Visual attention can be seen in action in a range of everyday situations. A basketball player directs his gaze to his teammate with the ball, while at the same time monitoring the movements of three other players. A gardener's eyes are drawn to the brilliant red of a male cardinal flying against the green backdrop of a lush lawn. A cook searching for a slotted spoon in a disorganized utensil drawer passes his gaze over his target several times before noticing it.

Central to the idea of attention is the fact that the identical retinal stimulus can be processed in very different ways. We can focus our processing resources (our 'attention') on the most relevant aspect of a visual scene, relegating others to the shadows of awareness. The examples above reveal different facets of the operation of visual attention. We can 'look out of the corner of our eye', that is, focus our attention on locations other than the centre of gaze (for example, the basketball player). Attention can be attracted automatically by highly salient external information that 'pops out' of the scene (for example, the cardinal). To find a particular target that shares many visual features with the items in its vicinity, we need to attend to each item in turn (for example, the slotted spoon).

How do we focus our attention on a particular aspect of a visual display, and what are the brain mechanisms that underlie this ability? Neuroimaging studies have shown that even when the retinal stimulus remains constant, attention can substantially affect neural activity in the specific cortical areas that perceptually analyse that stimulus\(^5\). These findings raise a host of questions. In this review we discuss four long-standing questions in attention research and describe the recent brain imaging findings that are beginning to provide some intriguing answers. First, at what stage(s) of the visual processing pathway does attention act? Second, what are the units of visual information that are selected by attention? Third, how does attention affect the neural response to a stimulus? Last, what is the source of these attentional signals?

What is the locus of attentional selection?

One of the classic issues in attention research concerns the locus of attentional selection\(^6\). According to the late selection view\(^7\), preattentive vision perceptually analyses the entire scene to a high level, including identification of objects. Attention then selects a subset of this highly processed information for further analysis and response planning. In contrast, the early selection view\(^8\) holds that only rudimentary perceptual processing is carried out preattentively, such that focused attention is necessary for object recognition and many other aspects of perceptual analysis.

The crux of this debate concerns the processing fate of unattended stimuli: how far do they progress up the visual pathway? Behavioural experiments have made substantial progress in answering this question through the use of various indirect measures of the processing of
All visually responsive areas of cortex except primary visual cortex.

EVENT-RELATED POTENTIALS

Electrical potentials generated in the brain as a consequence of synchronized activation of neuronal networks by external stimuli. These evoked potentials are recorded at the scalp and consist of precisely timed sequences of waves or ‘components’ (Fig. 1).

EXTRASTRIATE CORTEX

All visually responsive areas of cortex except primary visual cortex.
fMRI procedure in which the borders of retinotopic visual areas (V1, V2, V3, and so on) are delineated, along with a representation of eccentricity and polar angle.

**VENTRAL AND DORSAL VISUAL PATHWAYS**

Visual information coming from V1 is processed in two interconnected but partly dissociable visual pathways, a 'ventral' pathway extending into the temporal lobe thought to be primarily involved in visual object recognition, and a 'dorsal' pathway extending into the parietal lobe thought to be more involved in extracting information about where an object is or 'how' to execute visually guided action towards it.

**RETRITOTOPIC MAPPING**

An fMRI procedure in which the borders of retinotopic visual areas (V1, V2, V3, and so on) are delineated, along with a representation of eccentricity and polar angle.

Study showed that the neural response to an irrelevant moving stimulus as measured in the motion-processing region MT/ MST is weaker when the primary task is difficult than when it is easy (see also Ref. 29). When early selection is difficult and response conflict results (for example, as in the Stroop task), several studies have shown that the anterior cingulate becomes active (Ref. 30). In conclusion, the functional brain imaging literature has provided an important answer to a long-standing question about visual attention — attention can strongly affect perceptual analysis at an anatomically early stage of processing in the visual pathway. Future research can now explore the mechanisms underlying these attentional effects and the precise conditions under which they occur.

### What exactly gets selected by attention?

Does attention operate on spatial locations, visual features or whole 'objects'? In most studies, attention is directed to a specific spatial location, whereas distracting information is present in other locations. Such spatial selection can be highly efficient, as implied by the 'spotlight' metaphor of attention (Ref. 30). Evidence that spatial location is often central in selection comes from behaviour (Ref. 32) and physiological (Ref. 33) studies showing enhancement of the perception of stimuli appearing near an attended target. However, behavioural studies in humans and single-unit studies in macaques indicate that attention can sometimes operate not on locations but on visual feature dimensions, such as colour or motion (Ref. 34, 35), or whole objects with all of their features (Ref. 36, 37). Brain imaging work has made a substantial contribution to our understanding of the 'units' of attentional selection.

Although spatial location clearly functions in attentional selection in many tasks, few imaging studies have shown unambiguous spatial attentional effects that cannot be accounted for in terms of feature-based or object-based selection. (Note that the retinotopically specific attentional effects discussed in the previous section need not indicate location-based selection, as they can also be explained in terms of interactions between higher-level object representations and the earlier retinotopic representations that give rise to them.) However, preliminary findings from one study (Ref. 38) show that the neural response to a task-irrelevant face or house stimulus is stronger when it is superimposed on an attended target shape than when it is superimposed on an unattended shape. Because the face and house probe stimuli neither share features with, nor are part of, the same object as the attended target, this effect can only be accounted for in terms of spatial selection.

Evidence for feature-based selection was provided by a classic experiment using PET (Ref. 1), in which subjects were asked to pay attention to different features of the same visual arrays (the colour, shape or speed of motion of the elements). Different regions in extrastriate cortex were

---

**Figure 1** | An event-related potential (ERP) attention experiment. In this experiment, subjects focus their eyes on a central fixation point, and pay attention to either the left or right visual field. Stimuli are presented to the left or right in a random order, and the subject is asked to respond to occasional targets embedded among more frequent distractors in the attended field. Grand average ERP waveforms from four scalp sites are shown, with the P1, N1 and C1 components indicated. As can be seen, the P1 and N1 components are larger for attended compared with unattended locations, whereas the C1 component is unaffected by attention. (Par, parietal; occ, occipital; contra, contralateral; ipsi, ipsilateral.) (Figure adapted from Ref. 115.)

---

**Figure 2** | Evidence for attentional baseline shifts. a | Areas in ventral visual cortex activated by the complex images in the unattended condition compared with the subsequent blank presentations (control), plotted into coronal slices of a single subject at different distances from the posterior pole of the brain. b | Activated voxels in the same subject and the same slices contrasting the expectation period (before the stimulus appeared) with the respective blank period preceding an unattended presentation (control). Note that the same areas that responded to the stimulus also responded to the expectation of the stimulus. (Figure adapted from Ref. 26.)
REVIEWS

Figure 3 | Attentional baseline shifts in V1. Curves show typical time courses of V1 activity from one subject. V1 responses were large for both pattern-present (blue) and pattern-absent (red) trials. Each curve represents the time course of the fMRI signal, averaged across time over many trials and spatially throughout the region of cortical grey matter corresponding to the V1 representation of the stimulus ring. (BOLD, blood oxygenation level dependent.) (Figure adapted from Ref. 40.)

active when subjects attended to different features of the same arrays. This result cannot be accounted for in terms of either spatial or object-based selection because all of the visual features were present in the same location and all were properties of the same objects. Instead, it argues strongly that attention can directly affect the extraction and/or representation of specific visual features (or feature dimensions). Related results have been reported using ERPs39–41 and fMRI2–5,42,43.

Evidence for both feature-based and object-based attention comes from a recent study42 in which two stimuli, a face and a house, were transparently superimposed in the same location (Fig. 4). On each trial, either the face or the house oscillated back and forth along one of four axes; and because the moving stimulus did not travel far, the face and house remained largely overlapping (movie online). Subjects’ attention was directed in different conditions to the face, the house, the direction of motion. The new result was that neural activity in each of the three cortical areas was higher if it was the face that was moving than if the house moved, even though all features were present in the same location and even though motion was completely irrelevant to the task. These data strongly indicate that objects function as the units of attentional selection over and above any tendency to select features or locations, even when the task requires only selection of a single visual attribute.

To summarize, we can attentionally select not only spatial locations, but also feature dimensions or whole visual objects with all of their features. However, some evidence indicates that we do not have perfect control over the deployment of these different modes of selection, and each of them can occur to some degree even when unintended45,46, sometimes causing interference with performance46.

How does attention affect neural responses?

How does the neural response differ for an attended versus an unattended stimulus? Considerable evidence from the monkey single-unit literature indicates that attention can modulate the gain of the neural response to visual stimuli44,45,46. That is, attention can act as a multiplier of the neural response, such that the response in an attended condition is equal to the response in the unattended condition multiplied by some gain factor. Another (non-exclusive) possibility is that attention may also produce an additive elevation of baseline firing rate, increasing neural activity by a constant amount independent of the strength (that is, contrast) of the stimulus. Although data from fMRI studies of attention are generally consistent with a gain modulation account, few imaging studies have successfully distinguished between (additive) baseline shifts and (multiplicative) gain modulations. The critical test case is one in which no stimulus is present at all, as any attention-induced increase in activity in this situation is most likely to reflect a baseline shift, not a gain modulation. Indeed, one single-unit study47 and several fMRI studies provide strong evidence that attention can indeed produce additive baseline increases in activity when no stimulus is present.

Kastner et al.48 found (Fig. 2) that during the ten-second interval when subjects were expecting a visual target to appear, neural activity increased in the retinotopically appropriate region within V2, V4 and TEO, as well as in parietal regions (discussed below) and (in two

Figure 4 | An example of a stimulus in which features and objects are superimposed in the same location. Either the face or the house oscillates back and forth. Because all relevant visual attributes of this stimulus (face, house and motion) occupy essentially the same spatial location, selective enhancement of the neural signal to any subset of these attributes indicates feature-based or object-based (rather than location-based) attention. (Figure adapted from Ref. 42.)

Movie online
unattended (and the magnitude of response when attended (that is, the magnitude of the response to an attended stimulus. If attention works by increasing neural activity in an additive rather than a multiplicative fashion, that is, the magnitude of the response to a given stimulus when attended (A) should be higher by a constant K than the magnitude of the response to the same stimulus when unattended (U), or U + K = A.

**Gain modulation**
The multiplicatively higher response to an attended compared with an unattended stimulus. If attention works by gain modulation then Ug = A, that is, the magnitude of the response to a given stimulus when attended (A) should equal the product of an attentional gain multiplier (g) and the magnitude of response to the same stimulus when unattended (U).

**Enhancement or inhibition.** Another long-standing question regarding the effect of attention on neural activity has been whether it exerts its influence by enhancing the representation of the attended stimulus or by inhibiting the representation of the unattended stimulus, or both. On the basis of behavioural experiments, it has been argued that both mechanisms are important, because performance is both enhanced by a valid location cue and disrupted by an invalid cue, in each case compared with a non-informative ‘neutral’ cue. In a similar vein, two recent fMRI studies have argued for the existence of suppressive (as well as enhancing) effects of attention. These studies found that baseline activity was lower in peripheral retinotopic cortex when subjects attended to a foveal stimulus than when they passively viewed the same stimulus, even if no stimulus was present in the periphery in either condition. Although these data are consistent with suppression in the most general sense, they do not necessarily imply an active inhibitory process or indeed any process beyond enhancement. Instead, they can be explained if: first, the passive condition entails a diffuse allocation of attention over the entire field; and second, focusing of the five subjects) in V1 (see also REF. 48). This effect is unlikely to reflect working memory for the position of the upcoming target, as it occurred even when subjects did not have to hold the information in working memory because the stimulus contained a small dot indicating the position of the expected target. In a related study, subjects were asked to detect the presence or absence of a low-contrast ring at a fixed one-second interval after the presentation of an auditory tone. An event-related fMRI technique was used (BOX 1), enabling a separate analysis of target-present and target-absent trials. As expected, the MR signal from the retinotopically appropriate part of V1 showed the typical evoked haemodynamic response for trials in which the stimulus was present, peaking at about six seconds post-stimulus, and decaying to baseline after about 20 seconds. The surprise (FIG. 3) was that a similar function was obtained for trials in which the stimulus was absent. This was not a response to the tone itself, as it was not found when subjects heard the auditory stimulus passively outside the visual task. Apparently, the tone cued subjects to attend to the location of the annulus, producing a large baseline response in V1 even when the stimulus did not appear. Furthermore, this effect was restricted to the region within V1 that responded to the location of the stimulus, so it cannot reflect a generalized increase in arousal in response to the tone. Finally, the baseline response was highly predictive of performance in the detection task.

Attention-induced baseline increases in activity in the absence of a stimulus are not always found in retinotopic regions, and are not restricted to retinotopic cortex. Shulman et al. (see also REF. 51) found increases in neural activity in area MT/MST when subjects viewed a stationary cue that indicated the likely direction of motion for a subsequent test stimulus (compared with viewing a neutral cue that provided no directional information). Related results have been reported in studies of mental imagery. Goebel et al. reported activity in the human motion-processing area M T/MST when subjects imagined moving compared with stationary stimuli (see also REF. 43,53). Similarly, O’Craven and Kanwisher found selective activation in the region of the fusiform face area during imaging of famous faces compared with imagining places, and selective activation in the region of the parahippocampal place area during imaging of places versus faces. Although the mechanisms involved in attention and mental imagery may differ in important respects, the imagery results provide further evidence that extrastriate cortex can be strongly driven by pure top-down signals when no stimulus is present at all.

The evidence is now clear that attention (and other phenomena) can create a top-down bias signal to both retinotopic cortex and higher-level visual areas (BOX 2). How do these baseline increases in activity enhance perception of the attended item? Ress et al. speculate that increasing baseline activity in the relevant neural population may bring these cells into a dynamic range where the same stimulus input will produce a larger response. In other words, the increase in baseline activity may result in an increase in the gain of the response to any stimulus that matches the expected target. However, Kastner et al. point out that, for most cortical areas, the magnitude of the baseline increase in activity when no stimulus was present was not strongly correlated with the magnitude of the attentional increase when a stimulus was present, indicating that the two effects may derive from different but partly overlapping populations of neurons. So the precise relationship between baseline effects and gain modulations remains to be determined.
attention entails not only increasing it at the target location but also withdrawing it (relative to the passive baseline) from all other locations. Therefore, current fMRI evidence does not resolve the question of whether attention involves two mechanisms, one enhancing and one suppressive. However, it has been argued that qualitatively different mechanisms may be involved in attentional enhancement and suppression, on the basis of evidence that attentional costs are associated with changes in early ERP components (80–130 ms), whereas attentional benefits are associated with changes in later ERP components (130–180 ms).

Where do attentional signals come from?
As the discussion above makes clear, neural representations throughout visual cortex can be strongly modified by bottom-up attentional signals. What is the source of these signals? Do dedicated neural systems exist for the direction of attention? If so, are common or different mechanisms involved in different kinds of attention (spatial versus nonspatial attention, overt versus covert attention, and visual versus auditory or tactile attention)?

A fronto-parietal network. The parietal and frontal lobes have long been implicated in the direction of visual attention, on the basis of patient studies showing that damage in these regions leads to attentional deficits such as neglect, single-unit studies showing that many neurons in these areas produce stronger responses to attended than to unattended stimuli. This work gave rise to the idea of an attention network composed of several frontal and parietal components, with the posterior, parietal component concerned primarily with the representation of, and orienting towards, spatial locations, and the anterior, frontal component relating to target detection, alerting and motor representation.

The evidence for a role of the fronto-parietal network in the direction of visual attention has been strengthened by functional brain imaging studies. The early studies that investigated spatial attention and orienting consistently reported parietal and frontal activations, but it was only recently that activity due to top-down control signals was distinguished from that representing attentional modulation of the sensory responses to visual stimuli. For example, the study described above showing increases in baseline neural activity during expectation of visual stimuli, found that these effects were substantially larger in parietal and frontal regions (SPL, IPS, FEF and SEF) than in retinotopic cortex. Importantly, only in parietal and frontal areas were these increases equally strong for directed attention in the absence and in the presence of visual stimuli. This suggests that the frontal and parietal activations reflect attentional operations per se, rather than attentional modulation of responses to visual stimuli. Likewise, several event-related studies found that similar parietal and frontal areas responded to attentional cues in the absence of the cued attribute. Together, these data provide support for the hypothesis that specific areas within the fronto-parietal system produce the top-down attention signals that modulate activity elsewhere in the visual system.

Do these parietal and frontal activations reflect covert attention or oculomotor intention? The general result from several imaging studies is that shifts of overt and covert attention are different. Indeed, several studies have used designs that distinguish eye movements, respectively) produce remarkably similar activations within the fronto-parietal network. This overlap is consistent with the hypothesis that all activity in these regions reflects oculomotor planning, not attention, because peripheral attention tasks might cause subjects to plan and suppress eye movements to attended stimuli even if they maintain fixation. The critical test of this hypothesis would be an attentional task that does not involve eye movement planning. Indeed, several studies have used designs that distinguish eye movements, respectively) produce remarkably similar activations within the fronto-parietal network. In one study, an attentionally demanding feature conjunction task was compared with a less demanding feature pop-out task. Crucially, the stimuli were presented in a rapid sequence at fixation, thereby eliminating any reason for subjects to plan, execute or suppress eye movements. Large activations were nonetheless found in the intraparietal sulcus, apparently reflecting pure attentional effects without the...
The parietal lobes have long been implicated in spatial processing\(^6,7,8\). But are these regions involved only in space-based selection, or also in nonspatial attention? Earlier imaging studies concentrated on spatial selection and, in particular, on covert shifts of spatial attention. For example, Corbetta et al.\(^3\) found increased activity in superior parietal and superior frontal cortex during attentional shifts to peripheral locations as compared with maintenance of attention at fixation. Later studies of similar shifting tasks localized these activations to parietal areas SPL, IPS, and frontal areas FEF, SEF, SMA, inferior frontal cortex and anterior cingulate\(^4,57,71-77\). Particularly interesting was the finding that the very same SPL area involved in attentional shifting was also more active during conjunction than during feature search, providing support for the hypothesis that conjunction search requires subjects to attend to each object’s location in turn (box 2).

However, new evidence arguing against a purely spatial account of parietal and frontal involvement in visual attention comes from several studies investigating foveal attention tasks. As described above, a non-spatial conjunction versus feature detection task carried out at the fovea activates large regions of the intraparietal sulcus\(^6\). Similarly, Le et al.\(^6\) found that SPL/IPS (and cerebelum) were more active when subjects had to alternately detect a target colour or shape, than when they had to detect just the colour or just the shape (all stimuli were foveally presented). Furthermore, Coull et al.\(^8\) report that parietal and frontal (for example, SMA, inferior frontal, insula) areas can be driven by orienting attention to different intervals in time in expectation of foveal targets. Finally, similar frontal and parietal activations were found\(^9\) when subjects had to detect motion among the stimuli presented at the fovea, and the same location was attended in the comparison conditions, so selection of different locations is unlikely to explain the observed activations. These data do not easily fit into the space-based account and therefore strongly implicate parietal regions in nonspatial attention (for converging neuropsychological evidence, see REFS 87,88).

The wide variety of attentional tasks that have been shown to activate apparently similar parietal regions indicate that these regions play a very general role in visual attention. However, comparing the activated loci across subjects and even across studies can be problematic because of the necessarily imperfect alignment of anatomically different brains. Stronger evidence for overlapping activations comes from a study\(^10\) that showed that, within individual subjects, identical voxels in the intraparietal sulcus produced significant activations in three very different attention tasks (FIG. 6), including spatial and nonspatial attention; but these same voxels were not activated by a difficult language task with minimal demands on visual attention. This finding is reminiscent of responses in monkey area LIP, in which visually sensitive neurons can show an increased firing rate related to attention, eye movements, working memory or expectation of a stimulus\(^11\). The

---

**Figure 6 | The generality of parietal involvement in visual attention.** a | Averaged group data showing overlapping activations (white) through the entire extent of the intraparietal sulcus. The overlap was tested for three visual attention tasks: spatial shifts of attention, shape matching and nonspatial attention. Other colours represent activations with partial or no overlap (colour scheme as in inset). b | Regions of the anterior (AIPS) and posterior (IPTO) intraparietal sulcus showing overlapping activations in individual subjects. (Figure adapted from REF. 81.)
Multitasking and attentional control in the brain

Are the parietal and frontal regions that are involved in directing attention specific to vision, or are they also engaged when attention is directed to information from other sensory modalities? In a study of auditory attention, Pugh et al. reported that discrimination of tones or syllables produced stronger activations in IPL, SPL and inferior frontal cortex under dichotic than binaural listening conditions, areas that resemble those involved in visual attention. In a direct within-subjects comparison of visual and auditory oddball detection tasks, Linden et al. found highly consistent activations in similar areas (inferior frontal and superior parietal) for the two types of targets, indicating that these regions are important in target detection both in audition and vision (see also Refs 186–190). In addition, similar frontal activations have also been reported for tactile discrimination and cross-modal tactile–visual shape matching. Although parietal activity tends to be more anterior for tactile than visual attention, indicating some specialization, a tactile task that involves spatially directed attention can activate the same intraparietal area as an analogous visuospatial task. Furthermore, Downar et al. found that several frontal areas as well as the temporoparietal junction (TPJ) were notably activated when subjects were monitoring for a stimulus change, independently of whether the change occurred in auditory, visual or tactile stimuli, indicating that attention-related activity in this region may be multimodal. So, although attention in audition and touch have been investigated less intensively than in vision, recent data indicate that several regions in frontal and parietal cortex may be involved in attentional selection independently of modality, or in an even broader function.

Conclusions

Attention is central to the construction of every visual experience. Although much has been learned about attention from several decades of intensive research, brain imaging has now begun to provide important new insights. First, attention affects processing at the first stage of cortical information processing, in the primary visual cortex. Second, attention not only modulates the gain on incoming visual information, but can also add a pure top-down signal that increases baseline activity in striate and extrastriate cortex. Third, attention can under different conditions select locations, features, objects or a combination thereof. Last, large regions within the fronto-parietal network, which apparently provide the source of top-down bias signals in visual areas, support a very heterogeneous set of attentional functions. In fact, the functions that have been ascribed to this network (or parts of it) include not only visual attention and visuomotor coordination, but also attention in other modalities (Box 3) and disparate functions that include spatial and verbal working memory, mathematical understanding, the representation of decision variables, and even the factor of general intelligence. The challenge for future research will be to determine what accounts for the breadth of function in these areas, and to determine how the different components of the network contribute to attentional selection and control.

FURTHER INFORMATION

Movie of Figure 4

...in earlier areas, and increased with the synaptic distance of an area from V1 along the dorsal stream processing stream.


O’Cra…

Heywood, A. & Ro…


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).

Cortical area MT was activated more strongly by irrelevant motion stimuli when subjects carried out an easy primary task than a difficult one, consistent with Lavie’s theory that attention selects early under conditions of high load and late under conditions of low load.


An fMRI study showing that mental imagery of motion activates cortical area MT; this action was also observed in earlier areas, and increased with the synaptic distance of an area from V1 along the dorsal stream processing stream.


O’Cra…

Heywood, A. & Ro…


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).


This study used both blocked and event-related fMRI to dissociate activity owing to an attentional cue, reflecting top-down control signals, versus detection of a relevant stimulus. Several areas (for example, precentral and intraparietal) were activated during the cue period, with others (for example, prefrontal cortex) activating just during target presentation (see also references 67,69).


REVIEWS

85. Corbetta, M., Shulman, G. L., Miezin, F. M. & Petersen, S. E. Systematic analysis of deficits in visual attention tasks (but not a difficult task with minimal attentional requirements) produce overlapping activations in the intraparietal sulcus, consistent with the hypothesis that these areas support several modes of visual selection. J. Neurophysiol. 80, 362–389 (1997).
90. Corbetta, M., Shulman, G. L., Miezin, F. M. & Petersen, S. E. Systematic analysis of deficits in visual attention tasks (but not a difficult task with minimal attentional requirements) produce overlapping activations in the intraparietal sulcus, consistent with the hypothesis that these areas support several modes of visual selection. J. Neurophysiol. 80, 362–389 (1997).
This paper reported that detection of changes in visual, auditory or tactile stimuli activates a right-lateralized multimodal network, including temporoparietal junction and several frontal areas.
Acknowledgements: We thank M. Chun, P. Downing, R. Epstein, Y. Jiang, M. Shuman and D. Somers for helpful comments on the manuscript. Work on this paper was supported by a Human Frontiers grant to N.K.