The Neuroscientist
XX(X) 1–14

DOI: 10.1177/1073858411409051
http://nro.sagepub.com
SAGE

The Frontoparietal Attention Network of the Human Brain: Action, Saliency, and a Priority Map of the Environment

Radek Ptak[1]

Abstract

The dorsal convexity of the human frontal and parietal lobes forms a network that is crucially involved in the selection of sensory contents by attention. This network comprehends cortex along the intraparietal sulcus, the inferior parietal lobe, and dorsal premotor cortex, including the frontal eye field. These regions are richly interconnected with recurrent fibers passing through the superior longitudinal fasciculus. The posterior parietal cortex has several functional characteristics—such as feature-independent coding, enhancement of activity by attention, representation of task-related signals, and access to multiple reference frames—that point to a central role of this region in the computation of a feature- and modality-independent priority map of the environment. The priority map integrates feature information elaborated in sensory cortex and top-down representations of behavioral goals and expectations originating in the dorsolateral prefrontal and premotor cortex. This review presents converging evidence from single-unit studies of the primate brain, functional neuroimaging, and investigations of neuropsychological disorders such as Bálint syndrome and spatial neglect for a decisive role of the frontoparietal attention network in the selection of relevant environmental information.

Keywords

frontoparietal network, saliency, priority map, attention, spatial neglect, frontal eye field

Three Problems of Attention

Consider yourself reading a novel while sitting in a coffee shop that faces a busy street. Though there are many potential distracters such as cars and people producing a variety of sounds your lecture is completely absorbing your attention. Suddenly, a small black shape slowly creeping across the table captures your gaze. How did your brain determine that the insect was more relevant than any other of the surrounding sensory stimuli?

This example illustrates three fundamental problems of attention, which have to do with capacity, control, and selection criterion. The capacity problem is a consequence of the fact that, although sensory systems are capable of processing a massive amount of information, the capacity of output systems is severely limited. As a result, a mechanism is needed that selects among all incoming stimuli those that might require an answer and hence are behaviorally relevant. The example given above also implies that attentional selection can be automatic (when attention is captured by the creeping insect) or voluntary (when attention is maintained on the text despite distracting stimuli). The control problem deals with the conditions specifying whether the deployment of attention is driven by environmental stimuli (stimulus-driven attention) or by goals and expectations of the observer (goal-driven attention), and how these two sources of control interact (Egeth and Yantis 1997; Pashler 1998). Current literature on the cognitive mechanisms visual attention is dominated by the question of whether attention may select a stimulus solely on the basis of its perceptual characteristics or whether behavioral predispositions may overwrite stimulus-driven capture of attention (Simons 2000; Theeuwes 2010; Yantis and Egeth 1999). The problem of selection criterion, a possibly more fundamental challenge for theories of attention, has received comparatively less

---

[1] Division of Neurorehabilitation, Geneva University Hospital and Faculty of Medicine, University of Geneva, Switzerland

Corresponding Author:
Radek Ptak, Division of Neurorehabilitation, Department of Clinical Neurosciences, Geneva University Hospital, 26, Av. de Beau-Séjour, 1211 Geneva 14, Switzerland
Email: radek.ptak@hcuge.ch

consideration. The pertinence of the criterion problem becomes clear when one considers the variety of sensory stimuli that are present in a situation such as the coffee shop example: Assuming that attention is a ubiquitous mental faculty (implying that there are not several selection functions proceeding in parallel), the filtering mechanism should be the same irrespective of the sensory quality of stimuli on which attention operates. A parsimonious way to select among stimuli with physically distinct characteristics (e.g., color and shape) or presented in different modalities (e.g., auditory and tactile) is to compute a neural criterion that allows judging and comparing their relevance. To specify the nature of this signal is the core issue of the criterion problem.

Evidence from single-unit studies, functional neuroimaging, and work with brain-injured patients suggests that the solution of the criterion problem depends on the function of a frontoparietal attention network (FPAN). The purpose of this review is to present recent findings in favor of a specialized brain system embedded in the FPAN, which encodes the priority of sensory inputs and constructs a feature-, modality-, and response-independent representation of the environment.

A Neural Solution for the Criterion Problem

The term *saliency* is commonly applied to denote the physical intensity of signals in relation to surrounding stimuli (Itti and Koch 2001). However, the physical appearance of a stimulus is determined not only by perceptual factors but also by top-down biases such as expectations or behavioral goals and by attention itself (Blaser and others 1999; Carrasco and others 2004). For example, the neural response to the same stimulus varies strongly as a function of whether this stimulus is an action goal or whether it is irrelevant for the current task (Constantinidis and Steinmetz 2001). Thus, the appropriate term for neural responses that integrate sensory and goal-related information and thus reflect the perceived quality of the signal rather than its absolute physical quality is *priority*.

Although some data suggest that priority is an emergent property of distributed representations in the brain (Treue 2003), several models of attention assume that it is encoded in a localizable priority map (Koch and Ullman 1985; Treisman 1998; Wolfe 1994). Figure 1 shows the basic cognitive architecture of a model in which priority is computed from perceptual features of the stimulus and high-level representations of the target. Primary and secondary sensory areas elaborate topographic feature maps by extracting basic perceptual features (such as curves, edges, and other shape primitives; intensity, or color) from the input image. In addition, computation of priority is biased by preferences of the observer or action goals held in working memory. Thus, the priority map is a topographically organized representation of space computed by integrating perceptual features and observer biases.

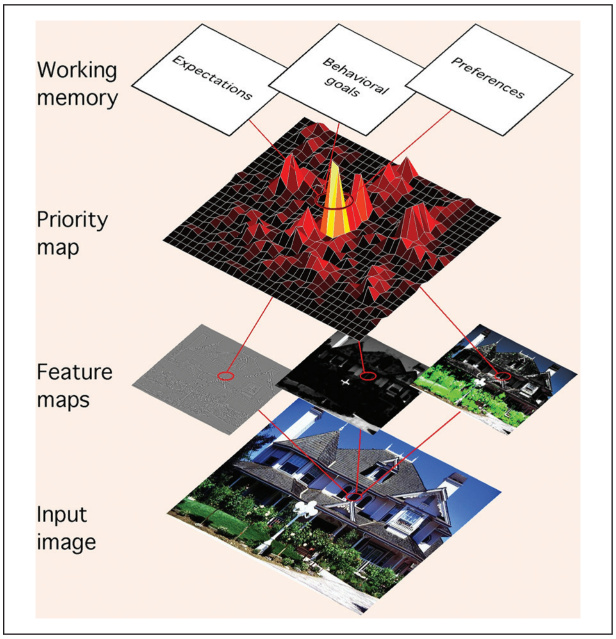

Figure 1. A model of the computation of attentional priority. Early sensory cortex (here, the visual cortex) decomposes the input stimulus into several independent maps representing distinct sensory features (e.g., spatial frequency, intensity, color, and so on). Feature maps are computed automatically and preattentively, that is, prior to the selection of a specific stimulus for conscious processing. The priority map integrates the converging inputs from multiple feature maps and combines them with top-down signals reflecting behavioral goals and expectations. Thus, the priority of a specific location in space reflects the sum of feature inputs and task-related signals converging at this location.

To constitute a biologically advantageous and neurally plausible solution of the criterion problem, the priority map must fulfill several criteria:

1. Feature-independent coding. Priority of stimuli is coded independently of their specific physical quality (Fecteau and Munoz 2006; Itti and Koch 2001). Feature-independent coding implies that the priority of two perceptually distinct stimuli presented in the same modality (e.g., two colors) or different modalities (e.g., shape and sound) is comparable when they trigger a similar neural response. Because priority is an abstract quality of environmental stimuli that reflects the integration of a multitude of sensory signals, brain regions computing priority should be capable of multisensory integration.

2. Priority predicts the locus of attention. The region of highest activity in the priority map is associated with the spatial location that is currently selected by attention. Attentional selection in the priority map follows a "winner-take-all" rule: The spatial location or the object currently exhibiting the greatest level of priority automatically becomes the locus of attention (Koch and Ullman 1985). Consequently, damage to the priority map impairs the focusing of attention on environmental stimuli and thus results in a severe deficit of spatial attention.
3. Response-independent coding. The priority map codes stimuli prior to the specification of the required response, which ensures that the computation of priority is independent of the intended action (eye movement, grasping movement, button press, or other).
4. Coding in multiple reference frames. To maintain a constant locus of selection across eye, head, or trunk movements, coding in the priority map has access to retinotopic, head-centered, and body-centered coordinates. This feature of the priority map is crucial for the programming of directed actions toward moving stimuli (e.g., catching a ball). Attention would seriously lack functionality if it used an exclusively retinotopic representation of space because highlighted locations would shift with every movement of the eyes. It is therefore essential for goal-directed activities to represent the environment in coordinates that remain stable irrespective of eye or head movements.
5. Integration of bottom-up and top-down inputs. The computation of priority integrates information about the perceptual features of the stimulus as well as high-level representations of expectations and action-goals (Bisley and Goldberg 2010). The priority map therefore receives convergent inputs from brain regions processing basic sensory features and associative cortex elaborating representations of action goals and task constraints. These connections are reciprocal, enabling information to flow back from the priority map and to bias sensory competition in favor of a perceptual feature or the competition between different intentions in favor of a specific action plan.

Although some of these functional characteristics can be found in several regions throughout the cortex, multiple findings indicate that the dorsal frontoparietal cortex is particularly important for priority coding. The term *frontoparietal attention network* designates dorsal brain regions that are often activated concurrently when participants are engaged in tasks requiring the shifting of attention in space. These regions comprise several areas situated in the posterior parietal cortex (PPC), premotor and prefrontal cortex (including the frontal eye field), which are strongly interconnected with fibers passing through the superior longitudinal fasciculus (SLF). Studies of the monkey and human brain agree on a subdivision of the SLF in three parts (Figure 2), respectively, connecting the superior parietal region with dorsal premotor and prefrontal cortex (SLF I), the inferior parietal cortex with middle premotor and dorsolateral prefrontal cortex (SLF II), and the supramarginal gyrus with ventral premotor cortex (SLF III; Makris and others 2005; Schmahmann and Pandya 2006). In monkeys and humans, the intraparietal sulcus subdivides the PPC in a superior and inferior parietal lobule. The intraparietal sulcus contains several areas whose response properties are relevant for priority coding: the anterior (AIP), middle (MIP), ventral (VIP), and lateral intraparietal area (LIP; Caminiti and others 2010; Colby and Goldberg 1999). Other areas within the FPAN whose functional characteristics are suggestive of priority coding are parietal areas 7a and 7b, situated in the inferior parietal lobule, and the frontal eye field (FEF).

Priority Coding in the FPAN of the Monkey

Areas lying in the intraparietal sulcus support sensory-motor transformations that are relevant for the programming of reaching (MIP), grasping (AIP), and eye movements (LIP; Colby and Goldberg 1999). Feature-independent coding is a widespread property of neurons situated in these areas and the neighboring area 7a. Evidence for feature-independent coding is the observation that the response of many parietal neurons is driven by inputs from different sensory modalities (Colby and Duhamel 1991; Gottlieb 2007). Thus, although some MIP cells respond to isolated visual or somatosensory stimulation, many others are activated by concurrent somatosensory and visual inputs during active reaching or looking. VIP cells respond to moving visual stimuli as well as to somatosensory stimulation. Such bimodal responses appear to be absent in LIP cells, as these mainly discharge in response to visual stimulation; however, even these neurons are modulated by signals from other modalities and exhibit enhanced responses when an auditory cue correctly predicts the position of a saccade target (Cohen and others 2004). A further argument for feature-independent coding is the observation that only a few parietal cells show selective responses to a specific stimulus. For example, only 14% of area 7a neurons are color selective, with the majority showing unselective responses

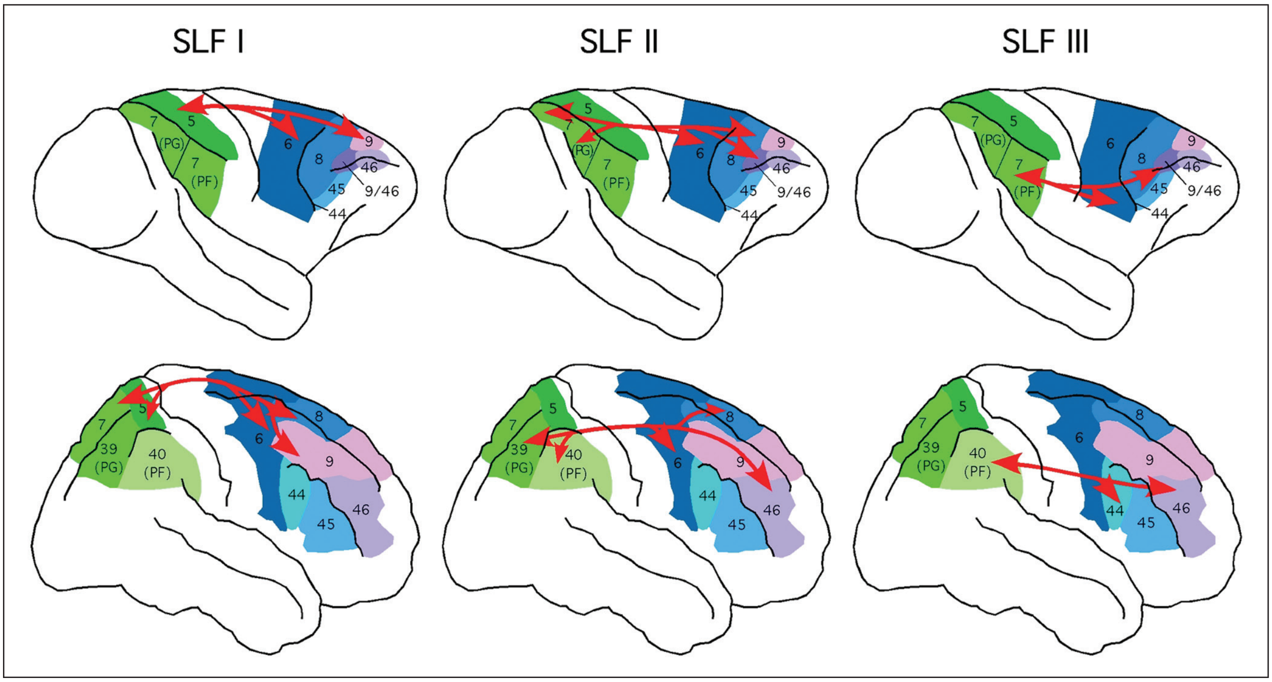

Figure 2. Comparison of the frontal and parietal regions of the monkey brain (upper row) and human brain (lower row) that constitute the frontoparietal attention network (numbers indicate Brodmann areas [BA]). The red arrows depict frontoparietal connections passing through subdivisions of the superior longitudinal fasciculus (SLF I-III). Note that the human homologues of monkey areas 7a and 7b correspond to the human BA 39 (angular gyrus) and 40 (supramarginal gyrus), whereas the human BA 7 is located in the superior parietal lobe. Despite this confusing terminology, the monkey and human parietal lobes are similar in terms of anatomy and connection pattern. SLF I connects the superior parietal region with the supplementary motor area (BA 6) and with BA 8 and 9. SLF II connects the inferior parietal cortex with dorsal frontal areas 6, 8, 9, and 46. SLF III connects the supramarginal gyrus with the ventral premotor cortex. In addition to these long-range fibers, there are numerous local interconnections between adjacent areas of the parietal and frontal cortex (not depicted).

to color (Constantinidis and Steinmetz 2001). In addition, the selectivity of response is itself subject to modulation by behavioral goals. For example, LIP cells exhibit color selectivity if color provides information about the planned action but not when color is irrelevant (Toth and Assad 2002). Thus, multisensory integration and the potential to respond differently as a function of whether a stimulus conveys information that is relevant for behavior indicate that feature-independent coding is a common property of parietal neurons.

In addition to feature-independent coding, the parietal components of the FPAN show responses that are strongly modulated by attention. For example, neurons in area 7 show enhanced activity when the monkey fixates an object that it desires or when it shifts attention to a peripheral visual stimulus (Bushnell and others 1981). Similar enhancement of responses by attention is observed in LIP, in which the effect is particularly strong for abruptly appearing peripheral distracters (Gottlieb and others 1998). This observation is consistent with the interpretation that the sudden appearance of a stimulus briefly increases its saliency and captures attention in a reflexive way. Bisley and Goldberg (2003) found that the population activity of LIP neurons predicts the locus of attention, be it captured by a task-irrelevant distracter or driven by a predefined saccade target. Consistent with response-independent coding, neural activity reflected the attentional priority of a location and did not change when the monkey made no eye movement or when it directed its response elsewhere.

A distinctive characteristic of the PPC is its capacity for coding in multiple reference frames. Visual responses of cells in area 7a and LIP are modulated by eye position, suggesting a purely retinotopic reference frame (Andersen and others 1985). However, the population activity of many cells with different eye position sensitivities is unique for each head-centered location. Thus, these areas are capable of computing a head-centered reference frame, even though such a frame is not explicitly coded by single neurons. Other neurons in these areas encode the spatial position of a stimulus with reference to the head or the body (Snyder and others 1998). Finally, receptive fields of VIP cells are organized along a continuum from eye to head coordinates (Duhamel and others 1997). Together, these results show that the PPC has access to multiple reference frames, which is a crucial property for a region that is involved in transforming information coded in a sensory frame of reference into a frame that can be used for the planning of movements.

A further property of neurons in the FPAN that is important for priority coding is the integration of sensory information and top-down signals that represent the constraints of the current task. Sensory information reaches the PPC through its direct or indirect connections with the sensory cortex. Thus, the parietal area PO receives projections from the primary visual cortex and visual association cortex and projects to the intraparietal sulcus and area 7a (Felleman and Van Essen 1991). The intraparietal sulcus in turn shares reciprocal connections with the premotor and dorsolateral prefrontal cortex (Schmahmann and Pandya 2006; see Fig. 2). Consequently, the response of single cells or cell populations in the PPC shows activity related to inputs from visual and from the premotor and prefrontal cortex. For example, neurons in area 7a respond strongly when a visual target, as contrasted with a neutral stimulus, is presented inside their receptive field (Constantinidis and Steinmetz 2001). Similarly, LIP neurons are strongly driven by a stimulus presented within their receptive field that has previously been defined as saccade goal but show much weaker activity when the same stimulus requires no response (Gottlieb and others 1998). These neurons are also strongly driven by an abrupt-onset stimulus as compared with a stimulus that has been presented some time before. These properties reflect the attentional priority of stimuli that capture attention either because of their sensory quality (e.g., abrupt onset) or because they are of significance for the ongoing activity (Bisley and Goldberg 2010). Ipata and others (2006) reported that responses of LIP neurons are actively suppressed when visual distracters tend to capture attention and thus perturb the visual search for a predefined target. Such active ignorance of a conspicuous stimulus suggests that top-down signals regulate the expression of priority in the parietal cortex by inhibiting the influence of bottom-up inputs.

Similarly to the PPC, response properties of the FEF satisfy some of the criteria that characterize a priority map. Activity of FEF cells is driven by visual stimuli prior to or during the execution of a saccade, indicating that the FEF is responsible for generating saccades of different amplitudes (Bruce and Goldberg 1985). Many neurons show nonselective responses to visual stimuli and enhanced activity if a stimulus in their receptive field is a saccade target (Schall and Thompson 1999; Thompson and others 1996). In addition, FEF cell activity is modulated by attention and behavioral predispositions (Buschman and Miller 2007; Fecteau and others 2004). For example, in a difficult search task requiring monkeys to discriminate the target from visually similar distracters, the activity of FEF neurons was sensitive to stimulus features that defined the target (Bichot and Schall 1999). However, in contrast to the PPC, activity of the FEF strongly depends on visual stimulation and on the necessity to use this stimulation for the generation of saccades. Thus, the PPC has all characteristics necessary for the computation of a feature-, modality-, and response-independent priority map, the FEF is specialized for visual aspects of spatial attention.

Functional Activity of the Human FPAN

Functional neuroimaging identified several areas in the human PPC that have similar response characteristics to areas lying in the monkey intraparietal sulcus (Culham and Kanwisher 2001; Wandell and others 2007). At least some of these areas exhibit feature-independent coding, as suggested by the observation that activity of the intraparietal sulcus increases similarly to visual, auditory, and tactile stimulation (Calvert 2001; Grefkes and others 2002). A recent fMRI study has shown that shifting attention in space in expectation of a visual or an auditory target results in very similar activations of the PPC and the FEF (Smith and others 2010), supporting the conclusion gained from neurophysiology that the FPAN encodes the environment in an abstract, feature-independent manner.

Neuroimaging studies of attention often use variants of a spatial cueing paradigm (Posner 1980), a task requiring participants to detect or discriminate a stimulus presented left or right of fixation following a brief cue that summons attention to the left or right visual field (Fig. 3). In this task, detection or discrimination of the target is faster when the cue indicates its correct position (valid cue) than when it orients attention opposite the target (invalid cue; Müller and Rabbitt 1989; Posner 1980). Several neuroimaging studies attempted to disambiguate activity related to the processing of the cue from activity related to the target. These studies observed an increase of activation along the intraparietal sulcus and the FEF when participants prepare to shift their attention (Corbetta and others 2000; Hopfinger and others 2000; Kincade and others 2005). These regions show cue-driven activity whether participants direct attention to a region in space or to a specific feature of the target, suggesting that the FPAN mediates spatial and nonspatial orienting of attention (Egner and others 2008). In contrast to the PPC and the FEF, the inferior parietal lobe is preferentially activated when a stimulus of high behavioral relevance (e.g., a stimulus that possesses some target-defining properties) appears at an unexpected position (Corbetta and others 2000; Indovina and Macaluso 2007; Serences and others 2005), suggesting that this region is important for the interruption of current cognitive activity and the reorienting of attention (Corbetta and others 2008). Based on these findings, an influential theory proposed that a

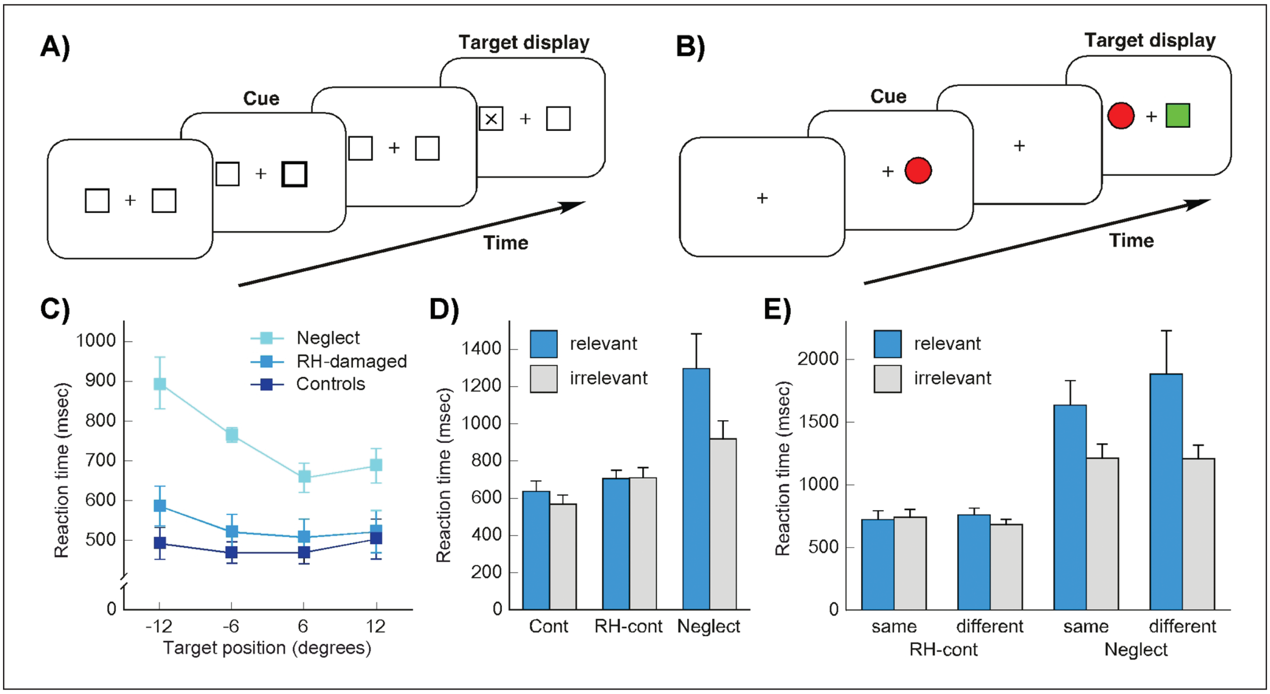

Figure 3. Patterns of contralesional slowing of patients with spatial neglect in simple detection and spatial cueing tasks. (A) Classic version of the spatial cueing paradigm. The target (letter *X*) is presented in one of two boxes that are continuously displayed on the screen. The cue is a brief brightening of one of these boxes on the same side as the upcoming target (valid cue) or on the opposite side (invalid cue). (B) Variant of the cueing task, which uses cues that either do or do not possess target-defining features. Here, the participant is asked to react to the red circle. Before the target display is presented, an identical red circle (relevant cue) or a different stimulus (e.g., a blue square; irrelevant cue) is briefly flashed to the left or right of fixation. (C) Performance of neglect patients in a simple reaction time task with stimuli presented at different peripheral locations left or right of fixation. In this task, no cues are provided. Note the characteristic increase of reaction times to stimuli presented in the left hemifield in patients with spatial neglect (data from Ptak and others 2007). (D) Performance of healthy participants (Cont), right-hemisphere–damaged patients without neglect (RH-cont), and neglect patients in the cueing task shown in B. Results show reaction times to targets in the left hemifield following an invalid cue, when the cue did (relevant cue) or did not (irrelevant cue) possess target-defining characteristics. Only neglect patients exhibit a significant relevance effect. (E) Adaptation of the cueing task shown in B using colors and words. The cue was either a colored form (e.g., red circle) or a word (e.g., *RED*), whereas the target was always a red circle. Neglect patients show a similar relevance effect when the cue and target are presented in the same modality (form cue—form target) or in different modalities (word cue—form target). No effect of relevance is observed in control patients.

dorsal attention network linking the intraparietal sulcus with the FEF is mainly responsible for voluntary orienting of attention, whereas a ventral attention network is involved in the detection of salient and unexpected events (Corbetta and others 2008; Corbetta and Shulman 2002).

The hypothesis that the PPC is primarily involved in voluntary attention appears to contradict the proposal that this region integrates bottom-up and top-down signals into a priority map mediating reflexive and voluntary aspects of attention. However, functional imaging studies attempting to differentiate between bottom-up and top-down processing or between activity related to the cue or the target base their conclusions on a technique with low temporal resolution. The buildup of the blood-oxygenation response measured with fMRI is in the order of seconds, whereas the deployment of reflexive and voluntary attention is at least 10 times faster (Müller and Rabbitt 1989). The capacity of brain-imaging techniques relying on hemodynamic responses to distinguish between sequential cognitive processes is therefore limited. This problem is of particular relevance for the assessment of the tiny temporal differences between bottom-up and top-down activity. It is therefore not surprising that cues and targets may activate the PPC, whether attention is shifted voluntarily or reflexively, which is consistent with a general importance of this region for attentional selection (Hopfinger and others 2000; Peelen and others 2004; Serences and others 2005). In addition, activity of the intraparietal sulcus is sensitive to bottom-up modulations of unattended stimuli, a finding interpreted as evidence for a priority map coding competition for attention between targets and distracters (Geng and Mangun 2009). Finally, the role of the inferior parietal lobe is not confined to the detection of salient events but also comprehends nonspatial aspects of attention such as maintaining alertness, sustaining attention, and detecting novelty (Singh-Curry and Husain 2009).

Thus, in agreement with neurophysiological studies, findings from functional brain imaging imply that the FPAN plays a decisive role in dynamic as well as sustained aspects of attention. The almost ubiquitous activation of the FPAN in these studies, the similar functional organization of the human and monkey parietal lobes, and the presence of feature-independent coding in the intraparietal sulcus support the conclusion that this region is crucial for attentional selection.

Integration of Bottom-up and Top-down Signals within the FPAN

A dominant idea in neuroscience is that sensory processing is organized hierarchically, progressing from simple to increasingly complex analysis (e.g., Felleman and Van Essen 1991). According to this view, the PPC and the FEF occupy relatively late stages of processing, which would be disadvantageous for a system that selects stimuli for further action. However, measures of latencies of visual response show that the FPAN receives information only shortly after early visual cortex and slightly in advance of inferior temporal cortex (Bisley and others 2004; Bullier 2001). This is a relevant property for a network that must be able to reorient attention to a suddenly appearing object even before this object has fully been identified.

Successful integration of sensory signals with behavioral goals entails a constant exchange of information between the FPAN, the prefrontal cortex, and sensory areas. Several findings indicate not only that the FPAN receives converging sensory information but also that representations of task constraints feed back from the premotor and prefrontal cortex into the FPAN and further down to the sensory cortex.

The FPAN Biases Responses of Sensory Cortex

Psychophysical experiments show that attention alters the subjective appearance of stimuli (Blaser and others 1999; Carrasco and others 2004). This effect suggests that a gating mechanism amplifies sensory responses when a stimulus is attended and attenuates them when it is ignored. Enhanced neural response to attended stimuli is a common property of several visual areas, as shown by single-unit (e.g., Moran and Desimone 1985; Motter 1994) and neuroimaging studies (e.g., Kastner and others 1999). Recent studies recording cell activity simultaneously in different cortical areas suggest that the FPAN is the origin of these biasing responses. For example, attention significantly modulates activity in LIP and area MT (a visual area processing motion information), but the modulation of responses begins earlier in the former than the latter area (Saalmann and others 2007). In addition, spikes registered from MT neurons closely follow spikes generated by LIP neurons. Such temporal contingency of activity suggests that LIP is the origin of attentional enhancement of MT neurons. In a similar vein, Moore and Armstrong (2003) showed that electric stimulation of FEF neurons enhances visual responses of neurons in extrastriate area V4 that have retinotopically corresponding receptive fields, whereas stimulation of noncorresponding sites attenuates V4 activity. Both studies indicate that the FPAN sends direct or indirect signals to sensory areas and thus modulates their activity according to the demands of the task. In addition, simultaneous measures of neural activity in areas belonging to the FPAN show that sensory-driven and goal-driven signals are communicated between the prefrontal and parietal cortex through this network. In a study by Buschman and Miller (2007), monkeys performed a search task in which the target was either detected without effort because it "popped out" from the distracters or was easily confounded with the distracters and therefore had to be searched for serially. Simultaneous recordings of neural activity revealed that in the pop-out task LIP activity predicted the location of the target approximately 40 ms prior to activity of FEF and prefrontal neurons, whereas in the difficult serial search task, this pattern was reversed. Thus, when attention is driven by perceptual features (as in the pop-out task), information within the FPAN is transmitted from posterior to anterior regions, whereas in a task requiring controlled processing, information spreads in the reverse direction. Such rapid shifts of activity between prefrontal and parietal regions are difficult to capture with functional brain imaging. However, a recent electrical neuroimaging study examined the sources of cortical activity in humans executing saccades in a visual search task, which triggered many error saccades directed to a distracter stimulus (Ptak and others 2011; Fig. 4). A common finding of electrophysiological studies is that the P1 component of the evoked potential is modulated by spatial attention. This has been interpreted in terms of a sensory gain-control mechanism that facilitates sensory processing by increasing the signal-to-noise ratio between targets and distracters (Hillyard and others 1998). In agreement with this hypothesis, an increased P1 component was found prior to reflexive saccades, suggesting that distracters captured attention when their saliency relative to the target was amplified. In addition, this amplification of sensory information was predicted by shifts of activity between the inferior

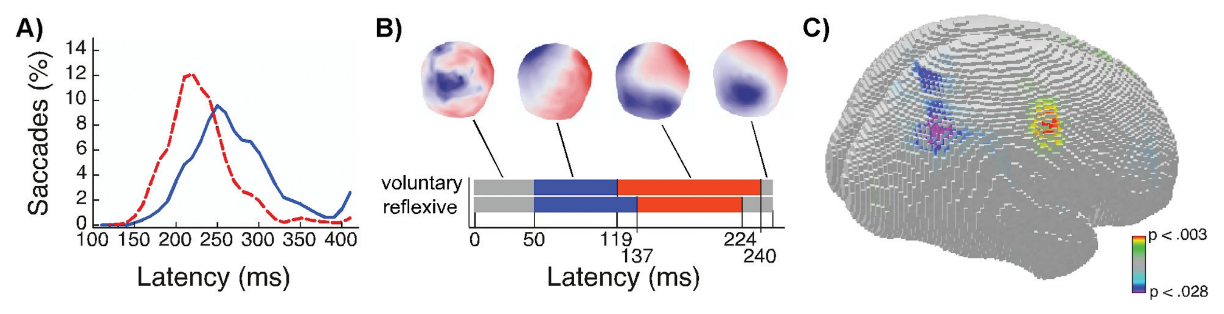

Figure 4. Electrocortical activity in the frontoparietal attention network predicts reflexive and voluntary attention. Participants executed saccades to colored targets presented in the visual periphery while attempting to inhibit reflexive glances to abruptly appearing distracters. Despite the instruction to disregard the distracter, the latter captured approximately 30% of all eye movements, suggesting a purely reflexive capture of attention. (A) Reflexive saccades (red) have a different distribution of saccade latency than voluntary saccades (blue), the latter being on average ˜30 ms slower. (B) A pattern analysis identifies four stable topographies of the electric field at the scalp. Compared with voluntary saccades, reflexive saccades are associated with prolonged processing between 50 and 137 ms (blue) and shortened processing between 137 and 224 ms (red). (C) The current sources predicting the difference in electric field topography observed between ˜120 and 140 ms after stimulus presentation are localized in the inferior parietal lobe and the ventral frontal eye field. These differences between voluntary and reflexive saccades occur well before initiation of the eye movement and are therefore not explained by motor activity associated with saccade execution. Modified figure reprinted with permission from John Wiley & Sons.

parietal lobe and the ventral FEF approximately 100 ms before the onset of the saccade. These findings support the idea that variations of activity in anterior and posterior parts of the FPAN determine whether attentional selection is triggered by sensory-driven or by goal-driven processes.

Working Memory Contents Bias Representations in the FPAN

Many tasks probing spatial attention require active maintenance of information relevant for successful performance in working memory. Neurophysiological (Fuster 2001; Miller and Cohen 2001), neuroimaging (Carlson and others 1998; Owen and others 1999), and lesion studies (D'Esposito and Postle 1999; Ptak and Schnider 2004) agree on the importance of the dorsolateral prefrontal cortex for the maintenance and mental manipulation of memory contents. Based on task requirements and abstract representations of actions, the prefrontal cortex generates templates of relevant stimuli and actions, maintains them in a transient form until the adequate response has been formulated, and protects them against distracting influences (Fuster 2001). The cortical areas that are most important for the working memory component of action planning are Brodmann areas 8, 9, and 46, which share extensive reciprocal connections with the superior and inferior parietal cortex (Miller and Cohen 2001; Schmahmann and Pandya 2006).

The effect of representations held in working memory on function of the FPAN has only recently been examined. fMRI studies have shown that an increased working memory load leads to enhanced sensory processing of visual distracters presented during a concurrent attention task (de Fockert and others 2001; Kelley and Lavie 2011), suggesting that working memory protects the primary task from distracting information. Although in these studies the working memory task primarily activated the lateral prefrontal and premotor cortex, significant activity was also measured in the PPC, suggesting that interactions between the prefrontal cortex and visual cortex are mediated by the FPAN. In fact, similarly to the prefrontal cortex, the intraparietal sulcus shows increased activity when items have to be maintained in working memory during a delay period. However, in contrast to the latter, delay-activity in prefrontal area 46 not only is associated with online maintenance of information but also predicts whether successful inhibition of distracting information has been achieved (Sakai and others 2002).

Together with the neuroimaging findings reported in the previous section, these results suggest that working memory contents bias sensory representations in the FPAN. The intraparietal region is activated when sensory information acts as a reorienting signal, such as when a spatial cue directs attention to the position of an upcoming target. It now becomes clear that this region is also strongly involved when relevant information has to be maintained in working memory. These results imply that the FPAN is a site of convergence and integration of sensory signals and working memory contents, whereas the maintenance of action plans and the prioritization of behaviorally relevant information over irrelevant sensory distracters rely on cognitive control signals originating in the prefrontal cortex and spreading through the FPAN.

Breakdown of the FPAN

Focal damage or dysfunction of the FPAN may result in Bálint syndrome, spatial extinction, or spatial neglect, which are characterized by major disorders of spatial attention. Experimental investigation of these syndromes constitutes a hard test for the hypothesis that the FPAN is critical for the computation of attentional priority.

Lesion studies often reveal dissociations between patterns of impairment and thus provide a logical argument for the fractionation of a global function into independent subfunctions. The first issue that such studies can address is what effect damage to the priority map has on attentional selection. Bálint syndrome results from bilateral damage to the PPC and is characterized by oculomotor disturbances, impaired reaching under visual guidance, and a dramatic limitation of spatial attention (Bálint 1909; Rafal 1997). A restricted window of attention makes it impossible for these patients to consciously perceive more than one object at a time. Shifting attention between different objects is slow and disorganized, and localization of stimuli in the visual or auditory modality is very poor (Phan and others 2000). In addition, Bálint patients may confound the features of two neighboring stimuli (e.g., they may report a red L when shown a red T and a green L), a phenomenon known as illusory conjunctions (Cohen and Rafal 1991; Friedman-Hill and others 1995; Valenza and others 2004). These devastating consequences of PPC damage indicate that this region is of central importance for attentional selection, the computation of coherent object representations based on the integration of multiple features, and the coding of space in coordinates that enable the programming of eye, reaching, and grasping movements. As outlined in previous paragraphs, these are the principal characteristics of a priority map. Thus, in agreement with neurophysiological studies, these findings suggest that the computation of a priority map of the environment relies heavily on the PPC.

Another line of evidence supporting the claim that attentional selection depends on the computation of priority comes from patients with spatial extinction and hemispatial neglect. In spatial extinction, a brief stimulus presented contralateral to the brain damage fails to reach consciousness when shown simultaneously with an ipsilesional stimulus. An influential hypothesis postulates that spatial extinction is the result of a biased competition for attentional selection (Duncan and others 1997). This hypothesis is supported by the finding that some perceptual factors (e.g., visual similarity between the two items; Ptak and Schnider 2005; Ward and others 1994) affect the degree of extinction. However, several studies have also shown that extinction is critically influenced by task constraints and expectations. Thus, in one study, extinction was diminished when the two stimuli represented objects (e.g., a bottle and a glass) that were spatially arranged so that they could be used together (e.g., the bottle being oriented as if one was pouring water in a glass), suggesting that the action relation between the two items critically affects attentional selection (Riddoch and others 2003). Another study found that a patient cued to attend to the color of two stimuli showed significantly less extinction when subsequently reporting their color than when he was unexpectedly asked to report their form, showing that extinction was influenced by the expectations of the patient (Ptak and others 2002).

Similarly to extinction, bottom-up and top-down factors modulate the deficits of attention observed in spatial neglect. Neglect is characterized by the failure to report or to act toward stimuli presented on the side contralateral to the damaged hemisphere, whether these are presented in the visual, auditory, or tactile modality. Patients with neglect exhibit a strong attentional bias toward stimuli in their preserved visual field and severely impaired reorienting of attention to contralesional stimuli (Fig. 3; Posner and others 1987). Several findings suggest that these attentional deficits reflect a bias in the parietal priority map (Pouget and Driver 2000). For example, the reorienting deficit may be observed whether patients shift their attention within the same modality (Morrow and Ratcliff 1988) or between modalities (Golay and others 2005), a finding suggesting feature-independent coding. Also, neglect patients show unilateral deficits in feature binding, which become manifest when they search for a target defined by the combination of two features (Eglin and others 1989; Ptak and Valenza 2005). Although they do not necessarily report illusory conjunctions, their search times for contralesional targets are disproportionately increased in conjunction tasks. Moreover, whereas early studies suggested that neglect patients orient their attention in a reflexive manner toward ipsilesional stimuli irrespective of their relevance for the current task (e.g., D'Erme and others 1992), more recent evidence has shown that the ipsilesional bias is significantly influenced by the relevance of the stimulus: When a stimulus shares task-relevant properties with the target, it captures attention easier than when all of its features are irrelevant for the task (Ptak and Golay 2006; Ptak and Schnider 2006). This effect is contingent on the representation of task relevance and cannot be explained by low-level factors such as the visual similarity between target and distracter (Fig. 3). Together, these findings indicate that neglect is the consequence of partial damage to a modality-independent representation of space encoding perceptual and task-related signals—in other words, the priority map of the FPAN.

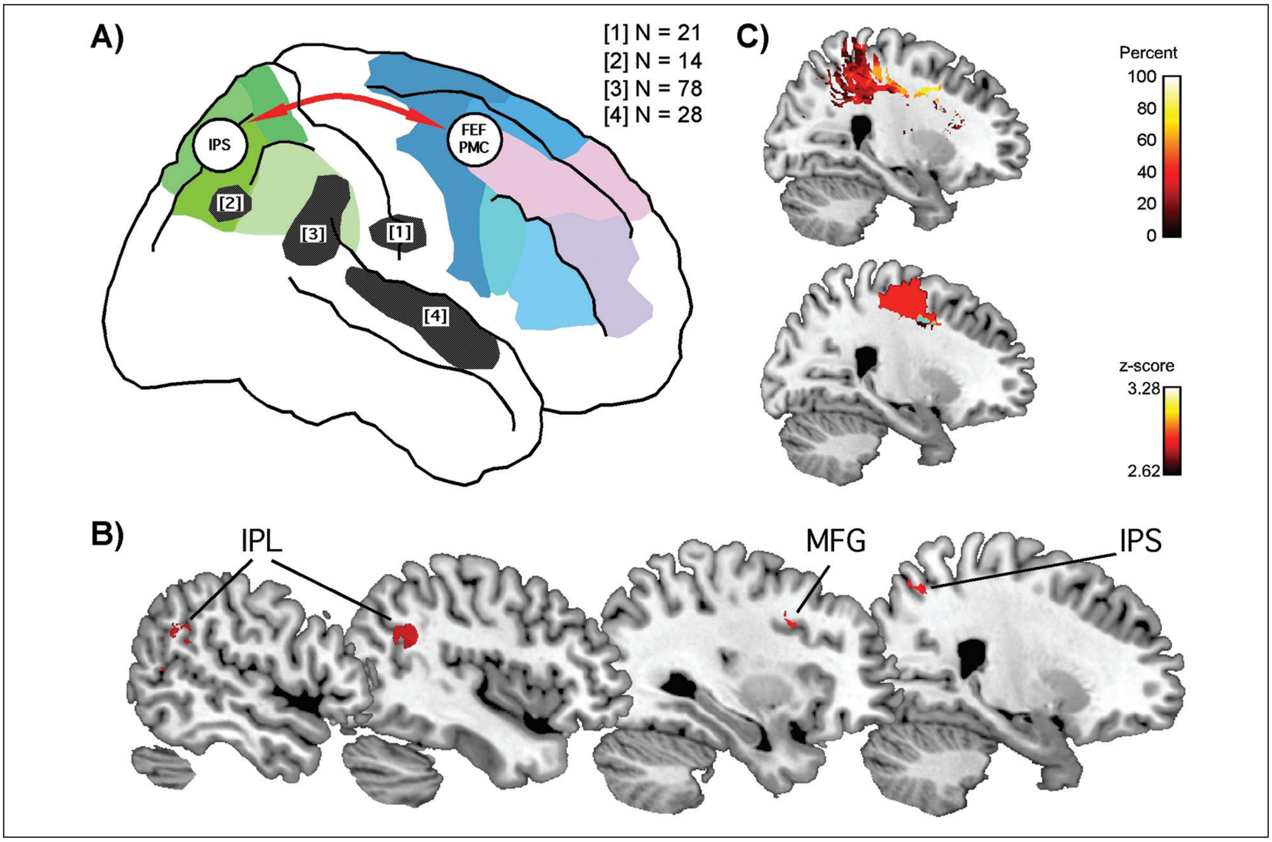

Figure 5. The frontoparietal attention network and spatial neglect. (A) Damage resulting in spatial neglect, as identified in lesion-overlap studies, is confined to the perisylvian cortex. It appears to spare the areas of activation identified by functional imaging studies of spatial attention, which are the intraparietal sulcus (IPS) and dorsal premotor cortex (PMC) including the frontal eye field (FEF). Gray areas show regions of maximal overlap in four lesion-overlap studies of spatial neglect (*Ns* indicate the number of neglect patients examined): [1] Doricchi and Tomaiuolo (2003); [2] Mort and others (2003); [3] Golay and others (2008); [4] Karnath and others (2004). (B) Areas of damage associated with spatial neglect as compared with right-hemisphere–damaged patients without neglect when a region-of-interest analysis is employed. Out of eight regions of interest, only the inferior parietal lobe, the intraparietal sulcus, and the middle frontal gyrus are significant predictors of spatial neglect. (C) The effect of task relevance on spatial orienting depends on the frontoparietal network. In neglect patients with damage to the dorsal premotor cortex, the FEF and the superior longitudinal fasciculus ipsilesional distracters impair contralesional shifts of attention regardless of their relevance for the current task. In contrast, patients with sparing of these regions are impaired only when distracters are task relevant. A lesion subtraction between these two groups of neglect patients (upper figure) and voxel-based lesion-symptom mapping (lower figure) independently confirm the importance of the frontoparietal attention network for this effect of task relevance. Modified figure reprinted with permission from the Society for Neuroscience.

However, when one compares results of neuroimaging studies with lesion studies of spatial neglect, one puzzling finding appears to challenge this conclusion: Whereas functional neuroimaging regularly reveals activations of the PPC and dorsal premotor cortex in tasks requiring the shifting of attention, lesion studies show that the critical damage underlying spatial neglect concerns more ventral regions, comprising the inferior parietal lobe, the temporal-parietal junction, and the superior temporal gyrus (Fig. 5A; Golay and others 2008; Karnath and others 2004; Mort and others 2003). How could these conflicting findings be reconciled? One possibility is that although it is structurally intact, the FPAN may nevertheless be functionally impaired (He and others 2007). Alternatively, the lesion-subtraction approach, which focuses on the critical region characterizing spatial neglect, may fail to identify areas that are not systematically damaged yet are important for specific functions. Neglect is a heterogeneous disorder that may affect attentional, intentional, or representational mechanisms to different degrees and as a function of whether the lesion extends into parietal, temporal, or prefrontal cortex (Milner and McIntosh 2005). A recent lesion-symptom mapping study examined which of eight regions of interest (including the intraparietal sulcus and FEF) predicts neglect patients' deficits of attention in a spatial cueing task (R. Ptak and A. Schnider unpublished work).

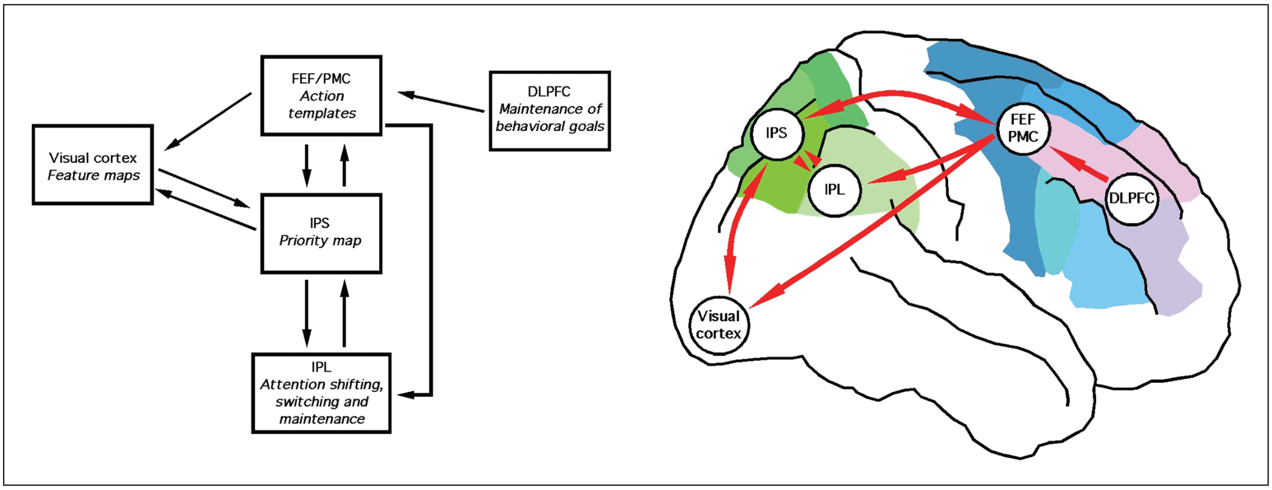

Figure 6. A model of attentional selection based on the computation of priority in the frontoparietal attention network (left) and its anatomical implementation (right). Feature maps computed in the sensory cortex and current behavioral goals as well as abstract representations of associated actions (action templates) generated in the prefrontal and premotor cortex (PMC) feed into the parietal priority map. The dorsolateral prefrontal cortex (DLPFC) maintains behavioral goals in working memory and protects them from distracting information. The inferior parietal lobe (IPL) initiates shifts of attention and maintains attention on the relevant stimulus. Attentional selection of the relevant stimulus is thus the result of complex functional interactions between frontal and parietal brain regions.

A comparison of the neglect group to control patients without neglect revealed that damage to the middle frontal gyrus, the inferior parietal lobe, and the intraparietal sulcus was a critical predictor of the occurrence of neglect (Fig. 5B). In addition, the intraparietal sulcus was the only region that also predicted the extent of contralesional slowing, the speed of attentional reorienting following an ipsilesional cue, and the degree to which reorienting was modulated by stimulus relevance. These findings strongly support the contention that the intraparietal sulcus is critical for stimulus selection and the deployment of spatial attention. The same data set provided evidence that the FPAN is crucially involved in the processing of task-selective signals, as damage to the FEF, the middle frontal gyrus, and the SLF was correlated with the degree to which a behaviorally relevant stimulus captured attention of neglect patients (Ptak and Schnider 2010). This finding is reminiscent of previous reports studying the involvement of the SLF in spatial neglect (Doricchi and Tomaiuolo 2003; Thiebaut de Schotten and others 2005) and suggests that an intact SLF is necessary for the transmission of task-related signals from premotor regions to the PPC and inferior parietal lobe.

Conclusions

Neurophysiological, neuroimaging, and neuropsychological studies provide conclusive arguments for a model of attentional selection based on the computation of priority in a network comprising several frontal and parietal areas (Fig. 6). The findings presented in this review support the hypothesis that the FPAN integrates bottom-up representations of perceptual features and top-down task-selective signals generated in the premotor and dorsolateral prefrontal cortex. They show that the FPAN biases sensory responses in upstream areas and is itself biased toward specific stimuli or actions through signals maintained in working memory. And they suggest that the PPC and premotor cortex including the FEF closely interact with the inferior parietal lobe, which is involved in sustained and dynamic aspects of attention.

The definition of attentional priority proposed in this article goes substantially beyond previous descriptions of saliency or priority computations in the LIP (Bisley and Goldberg 2010), FEF (Fecteau and Munoz 2006), or ventral stream areas such as V4 (Mazer and Gallant 2003; Reynolds and Chelazzi 2004). It is probable that no single neuron in the PPC exhibits all functional features characterizing the priority map. The parietal priority map must therefore rely on population activity of neurons distributed in adjacent areas of the PPC, but how these signals are integrated into a unique response is not known. Computational modeling of priority proposes biologically plausible models of attention (Itti and Koch 2001); however, it has yet to be shown how these computations are implemented in the complex neuronal circuitry of the human brain. Although we are far from a complete understanding of the brain's solution of the criterion problem, we have strong evidence that it emerges from complex interactions between cortical areas constituting the FPAN.

Acknowledgments

The author is indebted to Armin Schnider, René Müri, and Laetitia Golay for their contributions to much of the work described in this article.

Declaration of Conflicting Interests

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

Funding

The author disclosed receipt of the following financial support for the research and/or authorship of this article: Studies presented in this article were supported by grants from the Swiss National Science Foundation, the De Reuter Foundation, and the Schmidheiny Foundation.

References

Andersen RA, Essick GK, Siegel RM. 1985. Encoding of spatial location by posterior parietal neurones. Science 230:456–8.

Bálint R. 1909. Seelenlähmung des ‘Schauens,’ optische Ataxie, räumliche Störung der Aufmerksamkeit. Msschr Psychiat Neurol 25:51–81.

Bichot NP, Schall JD. 1999. Effects of similarity and history on neural mechanisms of visual selection. Nat Neurosci 2(6):549–54.

Bisley JW, Goldberg ME. 2003. Neuronal activity in the lateral intraparietal area and spatial attention. Science 299:81–6.

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

Bisley JW, Krishna BS, Goldberg ME. 2004. A rapid and precise on-response in posterior parietal cortex. J Neurosci 24(8):1833–8.

Blaser E, Sperling G, Lu Z-L. 1999. Measuring the amplification of attention. Proc Natl Acad Sci U S A 96:11681–6.

Bruce CJ, Goldberg ME. 1985. Primate frontal eye fields. I. Single neurons discharging before saccades. J Neurophysiol 53(3):603–35.

Bullier J. 2001. Integrated model of visual processing. Brain Res Rev 36:96–107.

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.

Bushnell MC, Goldberg ME, Robinson DL. 1981. Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. J Neurophysiol 46(4):755–72.

Calvert GA. 2001. Crossmodal processing in the human brain: insights from functional neuroimaging studies. Cereb Cortex 11(12):1110–23.

Caminiti R, Chafee MV, Battaglia-Mayer A, Averbeck BB, Crowe DA, Georgopoulos AP. 2010. Understanding the parietal lobe syndrome from a neurophysiological and evolutionary perspective. Eur J Neurosci 31(12):2320–40.

Carlson S, Martinkauppi S, Rämä P, Salli E, Korvenoja A, Aronen HJ. 1998. Distribution of cortical activation during visuospatial n-back tasks as revealed by functional magnetic resonance imaging. Cereb Cortex 8:743–52.

Carrasco M, Ling S, Read S. 2004. Attention alters appearance. Nat Neurosci 7(3):308–13.

Cohen A, Rafal RD. 1991. Attention and feature integration: illusory conjunctions in a patient with a parietal lobe lesion. Psych Sci 2(2):106–10.

Cohen YE, Cohen IS, Gifford GW. 2004. Modulation of LIP activity by predictive auditory and visual cues. Cereb Cortex 14:1287–301.

Colby CL, Duhamel JR. 1991. Heterogeneity of extrastriate visual areas and multiple parietal areas in the macaque monkey. Neuropsychologia 29(6):517–37.

Colby CL, Goldberg ME. 1999. Space and attention in parietal cortex. Ann Rev Neurosci 22:319–49.

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.

Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL. 2000. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nat Neurosci 3:292–7.

Corbetta M, Patel G, Shulman GL. 2008. The reorienting system of the human brain: from environment to theory of mind. Neuron 58:306–24.

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

Culham JC, Kanwisher NG. 2001. Neuroimaging of cognitive functions in human parietal cortex. Curr Opin Neurobiol 11(2):157–63.

D’Erme P, Robertson I, Bartolomeo P, Daniele A, Gainotti G. 1992. Early rightwards orienting of attention on simple reaction time performance in patients with left-sided neglect. Neuropsychologia 30(11):989–1000.

D’Esposito M, Postle BR. 1999. The dependence of span and delayed-response performance on prefrontal cortex. Neuropsychologia 37:1303–15.

de Fockert JW, Rees G, Frith CD, Lavie N. 2001. The role of working memory in visual selective attention. Science 291:1803–6.

Doricchi F, Tomaiuolo F. 2003. The anatomy of neglect without hemianopia: a key role for parietal-frontal disconnection? NeuroReport 14(17):2239–43.

Duhamel JR, Bremmer F, BenHamed S, Graf W. 1997. Spatial invariance of visual receptive fields in parietal cortex neurons. Nature 389(6653):845–8.

Duncan J, Humphreys G, Ward R. 1997. Competitive brain activity in visual attention. Curr Opin Neurobiol 7:255–61.

Egeth HW, Yantis S. 1997. Visual attention: control, representation, and time course. Ann Rev Psychol 48:269–97.

Eglin M, Robertson LC, Knight RT. 1989. Visual search performance in the neglect syndrome. J Cogn Neurosci 1(4):372–85.

Egner T, Monti JM, Trittschuh EH, Wieneke CA, Hirsch J, Mesulam MM. 2008. Neural integration of top-down spatial and feature-based information in visual search. J Neurosci 28(24):6141–51.

Fecteau JH, Bell AH, Munoz DP. 2004. Neural correlates of the automatic and goal-driven biases in orienting spatial attention. J Neurophysiol 92:1728–37.

Fecteau JH, Munoz DP. 2006. Salience, relevance, and firing: a priority map for target selection. Trends Cogn Sci 10(8):382–90.

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

Friedman-Hill SR, Robertson LC, Treisman A. 1995. Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. Science 269:853–5.

Fuster JM. 2001. The prefrontal cortex—an update: time is of the essence. Neuron 30:319–33.

Geng JJ, Mangun GR. 2009. Anterior intraparietal sulcus is sensitive to bottom-up attention driven by stimulus salience. J Cogn Neurosci 21(8):1584–601.

Golay L, Hauert CA, Greber C, Schnider A, Ptak R. 2005. Dynamic modulation of visual detection by auditory cues in spatial neglect. Neuropsychologia 43(9):1258–65.

Golay L, Schnider A, Ptak R. 2008. Cortical and subcortical anatomy of chronic spatial neglect following vascular damage. Behav Brain Funct 4:43.

Gottlieb J. 2007. From thought to action: the parietal cortex as a bridge between perception, action, and cognition. Neuron 53:9–16.

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

Grefkes C, Weiss PH, Zilles K, Fink GR. 2002. Crossmodal processing of object features in human anterior intraparietal cortex: an fMRI study implies equivalencies between humans and monkeys. Neuron 35(1):173–84.

He BJ, Snyder AZ, Vincent JL, Epstein A, Shulman GL, Corbetta M. 2007. Breakdown of functional connectivity in frontoparietal networks underlies behavioral deficits in spatial neglect. Neuron 53:905–18.

Hillyard SA, Vogel EK, Luck SJ. 1998. Sensory gain control (amplification) as a mechanism of selective attention: electrophysiological and neuroimaging evidence. Phil Trans R Soc Lond B 353:1257–70.

Hopfinger JB, Buonocure MH, Mangun GR. 2000. The neural mechanisms of top-down attentional control. Nat Neurosci 3(3):284–91.

Indovina I, Macaluso E. 2007. Dissociation of stimulus relevance and saliency factors during shifts of visuospatial attention. Cereb Cortex 17:1701–11.

Ipata AE, Gee AL, Gottlieb J, Bisley JW, Goldberg ME. 2006. LIP responses to a popout stimulus are reduced if it is overtly ignored. Nat Neurosci 9(8):1071–6.

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

Karnath HO, Fruhmann Berger M, Küker W, Rorden C. 2004. The anatomy of spatial neglect based on voxelwise statistical analysis: a study of 140 patients. Cereb Cortex 14:1164–72.

Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG. 1999. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron 22(4):751–61.

Kelley TA, Lavie N. 2011. Working memory load modulates distractor competition in primary visual cortex. Cereb Cortex 21:659–65.

Kincade JM, Abrams RA, Astafiev SV, Shulman GL, Corbetta M. 2005. An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. J Neurosci 25(18):4593–604.

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

Makris N, Kennedy DN, McInerney S, Sorensen AG, Wang R, Caviness VS, and others. 2005. Segmentation of subcomponents within the superior longitudinal fascicle in humans: a quantitative, in vivo, DT-MRI study. Cereb Cortex 15:854–69.

Mazer JA, Gallant JL. 2003. Goal-related activity in V4 during free viewing visual search: evidence for a ventral stream visual salience map. Neuron 40(6):1241–50.

Miller EK, Cohen JD. 2001. An integrative theory of prefrontal cortex function. Ann Rev Neurosci 24:167–202.

Milner AD, McIntosh RD. 2005. The neurological basis of visual neglect. Curr Opin Neurol 18:748–53.

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

Moran J, Desimone R. 1985. Selective attention gates visual processing in the extrastriate cortex. Science 229:782–4.

Morrow LA, Ratcliff G. 1988. The disengagement of covert attention and the neglect syndrome. Psychobiology 16(3): 261–9.

Mort DJ, Malhotra P, Mannan SK, Rorden C, Pambakian A, Kennard C, and others. 2003. The anatomy of visual neglect. Brain 126:1986–97.

Motter BC. 1994. Neural correlates of attentive selection for color or luminance in extrastriate area V4. J Neurosci 14(4):2178–89.

Müller HJ, Rabbitt PMA. 1989. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. J Exp Psychol Hum Percept Perf 15(2): 315–30.

Owen AM, Herrod NJ, Menon DK, Clark JC, Downey SPMJ, Carpenter TA, and others. 1999. Redefining the functional organization of working memory processes within human lateral prefrontal cortex. Eur J Neurosci 11:567–74.

Pashler HE. 1998. The Psychology of Attention. Cambridge, MA: MIT Press.

Peelen MV, Heslenfeld DJ, Theeuwes J. 2004. Endogenous and exogenous attention shifts are mediated by the same large-scale neural network. NeuroImage 22(2):822–30.

Phan ML, Schendel KL, Recanzone GH, Robertson LC. 2000. Auditory and visual spatial localization deficits following bilateral parietal lobe lesions in a patient with Balint's syndrome. J Cogn Neurosci 12(4):583–600.

Posner MI. 1980. Orienting of attention. Q J Exp Psychol 32:3–25.

Posner MI, Walker JA, Friedrich FA, Rafal RD. 1987. How do the parietal lobes direct covert attention? Neuropsychologia 25(1A):135–45.

Pouget A, Driver J. 2000. Relating unilateral neglect to the neural coding of space. Curr Opin Neurobiol 10:242–9.

Ptak R, Camen C, Morand S, Schnider A. 2011. Early event-related cortical activity originating in the frontal eye fields and inferior parietal lobe predicts the occurrence of correct and error saccades. Human Brain Mapp 32(3):358–69.

Ptak R, Golay L. 2006. Temporal dynamics of attentional control settings in patients with spatial neglect. Brain Res 1092:190–7.

Ptak R, Schnider A. 2004. Disorganised memory after right dorsolateral prefrontal damage. Neurocase 10(1):52–9.

Ptak R, Schnider A. 2005. Visual extinction of similar and dissimilar stimuli: evidence for level-dependent attentional competition. Cogn Neuropsychol 22(1):111–27.

Ptak R, Schnider A. 2006. Reflexive orienting in spatial neglect is biased towards behaviourally salient stimuli. Cereb Cortex 16:337–45.

Ptak R, Schnider A. 2010. The dorsal attention network mediates orienting toward behaviorally relevant stimuli in spatial neglect. J Neurosci 30(38):12557–65.

Ptak R, Schnider A, Golay L, Müri R. 2007. A non-spatial bias favouring fixated stimuli revealed in patients with spatial neglect. Brain 130:3211–22.

Ptak R, Valenza N. 2005. The inferior temporal lobe mediates distracter-resistant visual search of patients with spatial neglect. J Cogn Neurosci 17(5):788–99.

Ptak R, Valenza N, Schnider A. 2002. Expectation-based attentional modulation of visual extinction in spatial neglect. Neuropsychologia 40:2199–205.

Rafal RD. 1997. Balint syndrome. In: Feinberg TE, Farah MJ, editors. Behavioral Neurology and Neuropsychology. New York: McGraw-Hill. p 337–56.

Reynolds JH, Chelazzi L. 2004. Attentional modulation of visual processing. Annu Rev Neurosci 27:611–47.

Riddoch MJ, Humphreys GW, Edwards S, Baker T, Willson K. 2003. Seeing the action: neuropsychological evidence for action-based effects on object selection. Nat Neurosci 6(1):82–9.

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

Sakai K, Rowe JB, Passingham RE. 2002. Active maintenance in prefrontal area 46 creates distractor-resistant memory. Nat Neurosci 5(5):479–84.

Schall JD, Thompson KG. 1999. Neural selection and control of visually guided eye movements. Ann Rev Neurosci 22: 241–59.

Schmahmann JD, Pandya DN. 2006. Fiber Pathways of the Brain. Oxford (UK): Oxford University Press.

Serences JT, Shomstein S, Leber AB, Golay X, Egeth HE, Yantis S. 2005. Coordination of voluntary and stimulus-driven attentional control in human cortex. Psychol Sci 16(2): 114–22.

Simons DJ. 2000. Attentional capture and inattentional blindness. Trends Cogn Sci 4(4):147–55.

Singh-Curry V, Husain M. 2009. The functional role of the inferior parietal lobe in the dorsal and ventral stream dichotomy. Neuropsychologia 47(6):1434–48.

Smith DV, Davis B, Niu K, Healy EW, Bonilha L, Fridriksson J, and others. 2010. Spatial attention evokes similar activation patterns for visual and auditory stimuli. J Cogn Neurosci 22(2):347–61.

Snyder LH, Grieve KL, Brotchie P, Andersen RA. 1998. Separate body- and world-referenced representations of visual space in parietal cortex. Nature 394:887–91.

Theeuwes J. 2010. Top-down and bottom-up control of visual selection. Acta Psychol 135(2):77–99.

Thiebaut de Schotten M, Urbanski M, Duffau H, Volle E, Lévy R, Dubois B, and others. 2005. Direct evidence for a parietal-frontal pathway subserving spatial awareness in humans. Science 309:2226–8.

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.

Toth LJ, Assad JA. 2002. Dynamic coding of behaviourally relevant stimuli in parietal cortex. Nature 415(6868): 165–8.

Treisman A. 1998. Feature binding, attention and object perception. Phil Trans R Soc Lond B 353:1295–306.

Treue S. 2003. Visual attention: the where, what, how and why of saliency. Curr Opin Neurobiol 13:428–32.

Valenza N, Murray MM, Ptak R, Vuilleumier P. 2004. The space of senses: impaired crossmodal interactions in a patient with Balint syndrome after bilateral parietal damage. Neuropsychologia 42:1737–48.

Wandell BA, Dumoulin SO, Brewer AA. 2007. Visual field maps in human cortex. Neuron 56(2):366–83.

Ward R, Goodrich S, Driver J. 1994. Grouping reduces visual extinction: neuropsychological evidence for weight-linkage in visual selection. Visual Cognition 1(1):101–29.Wolfe JM. 1994. Guided Search 2.0. A revised model of visual search. Psychonom Bull Rev 1(2):202–38.

Yantis S, Egeth HE. 1999. On the distinction between visual salience and stimulus-driven attentional capture. J Exp Psychol Hum Percept Perform 25(3):661–76.