CONTROL OF GOAL-DIRECTED AND STIMULUS-DRIVEN ATTENTION IN THE BRAIN

Maurizio Corbetta and Gordon L. Shulman

We review evidence for partially segregated networks of brain areas that carry out different attentional functions. One system, which includes parts of the intraparietal cortex and superior frontal cortex, is involved in preparing and applying goal-directed (top-down) selection for stimuli and responses. This system is also modulated by the detection of stimuli. The other system, which includes the temporoparietal cortex and inferior frontal cortex, and is largely lateralized to the right hemisphere, is not involved in top-down selection. Instead, this system is specialized for the detection of behaviourally relevant stimuli, particularly when they are salient or unexpected. This ventral frontoparietal network works as a 'circuit breaker' for the dorsal system, directing attention to salient events. Both attentional systems interact during normal vision, and both are disrupted in unilateral spatial neglect.

TOP-DOWN PROCESSING
The flow of information from 'higher' to 'lower' centres, conveying knowledge derived from previous experience rather than sensory stimulation.

BOTTOM-UP PROCESSING
Information processing that proceeds in a single direction from sensory input, through perceptual analysis, towards motor output, without involving feedback information flowing backwards from 'higher' centres to 'lower' centres.

Departments of Neurology, Radiology, and Anatomy and Neurobiology, Washington University School of Medicine, St Louis, Missouri 63110, USA. Correspondence to M.C. e-mail: mau@npg.wustl.edu
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Picture yourself at the Museum El Prado in Madrid while a guide explains the painting *The Garden of Earthly Delights* by the fifteenth-century Flemish painter Hieronymous Bosch (FIG. 1). Bosch depicts a fantastic, surreal and satirical world, which is in stark contrast to anything else represented until that time. The guide's words cue us to attend to different aspects of the painting, such as its colour, spatial configuration or meaning. For example, if he notes "a small animal playing a musical instrument", we can use this information to spot the rabbit playing the horn near a black-and-white dice. Knowledge and expectations allow us to focus on elements, parts or details of a visual scene that we might otherwise have missed. Cognition aids vision by enabling the brain to create, maintain and change a representation of what is important while we scan a visual scene.

At the other extreme, visual perception can be dominated by external events. Initially, our eyes might have been drawn to the more salient objects in the painting, such as the large wooden musical instrument (a lute in construction) at the centre of the scene, rather than to more subtle aspects of the painting that are discussed by the guide. An event might even distract us from the painting altogether. If an alarm system started to ring and flash in a nearby room, everyone's attention would instantly be drawn towards the source of the alarm. Unexpected, novel, salient and potentially dangerous events take high priority in the brain, and are processed at the expense of ongoing behaviour and neural activity.

In everyday life, visual attention is controlled by both cognitive (TOP-DOWN) factors, such as knowledge, expectation and current goals, and BOTTOM-UP factors that reflect sensory stimulation. Other factors that affect attention, such as novelty and unexpectedness, reflect an interaction between cognitive and sensory influences. The dynamic interaction of these factors controls where, how and to what we pay attention in the visual environment. In this review, we propose that visual attention is controlled by two partially segregated neural systems. One system, which is centred on the dorsal posterior parietal and frontal cortex, is involved in the cognitive selection of sensory information and responses. The second system, which is largely lateralized to the right hemisphere and is centred on the temporoparietal and ventral frontal cortex, is recruited during the detection of behaviourally relevant sensory events, particularly when they

Figure 1 | ***The Garden of Earthly Delights*** **by Hieronymous Bosch.** Courtesy of the Corbis Picture Library.

are salient and unattended. Here, we review the psychological, neuropsychological and physiological evidence for these two systems.

Top-down control of attention

Human observers are better at detecting an object in a visual scene when they know in advance something about its features, such as its location, motion or colour[1–5]. This facilitation depends on our ability to represent this advance information (a 'perceptual set'), and to use it to bias the processing of incoming visual information. Similarly, responses to a stimulus are quicker when subjects know in advance what type of movement they have to make (such as which arm to move or the direction of the movement — a 'motor set')[6,7]. As most studies involve the selection of both stimuli and responses, it is sensible to define perceptual and motor sets as processes that link relevant sensory information to relevant motor information. We use the more general term of 'attentional set' to define the representations involved in the selection of task-relevant stimuli and responses.

Conceptually, it is important to distinguish control signals for the generation and maintenance of an attentional set from the top-down effects of that set on the neural activity evoked by the target stimulus that the subject must detect or identify. One way to distinguish these control signals is to separate in time the neural responses to the advance information from the responses to the target stimulus. Therefore, this review focuses on studies that have isolated these preparatory control signals. Recent reviews have discussed how attentional sets modulate the neural response to a target[8,9].

Top-down signals for spatial attention. In studies of attention, advance information is typically provided in the form of a cue (for example, a small arrow) that instructs observers about some relevant aspect of the forthcoming visual scene (such as the location or direction of motion of a target stimulus). FIGURE 2a shows the results of a functional magnetic resonance imaging (fMRI) experiment in which subjects view, for two seconds, an arrow cue that tells them to direct covertly (without moving their eyes or head) their attention to a location in the periphery of the visual field[10]. The pattern of brain activation is displayed on the surface of the brain. Areas in the occipital lobe (fusiform and MT+) respond transiently to the cue, whereas areas in the dorsal posterior parietal cortex along the intraparietal sulcus (IPs) and in the frontal cortex (at or near the putative human homologue of the FRONTAL EYE FIELD, FEF) show a more sustained response. The transient response in occipital areas might reflect the sensory analysis of the cue. We know that the sustained part of the response (grey arrow) is endogenous, because it is not related to either visual stimuli or motor responses, and it is time-locked to the period in which subjects pay attention to the peripheral location. The activation is predominantly bilateral for attention to either visual field[10–12], but in a subset of parietal (ventral IPs) and frontal (FEF) areas, the response is spatially selective (stronger when attention is directed towards the contralateral visual field[12,13]). This pattern of brain activation indicates that parietal and frontal regions are involved in controlling the location of attention.

FIGURE 2c (left) shows results from other recent brain-imaging studies that have separated preparatory signals for attending to visual objects from signals that are related to the visual analysis of, detection of or response to those objects[10–12,14]. The areas most consistently activated by attention to stimulus attributes include the dorsal parietal cortex along the IPs, extending dorsomedially into the superior parietal lobule (SPL) and anteriorly towards the postcentral sulcus, and the dorsal frontal cortex at the intersection of the precentral and superior frontal sulci (the putative human FEF). During the cue period, these frontoparietal activations are sometimes accompanied by sustained activity in early occipital regions[11], but these lower-level activations are not always observed[10,14] (FIG. 2a), and might depend on the complexity of the cued information or on other factors. These findings complement an earlier body of imaging work using positron emission tomography (PET) and fMRI in which attention signals were not recorded in isolation but were mixed with signals that reflected the target stimulus and motor response. In various detection and discrimination paradigms, voluntary or endogenous visual selection most consistently activated the dorsal parietal and frontal cortex[15–21] (FIG. 2c, right, and see REF. 22).

The human parietal areas that are active during spatial attention might be homologous to areas in the monkey IPs[23], whereas the frontal area might be the human homologue of the FEF[24]. Accordingly, neurons in macaque

FRONTAL EYE FIELD
An area in the frontal lobe that receives visual inputs and produces movements of the eye.

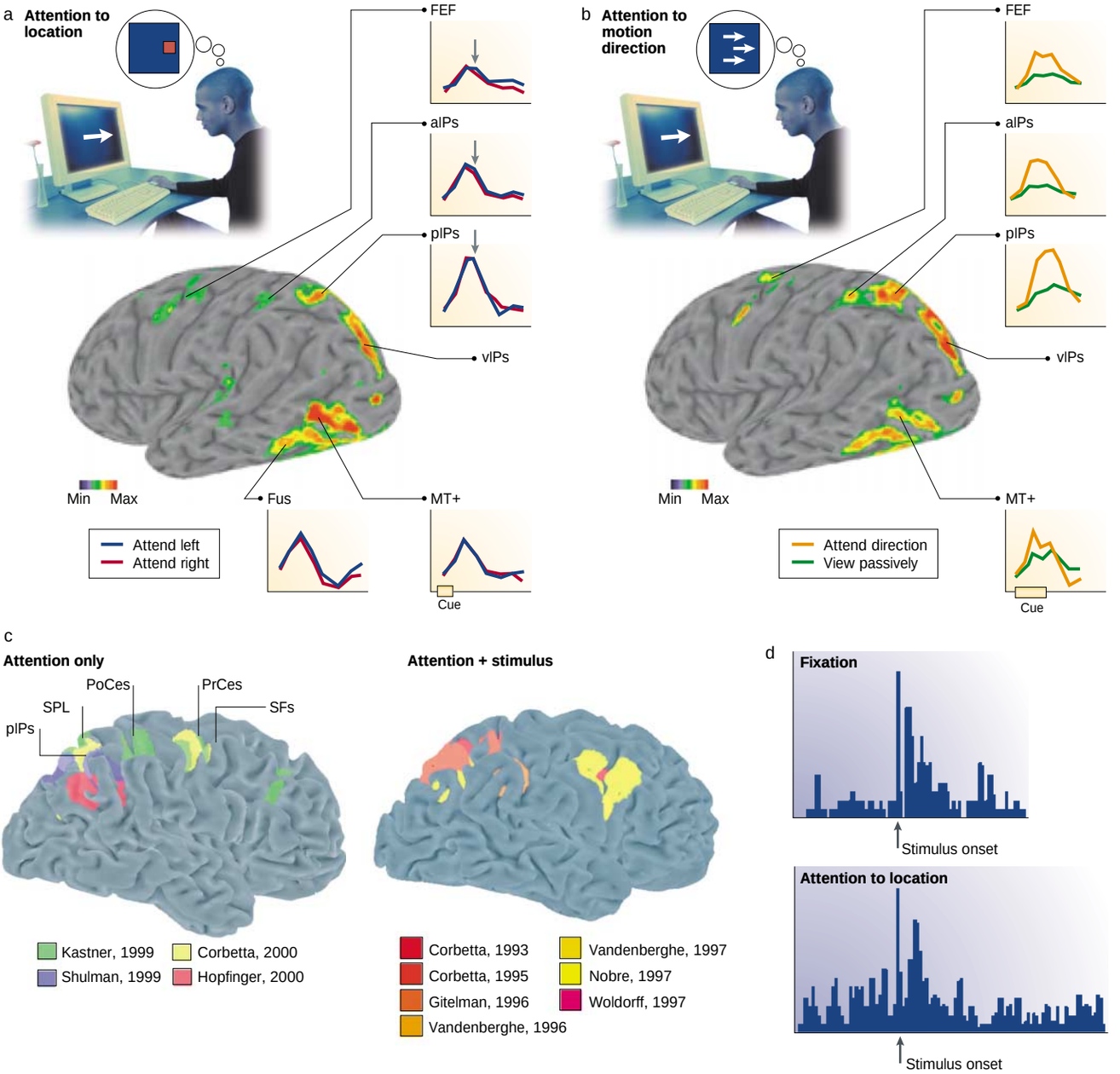

Figure 2 | **Dorsal frontoparietal network for top-down control of visual attention. a** | Human brain activity produced by attending to a location. Subjects see an arrow that cues one of two locations and covertly attend to the location indicated in preparation for a target at that location. The functional magnetic resonance imaging (fMRI) response is averaged over 13 subjects[10]. The graphs show the time course of the fMRI signal after the cue. Signals are transient in occipital regions, but sustained (grey arrow) in the parietal cortex and frontal eye field (FEF). aIPs, anterior intraparietal sulcus; Fus, fusiform cortex; MT+, middle temporal complex; pIPs, posterior IPs; vIPs, ventral IPs (junction of the vIPs and transverse occipital sulcus). **b** | Human brain activity produced by attending to a direction of motion. Subjects see an arrow that cues a direction of motion and prepare for a subsequent target moving in that direction. The response is averaged over 14 subjects[14]. The graphs contrast the response seen when the arrow cues a direction of motion with that observed when a cue instructs the subject to view the display passively. Directional cues produce sustained signals in frontal (FEF) and parietal (aIPs, pIPs) areas, but transient signals in occipital areas (MT+). **c** | Left: meta-analysis of studies of visual attention. Subjects expected a simple visual attribute, such as location[10,12] or direction of motion[14], or a more complex array[11]. Foci of activation from the expectation period are smoothed and projected onto the Visible Human Brain[117]. The area of maximal overlap between studies is in the pIPs. PoCes, postcentral sulcus; PrCes, precentral sulcus; SFs, superior frontal sulcus; SPL, superior parietal lobule. Right: meta-analysis of imaging studies of visual attention and detection (adapted with permission from REF. 22 © 1998 National Academy of Sciences, USA). The figure shows regions that are activated by attending to and detecting visual stimuli (preparatory activity has been averaged with visual- and motor-detection activity). **d** | Anticipatory activity in a macaque V3A neuron during a memory-guided task (adapted with permission from REF. 27 © 2000 The American Physiological Society). The graph shows the single-unit activity as the monkey performs two tasks while fixating the centre of the screen. In the fixation task, a small stimulus is presented peripherally and the monkey is rewarded for maintaining fixation. In the memory-guided task, the monkey has to remember the location of the stimulus and after a variable delay make a saccade to that location. Activity is increased in the memory-guided task before stimulus onset, perhaps reflecting attention to the stimulus location.

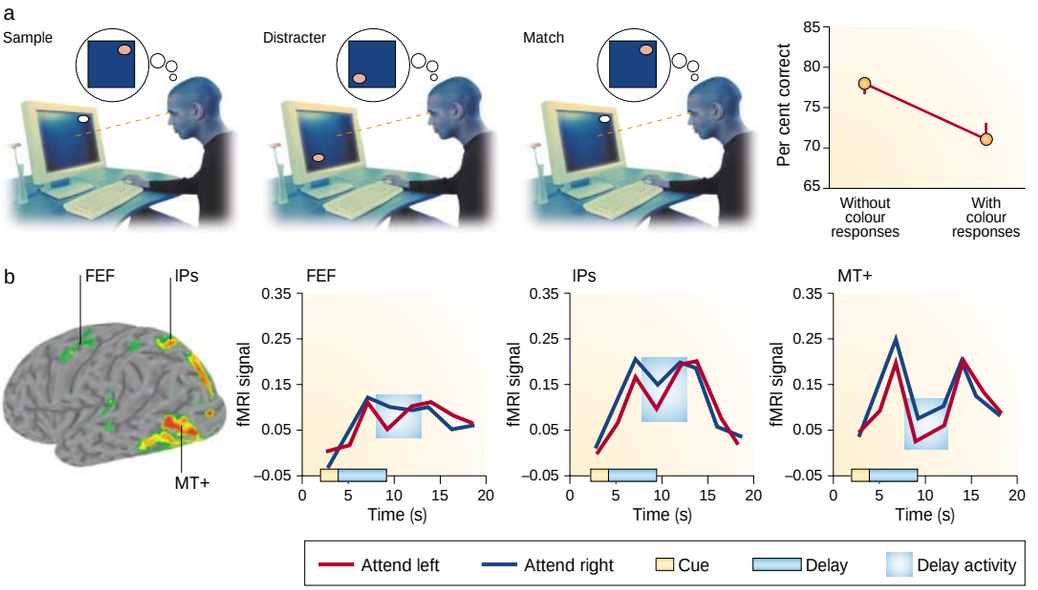

Figure 3 | **Overlap between working memory and attention. a** | In a match-to-sample task, subjects remember the location of the sample stimulus and decide after a variable delay whether it corresponds to the location of the match stimulus. Accuracy is significantly impaired when subjects have to shift attention to the distracter and report its colour ("with colour responses"). Control experiments show that this decrement is not due to increases in task difficulty. These results indicate that spatial rehearsal (maintaining a spatial location in memory) depends on spatially attending to the location (adapted with permission from REF. 36 © 2001 Elsevier Science). **b** | The dorsal frontoparietal network is active during spatial rehearsal[13]. The task is the same as that in FIG. 2a, except that subjects have to maintain attention to a peripheral location for ~7 s (2.4-s cue period + 4.7-s delay period). The functional magnetic resonance imaging (fMRI) signal remains sustained during the delay (delay activity shaded in blue) in regions of the dorsal frontoparietal system (FEF, IPs), but returns to baseline in MT+ after the sensory analysis of the arrow cue. FEF, frontal eye field; IPs, intraparietal sulcus; MT+, middle temporal complex.

frontal and parietal cortex (FEF, lateral intraparietal area (LIP), and areas 7a and V3A) show increases in baseline firing rate when the monkey anticipates the onset of a stimulus[25–27] (FIG. 2d). This prestimulus anticipatory activity could correspond to the fMRI signal that is recorded in human subjects during anticipatory attention.

These regions in dorsal parietal and frontal cortex, which respond when both human and monkey observers covertly pay attention to a peripheral location in anticipation of a stimulus, might form a network (dorsal frontoparietal network) for the control of visuospatial attention. However, they also carry neuronal signals that are related to the preparation of eye and arm movements, and to stimulus processing (see below).

Top-down signals for feature or object attention. Attending to location is just one way in which we can select relevant visual information. We can also attend to different features of an object, such as its shape, colour or direction of motion, or to objects, such as a familiar face in a crowd, which can be defined by many different features[28]. There is growing evidence that the frontoparietal cortical network that is recruited for spatial attention is also involved in other types of visual selection. FIGURE 2b shows a map of the brain activation that occurs when subjects expect to see moving stimuli. The arrow cue (as in FIG. 2a) provides advance information about the direction of motion (left or right) of a subsequent display that contains a few coherently moving dots (the target) among many randomly displaced dots (the distracters). Subjects cannot use location as a cue to find the target. Similar parietal, frontal and occipital areas are recruited by the cue as were activated by the spatial cue, and this activity is sustained only in frontal and parietal regions[14]. Interestingly, a region in the posterior IPs that is well activated by cues for motion is poorly activated by cues for colour, indicating that there is some specialization within the parietal cortex for the type of information attended[29]. Posterior parietal regions are also active when subjects switch their attention between two objects at the same location[30]. The location of these parietal regions might be different from those that are active in attending to location or direction of motion, but this will need to be confirmed by within-experiment or within-laboratory comparisons. Finally, several studies that did not specifically isolate attention signals have reported modulations in posterior parietal cortex during tasks that require the identification of features of foveal stimuli[19,31].

There is also evidence from single-unit studies for a possible role of these regions in coding an attentional set for features such as motion or colour. Neurons in area LIP show directional motion-selective activity when a monkey expects the reappearance of an object that is moving behind another one, consistent with an expectation signal for moving objects[32]. Neurons in LIP flexibly code colour information, when colour indicates a task-relevant location for an eye movement[33].

The dorsal frontoparietal network that is recruited when subjects expect to see object features other than location clearly overlaps with regions that are recruited by attending to location (FIG. 2a,b), but the exact overlap between regions recruited by different kinds of advance information is unclear, and many visual features have yet to be tested.

Maintaining attentional sets in memory. What psychological and neural mechanisms are responsible for the maintenance of attentional sets? One likely candidate is working memory, which is defined as the ability to maintain and manipulate information online in the absence of incoming sensory or motor stimulation. Attentional set and working memory mechanisms overlap functionally. For example, it is possible to maintain a memory of a visual attribute for many seconds without any apparent decrement in the precision of the visual information[34,35]. A more direct link is provided by reports that directing attention away from a location during a delay disrupts working memory for that location[36] (FIG. 3a). Therefore, spatial rehearsal, or the ability to maintain spatial information online in memory, depends crucially on spatial attention.

The parietal and frontal regions that are recruited by an attentional set (FIG. 2a–c) show sustained activation during a memory delay in which the set is maintained online for up to ten seconds[13,37] (FIG. 3b). The localization of working memory signals in dorsal frontoparietal areas is consistent with the presence of memory activity in neurons in macaque FEF and IPs[38,39]. In macaques, strong memory-related activity has also been found more anteriorly in the lateral prefrontal cortex[39], which has been considered in both species to be the main source of top-down control signals to the visual cortex[40,41]. However, in humans, the current neuroimaging evidence does not support the involvement of dorsolateral prefrontal cortex during the encoding and maintenance of a simple visual cue in a well practised task. This discrepancy might represent a species-specific difference in the neural systems that are involved in attentional control. More anterior prefrontal areas might be recruited in monkeys because of their low memory span[42]. These regions are probably recruited in humans when the task is initially learned or as the selected items become more complex or increase in number. For example, human prefrontal regions are active during the delay period of match-to-sample tasks in which a sample face is maintained over a delay period and then matched to a test face[37].

Top-down signals for attending to effectors. Our discussion so far has emphasized a role for the dorsal frontoparietal network in preparatory aspects of stimulus selection, but other results indicate that these areas are also important for response or action selection. Different regions of macaque IPs show preparatory activity that is selective for different effectors. For example, neurons in area LIP code for impending SACCADIC EYE MOVEMENTS, whereas neurons in a more medial area (parietal reach region, PRR) code for impending reaching movements[43] (FIG. 4a), and neurons in a more anterior area of the IPs code for impending grasping movements and three-dimensional objects[44]. Preparatory activity has been observed for eye movements in the FEF[45], and for arm movements in the premotor cortex[46]. Brain-imaging studies have reported both eye- and arm-related activity in the frontal cortex and IPs[47–49], although these studies did not separate preparatory signals from those involved in executing the response. More recent event-related studies have begun to isolate preparatory signals that are related to response selection in what are presumed to be corresponding human areas[50].

Because eye movements are important in stimulus selection, mechanisms for directing attention to a location might be similar to mechanisms for preparing an eye movement, as proposed by the premotor theory of attention[51]. Imaging studies that have compared covert spatial attention with overt oculomotor shifts have found strong overlap in activations of both the FEF and IPs[18,52,53] (FIG. 4b).

Top-down signals for task sets. Although stimulus and response selection can be separated in the laboratory, stimuli and responses are inextricably linked in real life. While looking at a canvas, the brain not only selects the stimuli at which to look, but also programs the eye movements with which to look at them. This close functional linkage is related to the convergence of stimulus- and response-selection signals in areas of the frontoparietal network. Neurons in LIP and FEF show signals that are related to attention, memory and eye movements[26,38,45]. However, in many circumstances, the association between stimulus and response must be learned. For instance, although the natural response to the museum alarm is flight, a firefighter will respond by actively looking for the source of a potential fire. So, a crucial aspect of attentional selection is not just the isolated selection of a stimulus or a response, but the assembly and coordination of stimulus–response associations or mappings. A recent study[54] found that online changes in the appropriate stimulus–response mapping for hand responses activated two clusters in posterior parietal cortex: one more posterior and medial, extending from the IPs into the SPL, and one more lateral, along the IPs (FIG. 4d, red regions). These regions were distinct from those involved in stimulus selection, more anteriorly in the IPs (FIG. 4d, green regions, and FIG. 2a,b). The spatial distribution of activity for stimulus selection and stimulus–(hand)-response mapping (specifically, the medial cluster) might correspond to the spatial distribution of the possibly homologous areas LIP and PRR in the macaque[54].

A change in the task that a person performs on a stimulus often changes the appropriate response (the stimulus–response mapping). Subtracting one digit from another results in a different response from that seen when adding the two digits. Performance analyses indicate that switching between task sets, particularly when they involve the same stimuli, is effortful and expensive in terms of resources and time[55,56]. For example, switching between categorizing numbers (as odd or even) or letters

SACCADIC EYE MOVEMENT
A rapid eye movement that brings the point of maximal visual acuity — the fovea — to the image of interest.

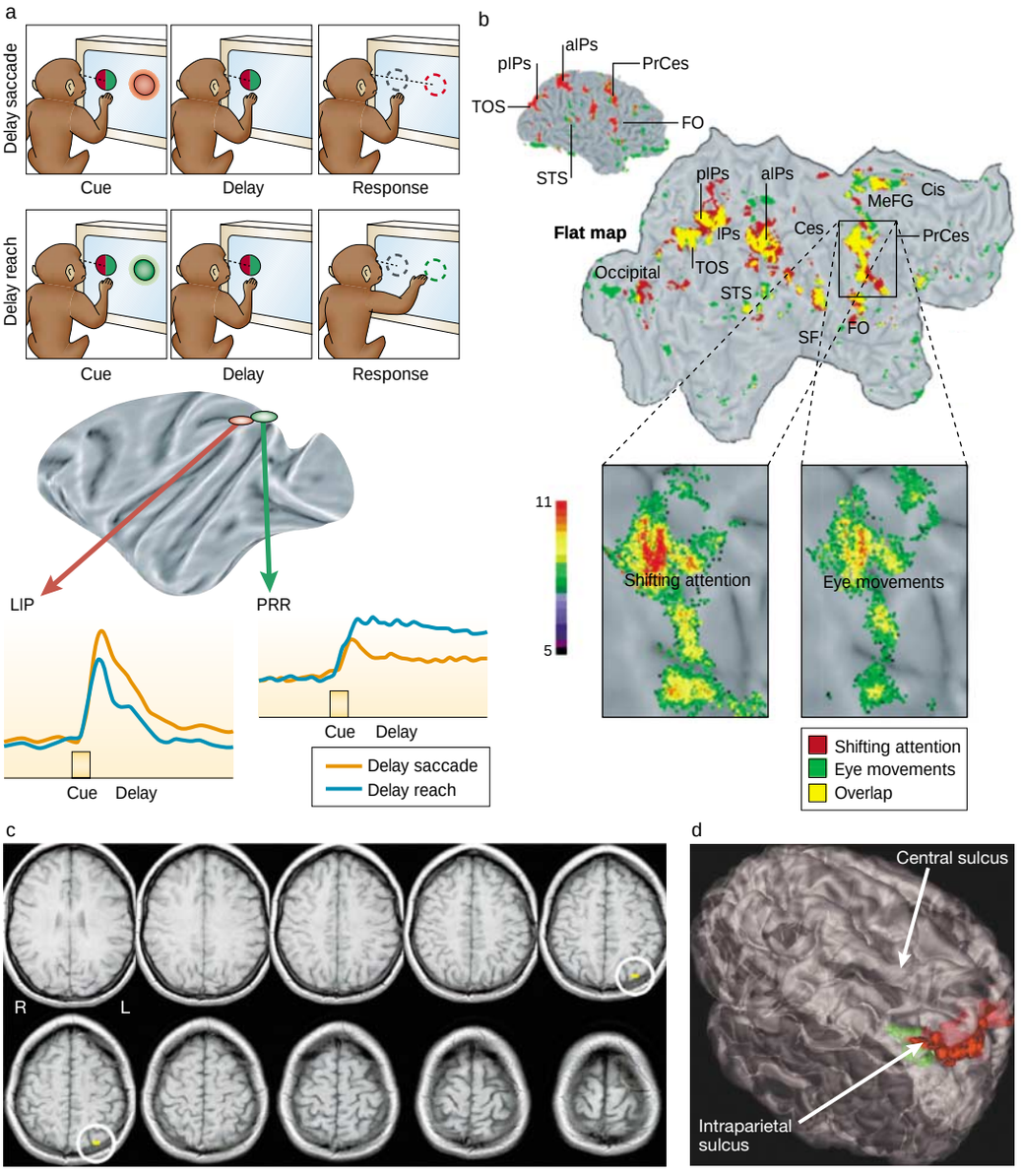

Figure 4 | **Dorsal frontoparietal network during response selection and stimulus–response mapping. a** | Response selection in the macaque intraparietal sulcus (IPs) (adapted with permission from *Nature* (REF. 43) © 1997 Macmillan Magazines Ltd). A monkey sees a brief coloured flash in the peripheral visual field that instructs either a saccadic (red cue) or pointing (green cue) movement. After a variable delay, the fixation point is turned off, and the monkey either looks at or points to the flashed location. Two areas in the IPs show effector-selective anticipatory activity during the delay. At the population level, neurons in the lateral intraparietal area (LIP) respond more strongly during eye-movement preparation, whereas neurons in a more posterior and medial region (the parietal reach region, PRR) respond more strongly during arm-movement preparation. **b** | Overlap of attention and eye-movement networks (reproduced with permission from REF. 52 © 1998 Elsevier Science). Functional magnetic resonance imaging (fMRI) activation during covert attentional (red) and overt oculomotor (green) shifts to different stimulus locations is shown for one subject. The functional data are projected onto a three-dimensional and a two-dimensional flattened representation of the subject's brain. Inset, activity in the dorsal and ventral precentral sulcus (PrCes). There is a strong overlap in frontal, parietal and temporal regions, indicating a functional relationship between the neural systems for shifting attention to locations and making eye movements. Ces, central sulcus; Cis, cingulate sulcus; FO, frontal operculum; MeFG, medial frontal gyrus; SF, sylvian fissure; STS, superior temporal sulcus; TOS, transverse occipital sulcus. **c** | Human left posterior parietal cortex is recruited during task switching (reproduced with permission from REF. 60 © 2000 Elsevier Science). An activation map is shown for a task-switching paradigm in which subjects switched between letter and number discrimination tasks in displays that contained both kinds of character. **d** | Intraparietal cortex and stimulus–response mapping (reproduced with permission from REF. 54 © 2001 Society for Neuroscience). The fMRI response in the IPs is shown during periods in which there was a change in either the stimulus–response mapping (red) or the stimulus feature that defined a task-relevant object (green). In one task (stimulus–response selection), a cue instructed subjects to respond with the left hand when they saw a triangle and with the right hand when they saw a square (or vice versa). In the other task (stimulus selection), a cue indicated whether a task-relevant object was defined by its colour or its shape.

(as vowels or consonants) that are presented simultaneously produces a decrease in performance known as a 'switch cost'[56]. Switch costs can be reduced, but not eliminated, if subjects are given sufficient time to prepare for the switch, indicating a role for preparatory processes in specifying the appropriate task set[57].

The neural bases of the preparatory processes that are involved in task switching are under investigation. Neurons in the macaque prefrontal cortex flexibly code for task-relevant information, including the appropriate stimuli and responses, and the rules that relate the two[41,58,59]. As with studies of endogenous orienting to stimuli and responses, it is important to separate preparatory signals that are involved in task switching from the signals that are evoked by performing the task. Recent studies have found that the left parietal cortex carries signals that might specify the appropriate task set in simple, practised tasks. In one experiment, subjects switched between letter and number discrimination tasks for displays that contained both kinds of character[60]. The left posterior parietal cortex (junction of the inferior parietal lobule, IPL, and the IPs) was the only area that was significantly active at the time of a switch (FIG. 4c). A second study that involved letter and number discrimination tasks reported left posterior parietal activity related to task switching both during a preparatory interval and during task performance[61]. Preparatory activity in the left posterior parietal cortex has also been reported for word cues that specified on each trial whether subjects must categorize the colour or motion of a forthcoming display with respect to a standard stimulus, whereas activity was weaker when the same dimension was cued for an entire block of trials[29]. This effect was found for both motion and colour cues, indicating that it generalizes over visual dimensions. These results indicate that, in humans, dorsal posterior parietal cortex, particularly in the left hemisphere, might be involved in assembling associations that link the appropriate stimuli and responses for a given task.

An important question for future work concerns the precise spatial relationship between parietal regions involved in task switching and those involved in selecting particular classes of stimulus or effector. As mentioned earlier, there is some evidence for spatial segregation of the mechanisms that specify stimulus–response mappings and task-relevant stimulus attributes[54].

Both stimulus and response selection involve activation of dorsal posterior parietal (IPs) and frontal (FEF) regions in monkey and human brains. Functional specialization in different subregions is expected on the basis of macaque anatomy, and mapping these specializations is an important goal for future research. However, the current evidence points to the generality of recruitment of dorsal frontoparietal regions during the top-down cognitive selection of stimuli and actions[19]. In addition, regions in the left posterior parietal cortex are recruited during the establishment or switching of task sets or stimulus–response associations for a wide variety of stimuli and perhaps responses. These results indicate that a primary function of the frontoparietal network is to link relevant sensory representations to relevant motor maps, and dynamically to control these links. Although experiments in the macaque indicate that the frontal cortex has an important role in attentional executive control, the parietal cortex has a crucial role in the human brain when the stimulus–response associations that are involved in a particular task set are simple or well learned, and can be prepared in advance.

Stimulus-driven control of attention

Often, we find ourselves drawn to stimuli that differ from the background ("very intense, voluminous, or sudden" in William James's terms[62]).

> "In involuntary attention of the immediate sensorial sort the stimulus is either a sense-impression, very intense, voluminous, or sudden; or it is an instinctive stimulus, a perception which, by reason of its nature rather than its mere force, appeals to some of our congenital impulses … these stimuli differ from one animal to another, and what most of them are in man: strange things, moving things, wild animals, bright things, pretty things, metallic things, blows, blood, etc."[62]

A red poppy will stand out in a field of green grass more than in a field of coloured tulips. Our ability to see the poppy depends on its difference from the distracters (the grass or the tulips) and on the relative similarity of the distracters (it is easier to spot the poppy if the tulips are all orange than if they are red, orange, purple and blue)[63].

The attention-grabbing effect of a sudden or distinctive stimulus can be shown by flashing a light at a location (a sensory cue) and measuring how long it takes for a subject to respond to a target stimulus at that location compared with another location in the visual field. Even when the sensory cue provides no information about the location of the forthcoming target, the cue facilitates detection and discrimination at the cued location. The facilitation produced by sensory cues appears more rapidly (within 50 ms) than that produced by cognitive cues[64,65]. Sensory cues also cause a prolonged inhibition of processing at the cued location (called 'inhibition of return') after the early facilitation[64,66]. These differences in the effects of cognitive and sensory cues have led to the idea of a functional distinction between sensory (exogenous) and cognitive (endogenous) orienting systems[67].

However, in real life, the salience of objects is strongly influenced by their behavioural relevance. For instance, if we are searching for a friend wearing a red hat in a crowd, we will notice more often people wearing red clothes, and less often people wearing clothes of other colours. The sensory (or bottom-up) distinctiveness of red objects interacts with the ongoing cognitive (top-down) goal of finding a red object. Early studies proposed that distinctive sensory stimuli attract attention automatically, independently of intention or of the current task, but more recent studies have revised this idea. Uninformative sensory stimuli are not effective in drawing attention when we are carefully attending to a specific location rather than diffusely attending over a

broad spatial extent[68]. Also, distinctive sensory stimuli attract attention more effectively when they are relevant to the task, as when they share attributes or features with the stimuli for which subjects are actively looking (for example, a red shirt when we are searching for someone wearing a red hat)[69]. This form of stimulus-driven orienting has been labelled 'contingent' to emphasize its dependence on the underlying task set. Although, in real life, there is no question that sudden unfamiliar stimuli can grab our attention no matter what we are thinking at that moment (for example, the museum alarm), it is also possible that some stimuli attract attention because of some form of contingency that is hard-wired in the brain by learning, development or genetics. This might explain why James's instinctive stimuli (blood, wild animals and so on) are powerful attractors of human attention.

Current psychological evidence supports the idea that orienting to sensory stimuli is modulated by both bottom-up and top-down signals. This dynamic interaction is central to current theories of visual attention. Top-down signals that reflect our expectations might influence the sensory salience of objects in the visual system. Activity in 'salience' maps, which sum the bottom-up and top-down signals for different object features, might determine which objects are selected for recognition and action[70]. Sensory stimuli also orient attention towards unexpected events of potentially high behavioural significance. Below, we discuss how these different influences on stimulus-driven attention are mediated by the interaction between the dorsal frontoparietal network and a recently recognized right dominant ventral frontoparietal network.

Dorsal frontoparietal network and stimulus salience. Neurophysiological studies indicate that the dorsal frontoparietal network, which is recruited for top-down selection, is also modulated by the bottom-up distinctiveness of objects in a visual scene. During a visual search task in which a monkey makes a saccade to the location of an oddball target (such as a red square among green squares), the visual response of FEF neurons discriminates between the target and distracters. This sensory modulation is independent of whether the monkey looks at the target, because similar effects can be obtained during covert detection[71] (FIG. 5a). The fact that the colour of the oddball is uncertain (sometimes a red target is presented with green distracters, and sometimes a green target is presented with red distracters) indicates that bottom-up sensory signals primarily drive the discrimination. Furthermore, it is possible that the monkey expects some 'oddness' in the display, a form of expectancy. Other results indicate that the response of FEF neurons to stimuli is modulated by cognitive factors, such as the relationship between target and distracter stimuli. Distracter stimuli produce larger responses when they are similar to the current target or when they have served as targets in a previous session[72]. Finally, these effects are observed for both colour and shape, indicating that the interaction of bottom-up and top-down signals in the FEF generalizes over visual dimensions (FIG. 5a).

Similarly, the response of neurons in the posterior parietal cortex is modulated by behavioural relevance. The visual response to a flash in area LIP is enhanced when the stimulus is relevant[26]. Moreover, LIP neurons show little or no response to static stimuli brought into their receptive field by saccades (producing the same transient input to the cell), unless the stimuli are behaviourally significant[73]. LIP neurons also respond to visual transients[26], and so might be sensitive to sensory salience. Therefore, macaque areas LIP and FEF are modulated by both the sensory distinctiveness of objects and top-down contextual information. These areas might be involved in generating the salience (activation) maps that are postulated in models of visual search[70], which combine bottom-up with top-down information to represent visual objects of interest (FIG. 5a).

Correspondingly, neuroimaging studies indicate that the human dorsal frontoparietal system is modulated during search and detection[19,74–77], consistent with the idea that this system maintains a salience map. FIGURE 5b shows the cortical distribution of fMRI activity as subjects search for a coherent motion target in a dynamic noise display, with regions that are involved in search labelled in red[76]. The response in these regions, which include the dorsal frontoparietal cortex and extrastriate cortex, is time-locked to the onset of the search display and is maintained until a target is detected (see time courses in FIG. 5c, middle, IPs function). This activity does not simply reflect a sensory response. Target detection produces a higher signal than do trials in which the target is missed (FIG. 5c, right). Moreover, after target detection, the signal drops off even though the search display is still present, indicating that the fMRI signal tracks processes that are engaged by search (FIG. 5c, right). Similar results have been reported for tasks in which subjects have to detect changes in a visual scene[77,78].

These findings indicate that the frontoparietal network is modulated during both visual search and detection. As this network also codes for top-down signals that are related to visual expectancy or goals, it shows some of the properties of salience maps, studied in the single-unit literature, in which top-down and bottom-up information interact to specify which relevant object to select.

Ventral frontoparietal network and sensory orienting. Whereas the above studies provide information on the neural systems that are recruited when stimuli are related to a task goal (as in studies of search and detection), sensory stimuli of potentially high behavioural significance, particularly when they are unexpected, as in the case of the museum alarm, can reorient attention. An inevitable consequence of orienting towards unexpected sensory events is that ongoing cognitive activity is interrupted. We suggest that this 'circuit-breaking' function lies outside the IPs–FEF network and is housed in a more ventral cortical network that includes the temporoparietal junction (TPJ) cortex and the ventral frontal cortex (VFC). This network is strongly lateralized to the right hemisphere: we call it the right ventral frontoparietal network. One of its key functions is to direct attention to behaviourally relevant sensory stimuli that are outside the focus of processing. Its

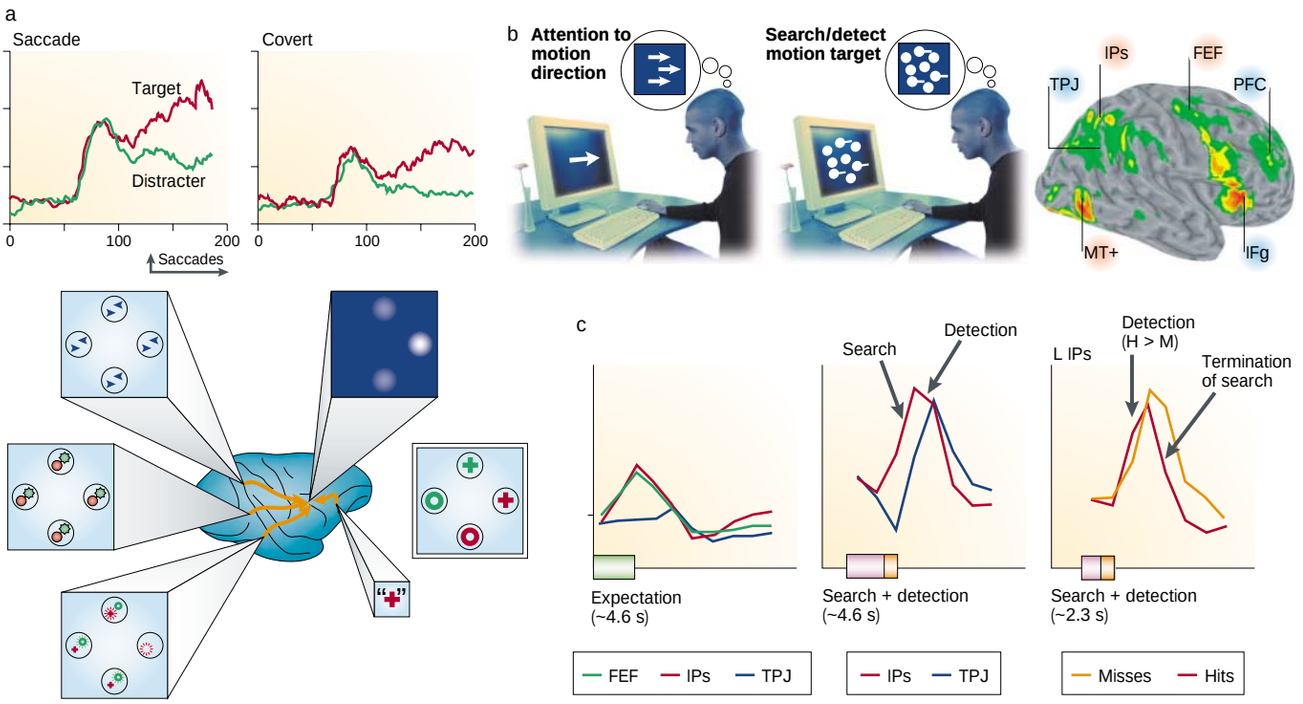

Figure 5 | **Dorsal frontoparietal network and salience. a** | The frontal eye field (FEF) and salience maps (reproduced with permission from REF. 118 © 2001 Massachusetts Institute of Technology). Top: neuronal response in macaque FEF during the detection of oddball targets or distracters in a visual search paradigm. Target detection was signalled by an eye movement to the target (left column) or was covert (right column). Within 120 ms, the single-unit response differentiated between target and distracters. Bottom: FEF as a salience map in which targets defined on the basis of different visual attributes can be selected. **b** | Human brain activity in the dorsal frontoparietal network during search and detection. Left: subjects see an arrow that cues a direction of motion and then search for (and detect) a moving target in a dynamic noise display. Right: functional magnetic resonance imaging (fMRI) map during search and detection. Areas in red are involved in searching for the target; areas in blue are recruited at or after detection. IFg, inferior frontal gyrus; IPs, intraparietal sulcus; MT+, middle temporal complex; PFC, prefrontal cortex; TPJ, temporoparietal junction. **c** | Time course of fMRI signals during cueing, search and detection (for the paradigm shown in **b**). Left: the IPs and FEF respond during the cue period as subjects establish a set for motion, but no activity is observed in the TPJ. Middle: the IPs is active from the onset of the search display, but the TPJ is recruited only when the target is detected. Right: the IPs response to hits (target was detected, H) and misses (target was not detected, M) during search and detection. The signal is initially enhanced on hit trials relative to miss trials, reflecting target detection, but it then falls off, reflecting the termination of search after detection. L IPs, left IPs.

strong right-hemisphere dominance, in contrast to the more bilateral organization of the IPs–FEF system, has important clinical implications for the pathophysiology of unilateral spatial NEGLECT, a common neuropsychological syndrome that occurs after injury to the right hemisphere. The existence of a ventral frontoparietal network is supported by a series of recent brain-imaging studies. First, we discuss some of its functional properties, before considering some hypotheses about its role in the control of visual attention.

In contrast to the dorsal frontoparietal network, the right ventral frontoparietal network is not engaged by cues that carry advance information about forthcoming stimuli. For example, FIG. 5c (left) contrasts the responses of the IPs, FEF and TPJ to the presentation of a cue that indicates the likely direction of motion of a subsequent stimulus. There is little activation in the TPJ for the cue or during the ensuing delay, which indicates that this network is not activated by generating or maintaining an attentional set. Moreover, again unlike the dorsal frontoparietal network, these regions are not activated by the application of this set during stimulus processing. FIGURE 5c (middle) shows that the TPJ is not active during search for a motion target (it is actually deactivated). However, it is strongly activated, predominantly in the right hemishere[10,21], by target detection (FIG. 5b, regions labelled in blue).

When the targets occur at an unexpected location, the activity in this network is further enhanced and even more lateralized to the right hemisphere. FIGURE 6a shows the cortical regions that are most active when stimuli are presented at unattended locations and subjects reorient towards them. They include areas that are centred on the right supramarginal and superior temporal gyrus (or TPJ), and on the inferior frontal gyrus (IFg). There is also activation in the right IPs and FEF[10]. FIGURE 6b shows a similar right-hemisphere network that was activated in another experiment that involved reorienting of attention to unattended (infrequently stimulated) locations[79].

An initial hypothesis about this network was that it is involved in spatial reorienting to an unattended location. However, it is now clear that activation of the right ventral frontoparietal network is independent of

NEGLECT
A neurological syndrome (often involving damage to the right parietal cortex) in which patients show a marked deficit in the ability to detect or respond to information in the contralesional field.

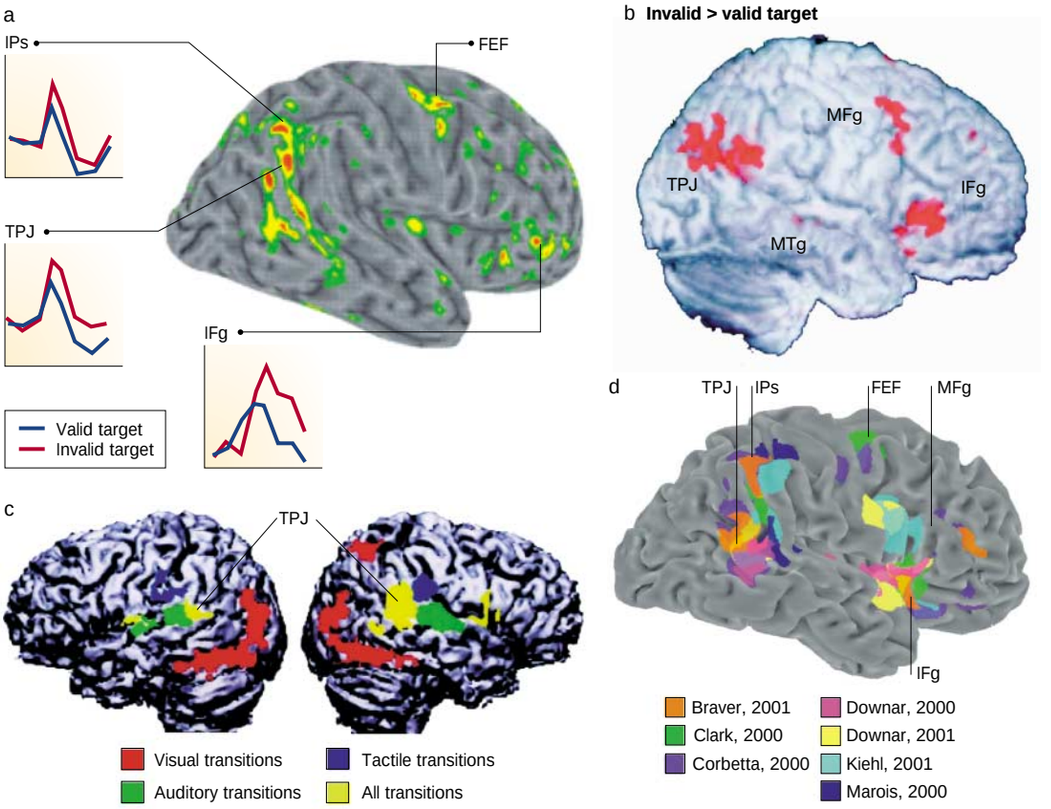

Figure 6 | **Ventral right frontoparietal network and target detection. a** | Spatial reorienting to unattended targets[13]. Maps of activation showing areas of differential activation for infrequent unattended spatial targets (invalid) versus frequent attended (valid) targets. The time course indicates that the response is stronger and more sustained to unattended targets than to attended targets. FEF, frontal eye field; IFg, inferior frontal gyrus; IPs, intraparietal sulcus; TPJ, temporoparietal junction. **b** | Spatial reorienting to unattended targets (reproduced with permission from REF. 79 © 2000 Massachusetts Institute of Technology). Similar areas of activation for spatial reorienting (invalid > valid targets) are observed. MFg, middle frontal gyrus; MTg, middle temporal gyrus. **c** | Detection of low-frequency multimodal stimuli (reproduced with permission from REF. 82 © 2000 Macmillan Magazines Ltd). A much larger volume of the TPJ is activated in the right than in the left hemisphere. **d** | Meta-analysis of imaging studies of the detection of low-frequency targets. A right dominant ventral frontoparietal network composed of the TPJ, IFg and MFg is consistently recruited during the detection of low-frequency events, independently of modality and response demands. Regions of the frontoparietal network (IPs and FEF) are co-activated in the right hemisphere. Foci of activation are smoothed and projected onto the Visible Human Brain[117].

whether the stimulus initiates a shift in spatial attention. In some experiments, the network was activated during the detection of low-frequency stimuli at an expected location; in other experiments, activation was observed when the stimuli were fixed at the centre of gaze[80,81]. Other results indicate that a similar right-hemisphere network is recruited by infrequent changes in a stimulus feature, independent of the modality of the change. Subjects were presented with simultaneous visual, auditory and tactile stimuli. Occasional changes in a feature of one of the stimuli (a change in colour of the visual stimulus from blue to red, or a change in the nature of the auditory stimulus from croaking frogs to running water), irrespective of the sensory modality, activated a set of cortical regions that included the right TPJ, IFg, anterior insula and anterior cingulate/supplementary motor area (AC/SMA), which strongly overlaps with the network that is activated for spatial reorienting[82] (FIG. 6c). Finally, the same network is recruited under a variety of response demands[83].

Therefore, a more general conclusion is that the ventral frontoparietal network is modulated by the detection of unattended or low-frequency events, independent of their location, sensory modality of presentation or response demands. These stimuli reorient attention, but not necessarily spatially. FIGURE 5d shows a meta-analysis of activation during the detection of low-frequency events. The areas of maximal overlap include the right TPJ and VFC (including the IFg, middle frontal gyrus and frontal operculum) and, in all studies, activation is lateralized to the right hemisphere. This figure also indicates that the detection of low-frequency targets co-activates the dorsal right IPs–FEF system. The link between TPJ–VFC activation and the detection of low-frequency events is reinforced by the observation that electrical evoked potentials associated with the detection of infrequent targets are localized to, and disrupted by, lesions of the TPJ and prefrontal cortex[84,85]. Finally, right prefrontal lesions specifically impair the detection of low-frequency events[86].

We previously discussed how stimulus-driven orienting is modulated by task relevance. Activity in the TPJ is also modulated by task relevance. This region is enhanced when oddball or infrequent stimuli in an attended modality (for example, vision) are detected, as compared with experiments in which the same stimuli are presented and subjects are monitoring for targets in a different modality[87]. A recent study shows a more direct demonstration of contingent orienting in the right TPJ[88]. Subjects searched for a red target at the centre of gaze while being presented with irrelevant distracters in the periphery of the visual field. When distracters were the same colour as the target, performance on the primary task was disrupted, presumably reflecting a shift of attention to the peripheral distracters and a resulting loss of targets at the centre. The right TPJ was specifically activated by task-contingent distracters, but not by distracters that did not attract attention.

The above studies indicate that the TPJ is differentially engaged by low-frequency stimuli that require reorienting of attention within the current task set (for example, responding to targets on a screen). We suggest that the TPJ is also strongly engaged by stimuli that are behaviourally relevant but require a change in the current task set. For example, the alarm at the museum is not part of the task set of listening to the guide's discussion of Hieronymous Bosch, but it is clearly a behaviourally relevant stimulus.

The TPJ is not well activated by low-frequency task-irrelevant stimuli that are embedded in trains of standard and oddball targets[87,89]. Typically, these stimuli, which do not require either a response or a change in the current task set, are novel to the subjects. Novel stimuli might activate more robustly prefrontal regions[89,90], damage to which specifically impairs novelty-related potentials[84,85]. Patients with prefrontal lesions have problems in adapting to novel situations and stimuli[91], and show a decreased autonomic response to novel stimuli[92]. It is possible that the differential response of the TPJ and frontal cortex to novel stimuli reflects a differential role in bottom-up attention. The frontal cortex might be necessary for evaluating the novelty of stimuli, whereas the TPJ might be more involved in detecting their behavioural valence.

Our discussion of the TPJ region has been limited to brain-imaging studies in humans. The parietal component of the TPJ response is located on the gyral surface of the IPL, which in monkey would correspond to area 7a. Neurons in area 7a respond more briskly when stimuli are presented at unattended than at attended locations[93,94], and when stimuli are behaviourally relevant[25]. Neurons in area 7a also code the location of distinctive stimuli that differ from the background (such as a red square in a field of green squares)[95]. These neuronal modulations for unattended and salient stimuli are consistent with the observed fMRI signals in the human TPJ. However, at present, it is unclear whether monkey area 7a is homologous to human TPJ.

In summary, the current evidence supports the existence of a right-lateralized ventral parietofrontal network that has many of the properties expected of a network that is involved in directing attention to a stimulus. We offer several related interpretations of its function.

Functions of the ventral frontoparietal network. First, this network might represent the exogenous orienting system, which directs attention to the spatial locations of salient stimuli. This hypothesis is most strongly supported by the modulation of the TPJ during the presentation of stimuli that induce a task-contingent shift of attention[30]. It is also consistent with the activation of TPJ–VFC during reorienting to spatially unexpected targets[10,79]. Although this right-hemisphere network is also engaged by low-frequency stimuli at attended or expected locations[80,81], this might reflect its involvement in orienting to segmented objects rather than just to spatial locations.

Alternatively, the ventral network could work in conjunction with the dorsal network during stimulus-driven orienting. Whereas sensory cues produce facilitation and inhibition with some spatial selectivity, the ventral network responds equally well to stimuli at different locations[10,21,81]. At present, there are no data on whether this network contains a spatial map that could direct attention to the location of the detected change. The spatial precision of exogenous orienting might depend on the co-activation of the TPJ with the more dorsal IPs–FEF network. The dorsal network might also be the source of the task-contingent properties of TPJ activation, as the TPJ is not active during cue or search periods in which attentional sets are generated and maintained. This influence might be direct or indirect through the top-down effects of the dorsal network on the visual cortex. Finally, the dorsal IPs–FEF network also has properties, such as sensitivity to stimulus distinctiveness for a range of visual features and task contingency, that are consistent with a role in exogenous orienting. Future studies will need to tease apart the relative contributions of the dorsal IPs–FEF and the ventral TPJ–IFg networks to stimulus-driven orienting.

We suggest several ways in which the two systems might interact. One possibility is that the ventral network serves as an alerting system that detects behaviourally relevant stimuli in the environment, but is not equipped with high-resolution spatial sensors. Once a relevant stimulus is detected, its precise localization depends on the dorsal IPs–FEF system. A related hypothesis is that the TPJ–VFC system acts as a circuit breaker of ongoing cognitive activity when a behaviourally relevant stimulus is detected. When subjects detect a low-frequency or unexpected event, they must break the current attentional set and adopt a new one on the basis of the incoming stimulus. In a recent set of experiments, we found a widely distributed set of endogenous signals that were related to the termination of an ongoing state of readiness for an event[96]. The pattern of activation in TPJ–VFC was consistent with the hypothesis that the ventral network generated the signal that terminated the task set.

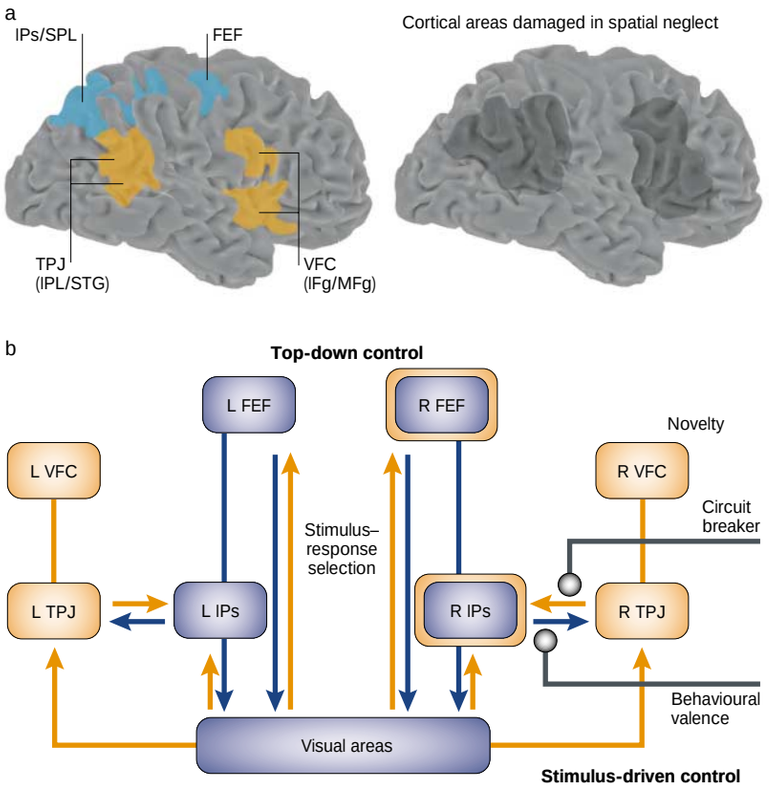

Figure 7 | **Neuroanatomical model of attentional control. a** | Dorsal and ventral frontoparietal networks and their anatomical relationship with regions of damage in patients with unilateral neglect. Areas in blue indicate the dorsal frontoparietal network. FEF, frontal eye field; IPs/SPL, intraparietal sulcus/superior parietal lobule. Areas in orange indicate the stimulus-driven ventral frontoparietal network. TPJ, temporoparietal junction (IPL/STG, inferior parietal lobule/superior temporal gyrus); VFC, ventral frontal cortex (IFg/MFg, inferior frontal gyrus/middle frontal gyrus). The areas damaged in neglect (right) better match the ventral network. **b** | Anatomical model of top-down and stimulus-driven control. The IPs–FEF network is involved in the top-down control of visual processing (blue arrows). The TPJ–VFC network is involved in stimulus-driven control (orange arrows). The IPs and FEF are also modulated by stimulus-driven control. Connections between the TPJ and IPs interrupt ongoing top-down control when unattended stimuli are detected. Behavioural relevance is mediated by direct or indirect (not shown) connections between the IPs and TPJ. The VFC might be involved in novelty detection. L, left; R, right.

Two orienting networks and spatial neglect

We propose that orienting is controlled in humans by two interacting networks. The model presented in FIG. 7 is a modification of earlier models[97,98]. A largely bilateral IPs–FEF system is involved in the generation of attentional sets — that is, goal-directed stimulus–response selection — and the application of those sets during stimulus processing. This system corresponds to the parietal and frontal cores of the attention network of Mesulam's model[98], and extends to the FEF the 'orienting' function of Posner's posterior attention system[97]. Our current hypothesis is that this system links relevant sensory representations to relevant motor representations.

A second system, which is strongly lateralized to the right hemisphere, detects behaviourally relevant stimuli and works as an alerting mechanism or circuit breaker for the first system when these stimuli are detected outside the focus of processing. We propose that this circuit-breaking function depends on a functional interaction between the TPJ and IPs. We also propose that the IPs provides the TPJ with information about the behavioural relevance of stimuli, either directly, or indirectly through top-down modulation of the visual cortex. The frontal component of the ventral network might be involved specifically in the evaluation of novel stimuli.

It is possible that part of the signal in the ventral network depends on noradrenergic modulation from the LOCUS COERULEUS. Cortically projecting noradrenergic terminals are most concentrated in the macaque inferior parietal cortex[99]. In humans, there is a denser concentration of noradrenaline in the right than in the left thalamus[100], which might be related to the right lateralization of the TPJ–VFC network. A similar right-hemisphere system is activated in humans during vigilance tasks[101] that are thought to depend on noradrenergic systems. The locus coeruleus noradrenergic system has been extensively implicated not only in arousal and vigilance, but also in selective attention, particularly to salient unexpected stimuli[102]. The delivery of noradrenaline to the rat prefrontal cortex is enhanced by unexpected changes in response/reward contingencies. The influx of noradrenaline to the prefrontal cortex for novel contingencies might serve to detect a mismatch between action and reward, and disengage ongoing actions in favour of new behavioural responses[103]. This characterization is akin to our proposal that the TPJ–VFC system works as a circuit breaker of ongoing cognitive activity when unexpected or novel stimuli are detected.

Our model has important implications for the neuroanatomy and neurophysiology of unilateral spatial neglect, a common and disabling result of unilateral brain damage. Patients with neglect tend to ignore stimuli towards the side of space opposite to their lesion. For instance, after a lesion to the right side of the brain, they ignore people on their left side, miss food on the left side of the plate, and fail to dress the left side of the body or to shave the left side of their face. In addition, neglect patients are forcefully attracted towards stimuli on their right side, as if attention were 'stickier' on the right side of space. They also have problems in directing actions (eye or arm movements) towards the contralateral side of space. Finally, neglect patients have low vigilance, which exacerbates deficits in spatial processing[98,104,105].

It has been proposed that neglect represents a dysfunction of the dorsal IPs–FEF network for spatial attention[98]. However, we propose that the anatomy of neglect better matches the ventral TPJ–VFC system[106]. First, lesions that cause neglect are located more ventrally in the brain than the core regions of the IPs–FEF network, and most frequently involve the right TPJ[107]. In cases without a visual field deficit, the right superior temporal gyrus is the most common site of damage[108]. In the frontal cortex, lesions that cause neglect are typically localized in right ventral prefrontal and opercular cortex, rather than in the more dorsal FEF region[104,109]. Therefore, the anatomical localization of neglect better matches the ventral TPJ–VFC attention network than the dorsal IPs–FEF attention network.

LOCUS COERULEUS
A nucleus of the brainstem. The main supplier of noradrenaline to the brain.

Second, neglect is more frequent after damage to the right than to the left hemisphere[110]. By contrast, activity in the IPs–FEF network is largely bilateral during spatial orienting to the left or right visual field[10–12], and becomes only slightly right lateralized during stimulus processing[15,16]. Activation of the right TPJ during stimulus detection is strongly lateralized to the right hemisphere, consistent with the hemispheric lateralization of neglect.

Finally, patients with neglect have deficits primarily in stimulus detection rather than in top-down goal-directed orienting. Neglect patients can voluntarily direct attention to the contralesional side, consistent with sparing of the IPs–FEF network, and can use cognitive cues to anchor attention to the left visual space during their rehabilitation[111]. The impairment in neglect matches more closely the dysfunction of a target detection system than an endogenous orienting system, particularly when the stimuli are unattended and outside the focus of processing[112]. This functional characterization is more consistent with a disruption of the stimulus-driven ventral frontoparietal attention network.

Whereas some aspects of neglect can be related to the TPJ, other aspects are more problematic. First, detection deficits in neglect show a gradient across the visual field. The deficit is worse at the most peripheral locations on the side of space opposite to the lesion (the left visual field), and decreases as the stimulus position moves towards the same side of space as the lesion[113]. However, as the right TPJ responds equally well to stimuli in the contralateral (left) and ipsilateral (right) visual fields[10,21], at least for eccentricities of up to ten degrees, TPJ lesions might be expected to cause bilateral deficits. Second, the TPJ is not well activated by motor preparation or execution, whereas neglect patients clearly show a deficit in initiating arm movements contralesionally[114].

These aspects of neglect might reflect dysfunction of the ipsilateral IPs–FEF network. Dorsal regions of the IPs–FEF system, for example, are involved in arm- and eye-movement selection. Also, although the spatial topography of the dorsal network in humans has not been investigated in detail, there is some evidence for an asymmetrical coding of space. The left hemisphere codes mainly for locations in the right visual field, but the right hemisphere codes for locations in both fields[13], consistent with a right visual field bias after right-hemisphere lesions. We suggest that right TPJ lesions might 'functionally' inactivate the right dorsal IPs–FEF network, either because of decreased input from the TPJ or because of damage to the underlying white matter. This functional inactivation might be exacerbated by a relative hyperactivation of the left IPs–FEF network, as indicated by hemispheric models of orienting[115].

Future directions

The proposed functional distinction between neural systems for goal-directed and stimulus-driven orienting raises many questions for future research. One issue concerns the anatomical relationship between regions of the dorsal frontoparietal network that are involved in attending to spatial location and non-spatial features such as motion, attending to effectors and linking stimuli to effectors. Specifying these relationships will require detailed studies in single subjects. Another issue concerns the functional relationship between dorsal and ventral networks during stimulus-driven orienting. For example, topographical mapping in both the TPJ and the dorsal network might indicate the relative role of each in directing attention to a location during exogenous orienting. Understanding spatial coding in both networks will also help to clarify the pathophysiology of neglect. It is also important to link these functional descriptions with neurophysiological and neuropharmacological descriptions of the same brain systems. Goal-directed orienting is influenced by cholinergic drugs, whereas stimulus-driven alerting is modulated by noradrenergic drugs[116]. If this neuropharmacological–behavioural correlation maps onto the anatomy of the dorsal and ventral attentional networks, then we might be able to use this information to treat more effectively acquired (stroke, trauma) or developmental (attention deficit) disorders of attention. Finally, all of these issues will be aided by a better understanding of the homologues of these networks in the human and monkey.

1. Eriksen, C. W. & Hoffman, J. E. The extent of processing of noise elements during selective encoding from visual displays. *Percept. Psychophys.* **14**, 155–160 (1973).
2. Posner, M. I., Snyder, C. R. R. & Davidson, B. J. Attention and the detection of signals. *J. Exp. Psychol.* **109**, 160–174 (1980).
3. Ball, K. & Sekuler, R. Models of stimulus uncertainty in motion perception. *Psychol. Rev.* **87**, 435–469 (1980).
4. Egeth, H. E., Virzi, R. A. & Garbart, H. Searching for conjunctively defined targets. *J. Exp. Psychol. Hum. Percept. Perform.* **10**, 32–39 (1984).
5. Dosher, B. A. & Lu, Z.-L. Mechanisms of perceptual attention in precuing of location. *Vision Res.* **40**, 1269–1292 (2000).
6. Rosenbaum, D. A. Human movement initiation: specification of arm, direction and extent. *J. Exp. Psychol.* **109**, 444–474 (1980).
7. Abrams, R. A. & Jonides, J. Programming saccadic eye movements. *J. Exp. Psychol. Hum. Percept. Perform.* **14**, 428–443 (1988).
   References 1–7 provide evidence that preparatory attention to stimuli and responses facilitates perception and action.
8. Kanwisher, N. & Wojciulik, E. Visual attention: insights from brain imaging. *Nature Rev. Neurosci.* **1**, 91–100 (2000).
9. Kastner, S. & Ungerleider, L. G. Mechanisms of visual attention in the human cortex. *Annu. Rev. Neurosci.* **23**, 315–341 (2000).
   References 8 and 9 review the effects of attention on neural mechanisms in the human visual cortex, and discuss the interaction between the frontoparietal network and the visual cortex.
10. Corbetta, M., Kincade, J. M., Ollinger, J. M., McAvoy, M. P. & Shulman, G. L. Voluntary orienting is dissociated from target detection in human posterior parietal cortex. *Nature Neurosci.* **3**, 292–297 (2000).
    Dissociates preparatory goal-directed activity in the IPs for stimulus location from stimulus-driven activity in the TPJ during reorienting to unattended targets.
11. Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R. & Ungerleider, L. G. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* **22**, 751–761 (1999).
12. Hopfinger, J. B., Buonocore, M. H. & Mangun, G. R. The neural mechanisms of top-down attentional control. *Nature Neurosci.* **3**, 284–291 (2000).
13. Corbetta, M., Kincade, J. M. & Shulman, G. L. Neural systems for visual orienting and their relationship with working memory. *J. Cogn. Neurosci.* **14** (in the press).
14. Shulman, G. L. *et al*. Areas involved in encoding and applying directional expectations to moving objects. *J. Neurosci.* **19**, 9480–9496 (1999).
    References 11–14 provide neuroimaging evidence that the human dorsal frontoparietal network is involved in preparing and maintaining expectations for stimulus location and motion.
15. Corbetta, M., Miezin, F. M., Shulman, G. L. & Petersen, S. E. A PET study of visuospatial attention. *J. Neurosci.* **13**, 1202–1226 (1993).
16. Nobre, A. C. *et al*. Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* **120**, 515–533 (1997).
17. Vandenberghe, R. *et al*. Attention to one or two features in left and right visual field: a positron emission tomography study. *J. Neurosci.* **17**, 3739–3750 (1997).
18. Culham, J. C. *et al*. Cortical fMRI activation produced by attentive tracking of moving targets. *J. Neurophysiol.* **80**, 2657–2670 (1998).
19. Wojciulik, E. & Kanwisher, N. The generality of parietal involvement in visual attention. *Neuron* **23**, 747–764 (1999).

20. Gitelman, D. R. *et al*. A large-scale distributed network for covert spatial attention: further anatomical delineation based on stringent behavioural and cognitive controls. *Brain* **122**, 1093–1106 (1999).
21. Perry, R. J. & Zeki, S. The neurology of saccades and covert shifts in spatial attention: an event-related fMRI study. *Brain* **123**, 2273–2288 (2000).
22. Corbetta, M. Frontoparietal cortical networks for directing attention and the eye to visual locations: identical, independent, or overlapping neural systems. *Proc. Natl Acad. Sci. USA* **95**, 831–838 (1998).
23. Van Essen, D. C. *et al*. Mapping visual cortex in monkeys and humans using surface-based atlases. *Vision Res.* **41**, 1359–1378 (2001).
24. Paus, T. Location and function of the human frontal eye-field: a selective review. *Neuropsychologia* **34**, 475–483 (1996).
25. Bushnell, M. C., Goldberg, M. E. & Robinson, D. L. Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective attention. *J. Neurophysiol.* **46**, 755–772 (1981).
26. Colby, C. L., Duhamel, J. R. & Goldberg, M. E. Visual, presaccadic, and cognitive activation of single neurons in monkey lateral intraparietal area. *J. Neurophysiol.* **76**, 2841–2852 (1996).
Shows how preparatory signals for visual attention and eye movements are combined in LIP neurons.
27. Nakamura, K. & Colby, C. L. Visual, saccade-related, and cognitive activation of single neurons in monkey exstrastriate area V3A. *J. Neurophysiol.* **84**, 677–692 (2000).
28. Pashler, H. E. *The Psychology of Attention* (MIT Press, Cambridge, Massachusetts, 1998).
29. Shulman, G. L., d'Avossa, G., Tansy, A. P. & Corbetta, M. Two attentional processes in the parietal lobe. *Soc. Neurosci. Abstr.* **27**, 722.20 (2001).
30. Serences, J. T., Schwarzbach, J. & Yantis, S. Control mechanisms of object-based visual attention in human cortex. *Soc. Neurosci. Abstr.* **27**, 348.9 (2001).
31. Le, T. H., Pardo, J. V. & Hu, X. 4T-fMRI study of nonspatial shifting of selective attention: cerebellar and parietal contributions. *J. Neurophysiol.* **79**, 1535–1548 (1998).
32. Assad, J. A. & Maunsell, J. H. R. Neuronal correlates of inferred motion in primate posterior parietal cortex. *Nature* **373**, 518–521 (1995).
33. Toth, L. J. & Assad, J. A. Dynamic coding of behaviourally relevant stimuli in parietal cortex. *Nature* **415**, 165–168 (2002).
34. Blake, R., Cepeda, N. J. & Hiris, E. Memory for visual motion. *J. Exp. Psychol. Hum. Percept. Perform.* **23**, 353–369 (1997).
35. Magnussen, S., Greenlee, M. W., Asplund, R. & Dyrnes, S. Stimulus-specific mechanisms of visual short-term memory. *Vision Res.* **31**, 1213–1219 (1991).
36. Awh, E. & Jonides, J. Overlapping mechanisms of attention and spatial working memory. *Trends Cogn. Sci.* **5**, 119–126 (2001).
Reviews the relationship between spatial working memory and attention.
37. Courtney, S. M., Ungerleider, L. G., Keil, K. & Haxby, J. V. Transient and sustained activity in a distributed neural system for human working memory. *Nature* **386**, 608–611 (1997).
38. Gnadt, J. W. & Andersen, R. A. Memory related motor planning activity in posterior parietal cortex of macaque. *Exp. Brain Res.* **70**, 216–220 (1988).
39. Funahashi, S., Bruce, C. J. & Goldman-Rakic, P. S. Neuronal activity related to saccadic eye movements in the monkey's dorsolateral prefrontal cortex. *J. Neurophysiol.* **65**, 1464–1483 (1991).
40. Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**, 193–222 (1995).
41. Miller, E. K. & Cohen, J. D. An integrative theory of prefrontal cortex function. *Annu. Rev. Neurosci.* **24**, 167–202 (2001).
References 40 and 41 review the role of the prefrontal cortex in attention and executive control.
42. Savage-Rumbaugh, S., Shanker, S. G. & Talbot, J. T. *Apes, Language, and the Human Mind* (Oxford Univ. Press, New York, 1998).
43. Snyder, L. H., Batista, A. P. & Andersen, R. A. Coding of intention in the posterior parietal cortex. *Nature* **386**, 167–170 (1997).
Presents evidence of different preparatory response mechanisms for eye and arm in the macaque posterior parietal cortex.
44. Sakata, H., Taira, M., Kusunoki, M., Murata, A. & Tanaka, Y. The parietal association cortex in depth perception and visual control of hand action. *Trends Neurosci.* **20**, 350–357 (1997).
45. Bruce, C. J. & Goldberg, M. E. Primate frontal eye fields. I. Single neurons discharging before saccades. *J. Neurophysiol.* **53**, 603–635 (1985).
46. Wise, S. P., Weinrich, M. & Mauritz, K. H. Motor aspects of cue-related neuronal activity in premotor cortex of the rhesus monkey. *Brain Res.* **260**, 301–305 (1983).
47. Kawashima, R., Roland, P. E. & O'Sullivan, B. Functional anatomy of reaching and visuomotor learning: a positron emission tomography study. *Cereb. Cortex* **5**, 111–122 (1995).
48. Petit, L., Clark, V. P., Ingeholm, J. & Haxby, J. V. Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. *J. Neurophysiol.* **77**, 3386–3390 (1997).
49. Connolly, J. D., Goodale, M. A., Desouza, J. F., Menon, R. S. & Vilis, T. A comparison of frontoparietal fMRI activation during anti-saccades and anti-pointing. *J. Neurophysiol.* **84**, 1645–1655 (2000).
50. Rowe, J. B., Toni, I., Josephs, O., Frackowiak, R. S. & Passingham, R. E. The prefrontal cortex: response selection or maintenance within working memory? *Science* **288**, 1656–1660 (2000).
51. Rizzolatti, G., Riggio, L., Dascola, I. & Umiltá, C. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* **25**, 31–40 (1987).
52. Corbetta, M. *et al*. A common network of functional areas for attention and eye movements. *Neuron* **21**, 761–773 (1998).
53. Nobre, A. C., Gitelman, D. R., Dias, E. C. & Mesulam, M. M. Covert visual spatial orienting and saccades: overlapping neural systems. *Neuroimage* **11**, 210–216 (2000).
54. Rushworth, M. F., Paus, T. & Sipila, P. K. Attention systems and the organization of the human parietal cortex. *J. Neurosci.* **21**, 5262–5271 (2001).
55. Allport, A., Styles, E. A. & Hsieh, S. in *Attention and Performance XV* (eds Umilta, C. & Moscovitch, M.) 421–452 (Erlbaum, Hillsdale, New Jersey, 1994).
56. Rogers, R. D. & Monsell, S. Costs of a predictable switch between simple cognitive tasks. *J. Exp. Psychol.* **124**, 207–231 (1995).
57. Meiran, N., Chorev, Z. & Sapir, A. Component processes in task switching. *Cogn. Psychol.* **41**, 211–253 (2000).
References 55–57 describe psychological processes involved in task switching.
58. Fuster, J. M. in *Cerebral Cortex* (eds Jones, E. G. & Peters, A.) 151–177 (Plenum, New York, 1985).
59. Goldman-Rakic, P. S. in *Handbook of Physiology, Section 1. Higher Functions of the Brain* (eds Plum, F. & Mountcastle, V.) 373–417 (American Physiological Society, Bethesda, Maryland, 1987).
60. Kimberg, D. Y., Aguirre, G. K. & D'Esposito, M. Modulation of task-related neural activity in task-switching: an fMRI study. *Brain Res. Cogn. Brain Res.* **10**, 189–196 (2000).
61. Sohn, M.-H., Ursu, S., Anderson, J. R., Stenger, V. A. & Carter, C. S. The role of prefrontal cortex and posterior parietal cortex in task switching. *Proc. Natl Acad. Sci. USA* **97**, 13448–13453 (2000).
62. James, W. *Principles of Psychology* Vol. 1 (Henry-Holt & Co., New York, 1890).
63. Duncan, J. & Humphreys, G. W. Visual search and stimulus similarity. *Psychol. Rev.* **96**, 433–458 (1989).
64. Posner, M. I. & Cohen, Y. in *Attention and Performance X* (eds Bouman, H. & Bowhuis, D.) 55–66 (Erlbaum, Hillsdale, New Jersey, 1984).
65. Muller, H. J. & Rabbitt, M. A. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J. Exp. Psychol.* **15**, 315–330 (1989).
66. Klein, R. M. Inhibition of return. *Trends Cogn. Sci.* **4**, 138–147 (2000).
67. Jonides, J. in *Attention and Performance XI* (eds Posner, M. I. & Marin, O.) 187–205 (Erlbaum, Hillsdale, New Jersey, 1981).
68. Yantis, S. & Jonides, J. Abrupt visual onsets and selective attention: voluntary versus automatic allocation. *J. Exp. Psychol. Hum. Percept. Perform.* **16**, 121–134 (1990).
69. Folk, C. L., Remington, R. W. & Johnston, J. C. Involuntary covert orienting is contingent on attentional control settings. *J. Exp. Psychol. Hum. Percept. Perform.* **18**, 1030–1044 (1992).
References 68 and 69 discuss cognitive influences on stimulus-driven orienting.
70. Wolfe, J. M. Guided search 2.0: a revised model of visual search. *Psychon. Bull. Rev.* **1**, 202–238 (1994).
71. Thompson, K. G., Bichot, N. P. & Schall, J. D. Dissociation of visual discrimination from saccade programming in macaque frontal eye field. *J. Neurophysiol.* **77**, 1046–1050 (1997).
72. Bichot, N. P. & Schall, J. D. Effects of similarity and history on neural mechanisms of visual selection. *Nature Neurosci.* **2**, 549–554 (1999).
73. Gottlieb, J. P., Kusunoki, M. & Goldberg, M. E. The representation of visual salience in monkey parietal cortex. *Nature* **391**, 481–484 (1998).
References 71–73 show that FEF and LIP neurons are modulated by stimulus salience and task relevance.
74. Corbetta, M., Shulman, G. L., Miezin, F. M. & Petersen, S. E. Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science* **270**, 802–805 (1995).
75. Leonards, U., Sunaert, S., Van Hecke, P. & Orban, G. A. Attention mechanisms in visual search — an fMRI study. *J. Cogn. Neurosci.* **12**, 61–75 (2000).
76. Shulman, G. L., Ollinger, J. M., Linenweber, M., Petersen, S. E. & Corbetta, M. Multiple neural correlates of detection in the human brain. *Proc. Natl Acad. Sci. USA* **98**, 313–318 (2001).
77. Huettel, S. A., Guzeldere, G. & McCarthy, G. Dissociating the neural mechanisms of visual attention in change detection using functional MRI. *J. Cogn. Neurosci.* **13**, 1006–1018 (2001).
78. Beck, D. M., Rees, G., Frith, C. D. & Lavie, N. Neural correlates of change detection and change blindness. *Nature Neurosci.* **4**, 645–650 (2001).
References 76–78 show that attentional search and target detection modulate the dorsal frontoparietal network and the visual cortex.
79. Arrington, C. M., Carr, T. H., Mayer, A. R. & Rao, S. M. Neural mechanisms of visual attention: object-based selection of a region in space. *J. Cogn. Neurosci.* **12**, 106–117 (2000).
80. Kirino, E., Belger, A., Goldman-Rakic, P. & McCarthy, G. Prefrontal activation evoked by infrequent target and novel stimuli in a visual target detection task: an event-related functional magnetic resonance imaging study. *J. Neurosci.* **20**, 6612–6618 (2000).
81. Marois, R., Leung, H. C. & Gore, J. C. A stimulus-driven approach to object identity and location processing in the human brain. *Neuron* **25**, 717–728 (2000).
82. Downar, J., Crawley, A. P., Mikulis, D. J. & Davis, K. D. A multimodal cortical network for the detection of changes in the sensory environment. *Nature Neurosci.* **3**, 277–283 (2000).
Presents evidence that the ventral frontoparietal network responds to stimulus changes in different sensory modalities.
83. Braver, T. S., Barch, D. M., Gray, J. R., Molfese, D. L. & Snyder, A. Anterior cingulate cortex and response conflict: effects of frequency, inhibition and errors. *Cereb. Cortex* **11**, 825–836 (2001).
84. Knight, R. T. & Scabini, D. Anatomic bases of event-related potentials and their relationship to novelty detection in humans. *J. Clin. Neurophysiol.* **15**, 3–13 (1998).
85. Daffner, K. R. *et al*. The central role of the prefrontal cortex in directing attention to novel events. *Brain* **123**, 927–939 (2000).
86. Wilkins, A. J., Shallice, T. & McCarthy, R. Frontal lesions and sustained attention. *Neuropsychologia* **25**, 359–365 (1987).
87. Downar, J., Crawley, A. P., Mikulis, D. J. & Davis, K. D. The effect of task relevance on the cortical response to changes in visual and auditory stimuli: an event-related fMRI study. *Neuroimage* **14**, 1256–1267 (2001).
88. Serences, J., Shomstein, S., Leber, A., Yantis, S. & Egeth, H. E. Neural mechanisms of goal-directed and stimulus-driven attentional control. *Psychon. Soc. Abstr.* **42**, 135 (2001).
89. Clark, V. P., Fannon, S., Lai, S., Benson, R. & Bauer, L. Responses to rare visual target and distractor stimuli using event-related fMRI. *J. Neurophysiol.* **83**, 3133–3139 (2000).
90. Kiehl, K. A., Laurens, K. R., Duty, T. L., Forster, B. B. & Liddle, P. F. Neural sources involved in auditory target detection and novelty processing: an event-related fMRI study. *Psychophysiology* **38**, 133–142 (2001).
91. Stuss, D. T. & Benson, D. F. *The Frontal Lobes* (Raven, New York, 1986).
92. Yokoyama, K., Jennings, R., Ackles, P., Hood, P. & Boller, F. Lack of heart rate changes during an attention-demanding task after right hemisphere lesions. *Neurology* **37**, 624–630 (1987).
93. Steinmetz, M. A. & Constantinidis, C. Neurophysiological evidence for a role of posterior parietal cortex in redirecting visual attention. *Cereb. Cortex* **5**, 448–456 (1995).
94. Robinson, D. L., Bowman, E. M. & Kertzman, C. Covert orienting of attention in macaques. II. Contributions of parietal cortex. *J. Neurophysiol.* **74**, 698–721 (1995).
95. Constantinidis, C. & Steinmetz, M. A. Neuronal responses in area 7a to multiple stimulus displays. II. Responses are suppressed at the cued location. *Cereb. Cortex* **11**, 592–597 (2001).
96. Shulman, G. L. *et al*. Reactivation of networks involved in preparatory states. *Cereb. Cortex* (in the press).

97. Posner, M. I. & Petersen, S. E. The attention system of the human brain. *Annu. Rev. Neurosci.* **13**, 25–42 (1990).
98. Mesulam, M. M. Spatial attention and neglect: parietal, frontal and cingulate contributions to the mental representation and attentional targeting of salient extrapersonal events. *Phil. Trans. R. Soc. Lond. B* **354**, 1325–1346 (1999).
Reviews the pathophysiology and anatomy of unilateral neglect.
99. Morrison, J. H. & Foote, S. L. Noradrenergic and serotoninergic innervation of cortical, thalamic and tectal visual structures in old and new world monkeys. *J. Comp. Neurol.* **243**, 117–128 (1986).
100. Oke, A., Keller, R., Mefford, I. & Adams, R. N. Lateralization of norepinephrine in human thalamus. *Science* **200**, 1411–1413 (1978).
101. Pardo, J. V., Fox, P. T. & Raichle, M. E. Localization of a human system for sustained attention by positron emission tomography. *Nature* **349**, 61–64 (1991).
102. Aston-Jones, G., Foote, S. L. & Bloom, F. E. in *Frontiers of Clinical Neuroscience* (ed. Ziegler, M. G.) (Williams & Wilkins, Baltimore, Maryland, 1984).
103. Dalley, J. W. *et al*. Distinct changes in cortical acetylcholine and noradrenaline efflux during contingent and noncontingent performance of a visual attentional task. *J. Neurosci.* **21**, 4908–4914 (2001).
Provides a possible link between activity in ventral frontoparietal networks and noradrenaline projection systems.
104. Heilman, K. M., Watson, R. T. & Valenstein, E. in *Clinical Neuropsychology* (eds Heilman, K. M. & Valenstein, E.) 243–293 (Oxford Univ. Press, New York, 1985).
105. Robertson, I. H., Mattingley, J. B., Rorden, C. & Driver, J. Phasic alerting of neglect patients overcomes their spatial deficit in visual awareness. *Nature* **395**, 169–172 (1998).
106. Corbetta, M., Kincade, M. J. & Shulman, G. L. in *The Cognitive and Neural Basis of Spatial Neglect* (eds Karnath, H. O., Milner, D. & Vallar, G.) (Oxford Univ. Press, Oxford, in the press).
107. Vallar, G. & Perani, D. in *Neurophysiological and Neuropsychological Aspects of Spatial Neglect* (ed. Jeannerod, M.) 235–258 (Elsevier, North-Holland, Amsterdam, 1987).
108. Karnath, H. O., Ferber, S. & Himmelbach, M. Spatial awareness is a function of the temporal not the posterior parietal lobe. *Nature* **411**, 950–953 (2001).
109. Husain, M. & Kennard, C. Visual neglect associated with frontal lobe infarction. *J. Neurol.* **243**, 652–657 (1996).
110. Stone, S. P., Patel, P., Greenwood, R. J. & Halligan, P. W. Measuring visual neglect in acute stroke and predicting its recovery: the visual neglect recovery index. *J. Neurol. Neurosurg. Psychiatry* **55**, 431–436 (1992).
111. Weinberg, J. *et al*. Visual scanning training effects on reading-related tasks in acquired brain-damage. *Arch. Phys. Med. Rehabil.* **58**, 479–486 (1977).
112. Posner, M. I., Walker, J. A., Friedrich, F. J. & Rafal, R. D. Effects of parietal injury on covert orienting of attention. *J. Neurosci.* **4**, 1863–1874 (1984).
113. Smania, N. *et al*. The spatial distribution of visual attention in hemineglect. *Brain* **121**, 1759–1770 (1998).
114. Mattingley, J. B., Husain, M., Rorden, C., Kennard, C. & Driver, J. Motor role of human inferior parietal lobe revealed in unilateral neglect patients. *Nature* **392**, 179–182 (1998).
115. Kinsbourne, M. in *Unilateral Neglect: Clinical and Experimental Studies* (eds Robertson, I. H. & Marshall, J.) 63–86 (Erlbaum, Hillsdale, New Jersey, 1993).
116. Witte, E. A., Villareal, M. & Marrocco, R. T. Visual orienting and alerting in rhesus monkeys: comparison with humans. *Brain Res. Behav. Brain Res.* **82**, 103–112 (1996).
117. Drury, H. A. *et al*. Computerized mappings of the cerebral cortex: a multiresolution flattening method and a surface-based coordinate system. *J. Cogn. Neurosci.* **8**, 1–28 (1996).
118. Thompson, K. G., Bichot, N. P. & Schall, J. D. in *Visual Attention and Cortical Circuits* (eds Braun, J., Koch, C. & Davis, J. L.) (MIT Press, Cambridge, Massachusetts, 2001).

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