortex automatically encodes the location of salient stimuli. J Neurosci 25(1):233–8.

Cook EP, Maunsell JH. 2002. Attentional modulation of behavioral performance and neuronal responses in middle temporal and ventral intraparietal areas of macaque monkey. J Neurosci 22(5):1994–2004.

Corbetta M, Shulman GL. 2002. Control of goal-directed and stimulus-driven attention in the brain. Nat Rev Neurosci 3(3):201–15.

Cutrell EB, Marrocco RT. 2002. Electrical microstimulation of primate posterior parietal cortex initiates orienting and alerting components of covert attention. Exp Brain Res 144(1):103–13.

Desimone R, Duncan J. 1995. Neural mechanisms of selective visual attention. Annu Rev Neurosci 18:193–222.

Douglas RJ, Martin KA. 2004. Neuronal circuits of the neocortex. Annu Rev Neurosci 27:419–51.

Douglas RJ, Martin KA. 2007. Recurrent neuronal circuits in the neocortex. Curr Biol 17(13):R496–500.

Duncan J, Humphreys GW. 1989. Visual search and stimulus similarity. Psychol Rev 96(3):433–58.

Ekstrom LB, Roelfsema PR, Arsenault JT, Kolster H, Vanduffel W. 2009. Modulation of the contrast response function by electrical microstimulation of the macaque frontal eye field. J Neurosci 29(34):10683–94.

Felleman DJ, Van Essen DC. 1991. Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1(1):1–47.

Fries P, Reynolds JH, Rorie AE, Desimone R. 2001. Modulation of oscillatory neuronal synchronization by selective visual attention. Science 291(5508):1560–3.

Gottlieb JP, Kusunoki M, Goldberg ME. 1998. The representation of visual salience in monkey parietal cortex. Nature 391(6666):481–4.

Gregoriou GG, Gotts SJ, Zhou H, Desimone R. 2009. High-frequency, long-range coupling between prefrontal and visual cortex during attention. Science 324(5931):1207–10.

Grill-Spector K, Henson R, Martin A. 2006. Repetition and the brain: neural models of stimulus-specific effects. Trends Cogn Sci 10(1):14–23.

Hegde J, Felleman DJ. 2003. How selective are V1 cells for pop-out stimuli? J Neurosci 23(31):9968–80.

Herrington TM, Assad JA. 2009. Neural activity in the middle temporal area and lateral intraparietal area during endogenously cued shifts of attention. J Neurosci 29(45): 14160–76.

Iba M, Sawaguchi T. 2003. Involvement of the dorsolateral prefrontal cortex of monkeys in visuospatial target selection. J Neurophysiol 89(1):587–99.

Ibos G, Duhamel JR, Ben Hamed S. 2013. A functional hierarchy within the parietofrontal network in stimulus selection and attention control. J Neurosci 33(19):8359–69.

Itti L, Koch C. 2001. Computational modelling of visual attention. Nat Rev Neurosci 2(3):194–203.

Katsuki F, Constantinidis C. 2012a. Early involvement of prefrontal cortex in visual bottom-up attention. Nat Neurosci 15(8):1160–6.

Katsuki F, Constantinidis C. 2012b. Unique and shared roles of the posterior parietal and dorsolateral prefrontal cortex in cognitive functions. Front Integr Neurosci 6:17.

Knierim JJ, van Essen DC. 1992. Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol 67(4):961–80.

Koch C, Ullman S. 1985. Shifts in selective visual attention: towards the underlying neural circuitry. Hum Neurobiol 4:219–27.

Kusunoki M, Gottlieb J, Goldberg ME. 2000. The lateral intraparietal area as a salience map: the representation of abrupt onset, stimulus motion, and task relevance. Vision Res 40(10–12):1459–68.

Lamme VA. 1995. The neurophysiology of figure-ground segregation in primary visual cortex. J Neurosci 15(2):1605–15.

Liu Y, Yttri EA, Snyder LH. 2010. Intention and attention: different functional roles for LIPd and LIPv. Nat Neurosci 13(4):495–500.

Luck SJ, Chelazzi L, Hillyard SA, Desimone R. 1997. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. J Neurophysiol 77(1):24–42.

McPeek RM, Keller EL. 2002. Saccade target selection in the superior colliculus during a visual search task. J Neurophysiol 88(4):2019–34.

Mitchell JF, Sundberg KA, Reynolds JH. 2007. Differential attention-dependent response modulation across cell classes in macaque visual area V4. Neuron 55(1):131–41.

Mitchell JF, Sundberg KA, Reynolds JH. 2009. Spatial attention decorrelates intrinsic activity fluctuations in macaque area V4. Neuron 63(6):879–88.

Monosov IE, Trageser JC, Thompson KG. 2008. Measurements of simultaneously recorded spiking activity and local field potentials suggest that spatial selection emerges in the frontal eye field. Neuron 57(4):614–25.

Moore T, Armstrong KM. 2003. Selective gating of visual signals by microstimulation of frontal cortex. Nature 421(6921):370–3.

Moore T, Fallah M. 2001. Control of eye movements and spatial attention. Proc Natl Acad Sci U S A 98(3):1273–6.

Moore T, Fallah M. 2004. Microstimulation of the frontal eye field and its effects on covert spatial attention. J Neurophysiol 91(1):152–62.

Niebur E, Koch C. 1996. Control of selective visual attention: modeling the "where" pathway. In: Touretzky DS, Mozer MC, and Hasselmo ME, editors. Neural information processing systems. Cambridge, MA: MIT Press. p. 802–8.

Ninomiya T, Sawamura H, Inoue K, Takada M. 2012. Segregated pathways carrying frontally derived top-down signals to visual areas MT and V4 in macaques. J Neurosci 32(20):6851–8.

Noudoost B, Chang MH, Steinmetz NA, Moore T. 2010. Top-down control of visual attention. Curr Opin Neurobiol 20(2):183–90.

Purcell BA, Heitz RP, Cohen JY, Schall JD. 2012. Response variability of frontal eye field neurons modulates with sensory input and saccade preparation but not visual search salience. J Neurophysiol 108(10):2737–50.

Purcell BA, Schall JD, Woodman GF. 2013. On the origin of event-related potentials indexing covert attentional selection during visual search: timing of selection by macaque frontal eye field and event-related potentials during pop-out search. J Neurophysiol 109(2):557–69.

Saalmann YB, Pigarev IN, Vidyasagar TR. 2007. Neural mechanisms of visual attention: how top-down feedback highlights relevant locations. Science 316(5831):1612–5.

Sato TR, Watanabe K, Thompson KG, Schall JD. 2003. Effect of target-distractor similarity on FEF visual selection in the absence of the target. Exp Brain Res 151(3):356–63.

Schall JD, Hanes DP. 1993. Neural basis of saccade target selection in frontal eye field during visual search. Nature 366(6454):467–9.

Schall JD, Hanes DP, Thompson KG, King DJ. 1995. Saccade target selection in frontal eye field of macaque, I: visual and premovement activation. J Neurosci 15(10):6905–18.

Schall JD, Pare M, Woodman GF. 2007. Comment on "top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices." Science 318(5847):44.

Schall JD, Purcell BA, Heitz RP, Logan GD, Palmeri TJ. 2011. Neural mechanisms of saccade target selection: gated accumulator model of the visual-motor cascade. Eur J Neurosci 33(11):1991–2002.

Serences JT, Yantis S. 2006. Selective visual attention and perceptual coherence. Trends Cogn Sci 10(1):38–45.

Shadlen MN, Newsome WT. 1998. The variable discharge of cortical neurons: implications for connectivity, computation, and information coding. J Neurosci 18(10):3870–96.

Shomstein S. 2012. Cognitive functions of the posterior parietal cortex: top-down and bottom-up attentional control. Front Integr Neurosci 6:38.

Shomstein S, Lee J, Behrmann M. 2010. Top-down and bottom-up attentional guidance: investigating the role of the dorsal and ventral parietal cortices. Exp Brain Res 206(2): 197–208.

Siegel M, Warden MR, Miller EK. 2009. Phase-dependent neuronal coding of objects in short-term memory. Proc Natl Acad Sci U S A 106(50):21341–6.

Steinmetz MA, Constantinidis C. 1995. Neurophysiological evidence for a role of posterior parietal cortex in redirecting visual attention. Cereb Cortex 5(5):448–56.

Suzuki M, Gottlieb J. 2013. Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. Nat Neurosci 16(1):98–104.

Taylor K, Mandon S, Freiwald WA, Kreiter AK. 2005. Coherent oscillatory activity in monkey area v4 predicts successful allocation of attention. Cereb Cortex 15(9):1424–37.

Thomas NW, Pare M. 2007. Temporal processing of saccade targets in parietal cortex area LIP during visual search. J Neurophysiol 97(1):942–7.

Thompson KG, Hanes DP, Bichot NP, Schall JD. 1996. Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. J Neurophysiol 76(6):4040–55.

Tiesinga P, Fellous JM, Sejnowski TJ. 2008. Regulation of spike timing in visual cortical circuits. Nat Rev Neurosci 9(2):97–107.

Treisman AM, Gelade G. 1980. A feature-integration theory of attention. Cogn Psychol 12(1):97–136.

Ungerleider LG, Haxby JV. 1994. 'What' and 'where' in the human brain. Curr Opin Neurobiol 4(2):157–65.

Ungerleider LG, Mishkin M. 1982. Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW, editors. Analysis of visual behavior. Cambridge, MA: MIT Press. p. 549–86.

Wardak C, Ibos G, Duhamel JR, Olivier E. 2006. Contribution of the monkey frontal eye field to covert visual attention. J Neurosci 26(16):4228–35.

Wardak C, Olivier E, Duhamel JR. 2004. A deficit in covert attention after parietal cortex inactivation in the monkey. Neuron 42(3):501–8.

Wardak C, Olivier E, Duhamel JR. 2002. Saccadic target selection deficits after lateral intraparietal area inactivation in monkeys. J Neurosci 22(22):9877–84.

Wolfe JM. 1994. Guided search 2.0: a revised model of visual search. Psychon Bull Rev 1:202–38.

Wolfe JM. 2010. Visual search. Curr Biol 20(8):R346–9.

Wolfe JM, Horowitz TS. 2004. What attributes guide the deployment of visual attention and how do they do it? Nat Rev Neurosci 5(6):495–501.

Zhou H, Desimone R. 2011. Feature-based attention in the frontal eye field and area V4 during visual search. Neuron 70(6):1205–17.

Zohary E, Shadlen MN, Newsome WT. 1994. Correlated neuronal discharge rate and its implications for psychophysical performance. Nature 370(6485):140–3.