VISUAL ATTENTION: INSIGHTS FROM BRAIN IMAGING

Nancy Kanwisher and Ewa Wojciulik‡*

We are not passive recipients of the information that impinges on our retinae, but active participants in our own perceptual processes. Visual experience depends critically on attention. We select particular aspects of a visual scene for detailed analysis and control of subsequent behaviour, but ignore other aspects so completely that moments after they disappear from view we cannot report anything about them. Here we show that functional neuroimaging is revealing much more than where attention happens in the brain; it is beginning to answer some of the oldest and deepest questions about what visual attention is and how it works.

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 (BOX 1) 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[1–5]. 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

*Department of Brain and Cognitive Sciences,
Massachusetts Institute of Technology, NE20-454,
77 Mass Avenue, Cambridge,
Massachusetts 02138, USA.
‡Medical Research Council,
Cognition and Brain Sciences Unit,
15 Chaucer Road,
Cambridge CB2 2EF, UK.
Correspondence to N.K.
e-mail: ngk@psyche.mit.edu

Box 1 | Functional brain imaging: a guide

When neural populations within a focal region of the brain become active, blood flow to this region increases to supply the increased metabolic demands. In positron emission tomography (PET), these focal changes in blood flow are traced with a radioactive substance that is injected into the bloodstream and carried into the brain. Although much of the pioneering work in visual attention was carried out using PET[1], this technique has relatively low spatial resolution and only a few scans can be run on each subject because of the radiation dose[96]. In contrast, functional magnetic resonance imaging (fMRI) is thought to be without risk, so individuals can be scanned several times within and across scanning sessions. fMRI therefore offers substantial advantages, including higher spatial and temporal resolution and the ability to study individual subjects in detail (FIG. 2).

fMRI uses essentially the same equipment and principles as those involved in conventional medical MRI scanning, with two exceptions. First, fMRI scanners can take images at a faster rate (ten or more images of individual brain slices per second). Second, the fMRI signal is sensitive to function (rather than just anatomical structure). The most commonly used fMRI signal is called BOLD (blood oxygenation level-dependent), and is based on changes in the relative concentrations of oxygenated and deoxygenated haemoglobin that occur when blood flow increases[97]. Because blood flow regulation is relatively slow, so too is the typical fMRI response, taking four to six seconds to peak after the onset of neuronal activity (FIG. 3). In 'blocked' experimental designs, many trials of one condition appear consecutively in an 'epoch' lasting tens of seconds. In 'event-related' designs, trials of different conditions are interleaved[98]. Blocked designs usually have more power, whereas event-related designs enable different stages of the neural response to be analysed separately.

fMRI is powerful, but has two important limitations. The temporal resolution is two or three orders of magnitude lower than that of single unit recording or event-related potentials (ERPs). So fMRI cannot separate different neural events underlying attention that occur only a few milliseconds (or tens of milliseconds) apart in the same brain area. Second, like other physiological recording techniques, fMRI can show only when neural activity occurs in particular tasks, not when such activity is necessary for the task at hand. Necessity can only be established through the use of disruption techniques, such as transcranial magnetic stimulation, or through studies of human patients with focal brain damage.

INATTENTIONAL BLINDNESS
In a typical experiment, the subject decides which is longer, the horizontal or vertical arm of a large cross presented at fixation. An unexpected stimulus is then presented in the region of the cross, and immediately after the subject responds to the cross they are asked if they saw anything else. On a substantial number of trials, subjects do not report noticing the presence of the object at all.

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.

unattended items[9,10]. However, with physiological measures, the neural response to unattended stimuli can be measured directly, online, and without the subject knowing what the experimenter is measuring, thereby bypassing the limitations of some behavioural techniques. For example, in the behavioural phenomenon of INATTENTIONAL BLINDNESS[11], subjects are frequently unable to report an unexpected distractor item that appears close to a target stimulus, even when queried just moments after the display disappears. Although behavioural data do not enable determination of whether this inability is owing to the failure to process the unexpected item or the rapid forgetting of that item, recent functional neuroimaging data provide evidence for the former interpretation[12].

Attention and primary visual cortex. Visual attention has long been studied using single neuron activity in monkeys and EVENT-RELATED POTENTIALS (ERPs) recorded from the human scalp. The predominant result from both lines of research is that substantial effects of attention can be found throughout EXTRASTRIATE CORTEX, but that the processing of attended and unattended items does not differ at the earliest stage of cortical visual processing, namely PRIMARY VISUAL CORTEX (V1). An extensive ERP literature shows large effects of spatial attention on the P1 and N1 components of the visual response (FIG. 1), thought to originate in extrastriate cortex, but no attentional modulation on the C1 response thought to originate in primary visual cortex[13]. Similarly, the single-unit literature includes many reports of attentional modulation of neural responses in both the VENTRAL[14] AND DORSAL[15] VISUAL PATHWAYS in the macaque, but until recently[16–18] few reports of attentional modulations in V1 (REFS 19,20). So both the monkey physiology and the human ERP literatures converged to suggest that attention can affect processing in extrastriate visual areas but not that conducted by primary visual cortex.

However, in the past two years, half a dozen functional magnetic resonance imaging (fMRI) studies have been published that completely overturn this conclusion. In one study[21], subjects maintained central fixation while judging the speed of one of two moving gratings displayed to the left and right of this point. RETINOTOPIC MAPPING was carried out in individual subjects to find the precise region within V1 that responded to each grating. In stark contrast to previous ERP and single unit recording studies, substantial attentional modulations of the V1 response were found (these attentional effects were about 25% of the size of those found by alternating the grating stimulus with a uniform field). Around the same time, similar results were reported in many other labs[22–26]. Collectively, these results provide a clear and crisp answer to one of the oldest questions regarding visual attention — neural responses to visual stimuli can be modulated at an early stage in the visual processing pathway.

How can these results be reconciled with the failure to find attentional modulation of the C1 ERP response from V1? Martinez *et al.*[25] suggest an intriguing answer. In essentially identical experiments using ERPs and fMRI, they found that attentional modulation of the V1 response was substantial as measured by fMRI but nonexistent as measured by the C1 ERP. Martinez *et al.* reasoned that the C1 wave reflected the initial response to visual information in V1, presumably the result of BOTTOM-UP, FEEDFORWARD PROCESSING. However, the temporal resolution of fMRI is very low, so this signal will reflect both initial feedforward processes and longer-latency, TOP-DOWN, FEEDBACK influences. Martinez *et al.* therefore argue that the attentional modulation observed in primary visual cortex with fMRI reflects feedback processes. On this interpretation, attentional selection operates early in the anatomical sense (that is, it affects an early stage of the visual pathway), but not in the temporal sense (that is, the effect may result from later feedback). This interpretation unifies the data obtained by ERP and fMRI. However, an alternative interpretation of the difference between the results from fMRI and ERPs is that the attentional effects measured with fMRI represent baseline increases in neural activity (FIGS 2,3) that may occur before the stimulus appears and that may be more difficult to detect with ERPs.

The fact that attention can apparently select at an anatomically early stage under some circumstances need not imply that it always does. Indeed, according to one theory of visual attention[27], the stage of selection depends on the processing load of the primary task, with early selection occurring when processing load is high and selection occurring at a later stage when processing load is low. Consistent with this hypothesis, one imaging

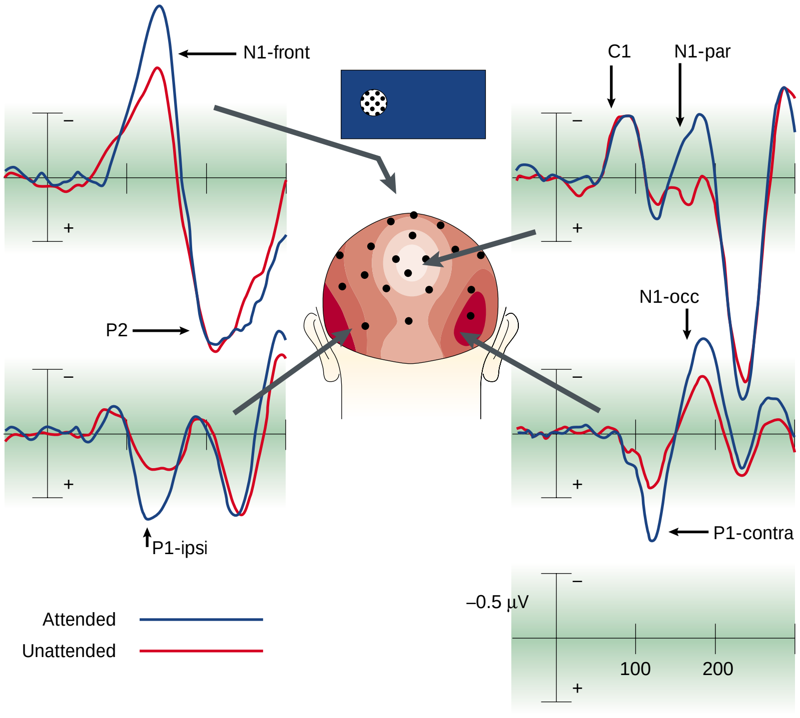


Figure 1 | **An event-related potential (ERP) attention experiment**. In this experiment, subjects focus their eyes on a central fixation point, and pay attention to either the left or right visual field. Stimuli are presented to the left or right in a random order, and the subject is asked to respond to occasional targets embedded among more frequent distractors in the attended field. Grand average ERP waveforms from four scalp sites are shown, with the C1, P1 and N1 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.)

PRIMARY VISUAL CORTEX
The cortical area that is the main recipient of visual information coming from the retinae (by way of the lateral geniculate nucleus, or LGN); also known as V1 or striate cortex.

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 lobes thought to be more involved in extracting information about 'where' an object is or 'how' to execute visually guided action towards it.

RETINOTOPIC 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[28] 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[30,31].

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.

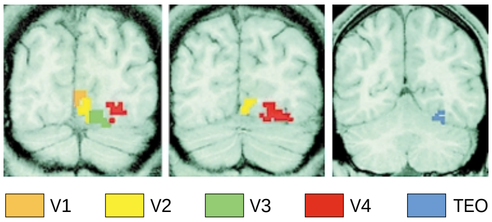
What exactly gets selected by attention?

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[32]. Evidence that spatial location is often central in selection comes from behavioural[32] and physiological[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[34,35], or whole objects with all of their features[16,36,37]. 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[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[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

a **Unattended presentations versus control**



b **Expectation versus control**

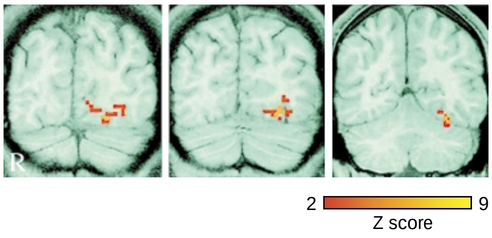


Figure 2 | **Evidence for attentional baseline shifts. a** | Areas in ventral visual cortex activated by the complex images in the unattended condition compared with the subsequent blank presentations (control), plotted into coronal slices of a single subject at different distances from the posterior 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.)

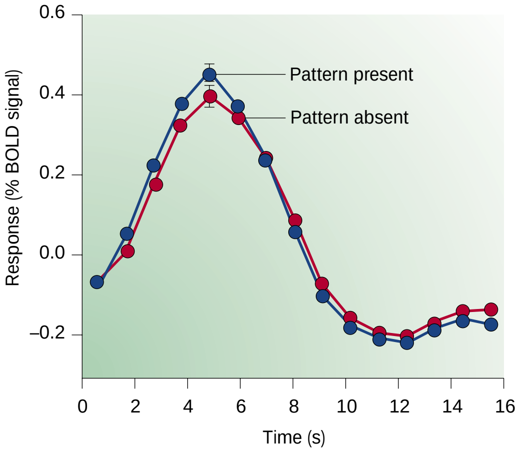


Figure 3 | **Attentional baseline shifts in V1.** Curves show typical time courses of V1 activity from one subject. V1 responses were large for both pattern-present (blue) and pattern-absent (red) trials. Each curve represents the time course of the fMRI signal, averaged across time over many trials 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. 49.)

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 ERPs[39–41] and fMRI[2–5,42,43].

Evidence for both feature-based and object-based attention comes from a recent study[42] 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 or the position of the stationary stimulus (which was displaced very slightly off centre). Consistent with feature-based selection, neural activity was higher in the face-selective FUSIFORM FACE AREA[44] when subjects attended to the faces, in the place-selective PARAHIPPOCAMPAL PLACE AREA[45] when subjects attended to the houses, and in MT/MST when subjects attended to the direction of motion. The new result was that neural activity in each of the three cortical areas was higher when the corresponding visual attribute was the irrelevant property of an attended object than when it was a property of the unattended object. For example, when attending to the face, the signal was higher in MT/MST 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 unintended[35,43], sometimes causing interference with performance[10].

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 stimuli[14,35,46,47]. 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 study[13] 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.*[26] 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

BOTTOM-UP, FEEDFORWARD 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.

TOP-DOWN FEEDBACK
The flow of information from 'higher' to 'lower' centres.

MT/MST
Middle temporal and medial superior temporal extrastriate areas involved in the analysis of visual motion information.

FUSIFORM FACE AREA (FFA)
A cortical region in the middle fusiform gyrus that responds at least twice as strongly in fMRI when subjects view faces as when they view various nonface stimuli.

PARAHIPPOCAMPAL PLACE AREA
A bilateral region in parahippocampal cortex that produces at least twice as strong a signal in fMRI when subjects view images of places (including indoor and outdoor scenes and houses) as when they view images of nonplaces (for example, objects and faces).

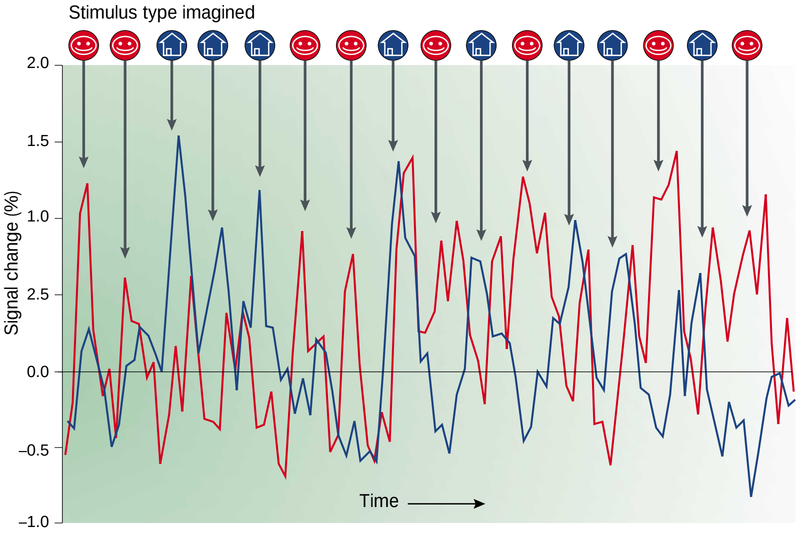


Figure 5 | **Neural correlates of single mental imagery events.** Unaveraged time course of percentage signal change in fusiform face area (FFA) region (red) and parahippocampal place area (PPA) region (blue) from a single scan in one subject. The arrows show the points in the sequence (one every twelve seconds) at which instructions were given (shifted by the estimated haemodynamic lag) to imagine either a particular famous face or a famous place. From a visual inspection of the raw time course of MR signal intensity in these two regions, it is possible to determine whether the subject was imagining a face or a place. (Figure adapted from REF. 54.)

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[49], 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[50,51]. Shulman *et al.*[50] (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.*[52] reported activity in the human motion-processing area MT/MST when subjects imagined moving compared with stationary stimuli (see also REFS 43,53). Similarly, O'Craven and Kanwisher[54] found selective activation in the region of the fusiform face area[44] when subjects closed their eyes and imagined faces (compared with imagining places), and selective activation in the region of the parahippocampal place area[45] during imagination of places versus faces (FIG. 5). 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.*[49] 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.*[26] point out that, for most cortical areas, the magnitude of the baseline attentional increase 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.

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[55], 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

BASELINE SHIFTS
The increased response in a given neural population in an attended compared with unattended condition when no stimulus is present at all. Such effects imply that attention increases 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).

Box 2 | Attention: integration, competition and top-down control

One theory that brings together all of the reviewed attention effects (top-down biases, gain modulation, enhancement and suppression) is Desimone and Duncan's[99,100] 'biased competition' model of attention. The theory rests on three assumptions. First, given the limits on our ability to process several stimuli at once, visual objects compete for representational resources, and only one or a small number of stimuli can be represented at one time. As the neural representations of visual stimuli are highly distributed, competitive processing occurs in many of the brain areas sensitive to visual input. Second, the competition is integrated across several areas, such that the neural populations that represent different aspects of a single object interact in a mutually facilitatory fashion. The gain in response to the selected object is accompanied by suppressed processing in the neural populations representing features of different objects. Therefore, as a 'winner' emerges in one system, the same object becomes dominant across the distributed network. Last, the competition can be biased not only by bottom-up factors (for example, stimulus intensity), but also by top-down influences that are based on current task demands. Top-down bias is reflected in neural priming (enhanced processing) of populations representing the relevant object attributes, resulting in a competitive advantage for the relevant stimulus. An important challenge for this theory (and other theories of attention) is to explain precisely how the distributed neural populations responding to a single object 'know' that they are representing the same object and so should enhance each other while supressing the neural representations of other objects (the binding problem).

One model of attention that specifically addresses the binding problem is Treisman's feature integration theory[86,101]. According to this theory, simple visual features, such as orientation, colour or motion, are analysed pre-attentively and in parallel across the visual scene. Serial shifts of spatial attention to each object's location allow binding of such separately represented attributes into coherent object representations. Features that are present at the attended location become integrated together into a stable percept by reference to a 'master map of locations', which maintains links to the feature maps. In this model, parietal cortex is hypothesized to represent the master map of locations and therefore play a privileged role in binding[102] (but see REF. 103). This model therefore places heavier emphasis on location as the unit of selection, and consequently on parietal cortex as the critical locus of integration, as compared with selection of objects and more distributed integration in the biased competition model.

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[56] 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 top-down 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[57–59], and single-unit studies showing that many neurons in these areas produce stronger responses to attended than to unattended stimuli[60,61]. 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[57,62].

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[63–65] 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[26], 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[66–69] 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[70] or oculomotor intention[71,72]? The general result from several imaging studies is that shifts of overt[73,74] and covert[63,64,75,76] attention (that is, with and without eye movements, respectively) produce remarkably similar activations within the fronto-parietal network[77–79]. 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 invoke eye movement planning. Indeed, several studies have used designs that distinguish eye-movement planning and visual attention by engaging attention at the fovea[66,68,80,81]. In one study[81], 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

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

POP-OUT
In displays composed of identical distractor stimuli (for example, red Xs), a stimulus with a unique feature (for example, a blue X) can be detected rapidly and effortlessly, with little or no increase in reaction time as the number of distractor stimuli increases.

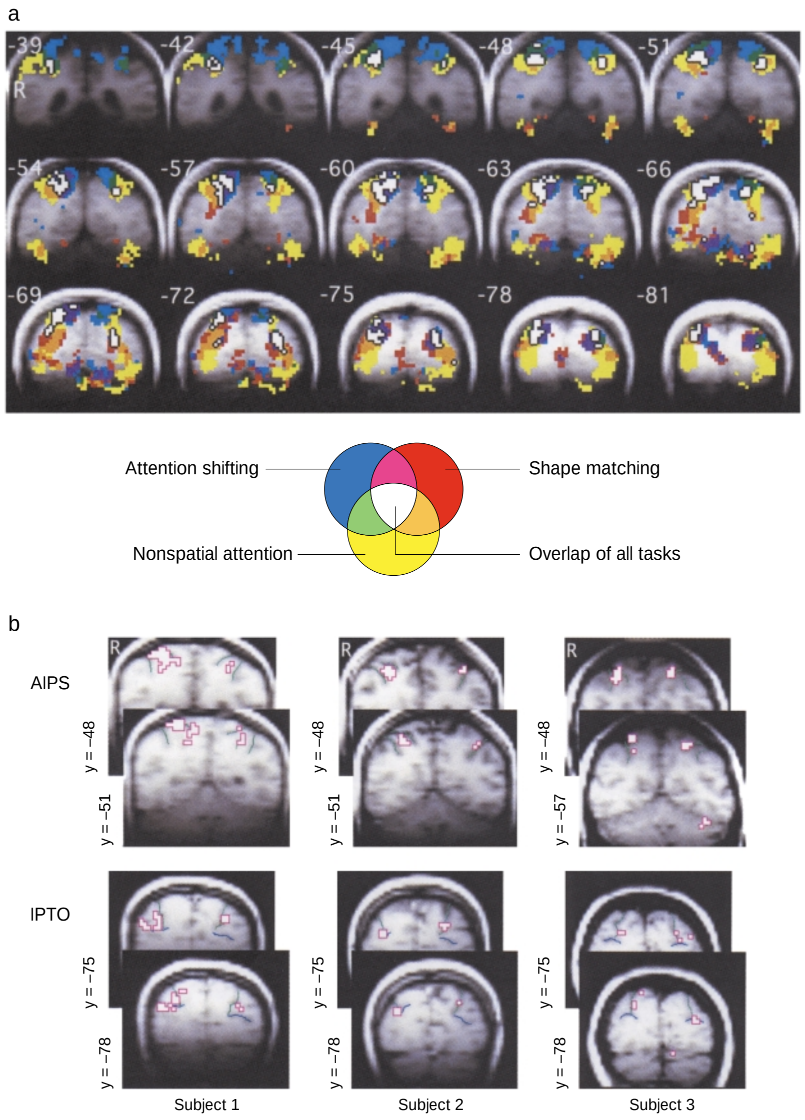


Figure 6 | **The generality of parietal involvement in visual attention. a** | Averaged group data showing overlapping activations (white) through the entire extent of the intraparietal sulcus. The overlap was tested for three visual attention tasks: spatial shifts of attention, shape matching and nonspatial 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.)

involvement of the eye movement system. This activation is unlikely to reflect the engagement of a system for maintaining fixation[82], because subjects fixated in both conditions. Other studies, investigating attention tasks in which the stimulus is presented at the fovea, obtained similar results in parietal and frontal cortex[66,68,80] (see below). Furthermore, activity in several areas, particularly in parietal cortex, was found to increase linearly with increasing task demands: as the number of attended stimuli increased, so did parietal activity. Such linear increases are difficult to explain in terms of covert eye movement plans or eye movement suppression[83]. So it seems that at least some of the parietal and frontal activity reflects 'pure' covert attention, distinct from oculomotor intention.

LIP
Lateral intraparietal area in the posterior parietal cortex of the monkey; single-unit physiological studies have shown that this area contains visually sensitive cells that increase their firing rate when a stimulus in their receptive field is attended, or is a target for a stimulus-driven or memory-guided saccade.

Just spatial attention? The parietal lobes have long been implicated in spatial processing[57,84]. 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.*[63] 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[64,75,77–79]. 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[81]. Similarly, Le *et al.*[80] found that SPL/IPS (and cerebellum) 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.*[68] 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[66] when subjects had to detect motion following an informative (versus neutral) cue. In all of these studies, all stimuli were 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[81] 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[89]. The

Box 3 | Attention in vision, audition and touch

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.*[104] 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.*[105] found highly consistent activations in similar areas (inferior frontal and inferior parietal) for the two types of targets, indicating that these regions are important in target detection both in audition and vision (see also REFS 106–108). In addition, similar frontal activations have also been reported for tactile discrimination[109] and cross-modal tactile–visual shape matching[110,111]. Although parietal activity tends to be more anterior for tactile than visual attention, indicating some specialization[109–111], a tactile task that involves spatially directed attention can activate the same intraparietal area as an analogous visuospatial task[112]. Furthermore, Downar *et al.*[113] 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[114].

fact that parts of parietal cortex activate to a wide variety of visually demanding tasks is consistent with the hypothesis that they contribute to top-down biases observed in ventral pathway. Indeed, this property is precisely what a top-down attentional system should have to bias activity in ventral visual areas based solely on the attended attribute, be it a complex object, a simple feature or a location.

Although many frontal and parietal areas participate in a diverse set of attention tasks, a greater degree of functional differentiation may ultimately be found, especially with the use of event-related methods. For example, a recent event-related study[66] found that several frontal and parietal regions responded both during an attentional cue (before target onset) and during target detection. However, some areas (for example, IPS) activated selectively to the cue, indicating a specific function in the maintenance of top-down bias signals, whereas others activated selectively during target detection (for example, prefrontal cortex). A related study investigating spatial cueing[67] confirmed that the IPS was primarily driven by a directional cue, with a weaker response to target detection, whereas the right temporo-parietal junction (TPJ) responded only to target detection (see also REF. 69). The TPJ response was larger on invalidly than on validly cued trials, indicating that it may be particularly important for reorienting of attention towards unattended locations. Interestingly, attentional reorienting to a different temporal interval (invalid versus valid temporal cues) may rely on a similar area close to the TPJ in the left hemisphere[68]. So event-related fMRI methodology could prove particularly useful in isolating the specific neural mechanisms that underlie distinct attentional operations.

Despite the few pieces of evidence for specialization within the attentional functions of the parietal and frontal lobes, the main picture that emerges from this literature is that these regions are involved broadly in several 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[90], but also attention in other modalities (BOX 3) and disparate functions that include spatial[91] and verbal[92] working memory, mathematical understanding[93], the representation of decision variables[94], and even the factor *g* of general intelligence[95]. 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.

Conclusions

Attention is central to the construction of every visual experience. Although much has been learned about attention from several decades of intensive behavioural 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 attention tasks. This suggests that new ways of thinking may be required to determine how the neural system segregates attentional control into distinct processes. So, neuroimaging research on visual attention has transcended mere phrenology and has begun to answer questions of substantial theoretical interest.

Links

FURTHER INFORMATION Movie of Figure 4

1. Corbetta, M. *et al.* Attentional modulation of neural processing of shape, color, and velocity in humans. *Science* **248**, 1556–1559 (1990).
   A classic early PET study showing that selective attention to speed, colour or shape can modulate activity in extrastriate cortex, enhancing activity in regions that are apparently specialized for processing information related to the selected attribute.
2. O'Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A. & Savoy. R. L. Voluntary attention modulates fMRI activity in human MT–MST. *Neuron* **18**, 591–598 (1997).
3. Wojciulik, E., Kanwisher, N. & Driver, J. Covert visual attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *J. Neurophysiol.* **79**, 1574–1578 (1998).
4. Beauchamp, M. S., Cox, R. W. & DeYoe, E. A. Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *J. Neurophysiol.* **78**, 516–520 (1997).
5. Clark, V. P. *et al.* Selective attention to face identity and color studied with fMRI. *Hum. Brain Mapp.* **5**, 293–297 (1997).
6. Broadbent, D. *Perception and Communication* (Pergamon, London, 1958).
7. Deutsch, J. A. & Deutsch, D. Attention: some theoretical considerations. *Psychol. Rev.* **87**, 272–300 (1963).
8. Broadbent, D. Task combination and selective intake of information. *Acta Psychol.* **50**, 253–290 (1982).
9. Tipper, S. P. & Driver, J. Negative priming between pictures and words in a selective attention task: evidence for semantic processing of ignored stimuli. *Mem. Cogn.* **16**, 64–70, (1988).
10. Driver, J. & Baylis, G. C. Movement and visual attention: the spotlight metaphor breaks down. *J. Exp. Psychol. Hum. Percept. Perform.* **15**, 448–456 (1989).
11. Rock, I., Linnett, C. M., Grant, P. & Mack, A. Perception without attention: results of a new method. *Cogn. Psychol,* **24**, 502–534 (1992).

12. Rees, G., Russell, C., Frith, C. D. & Driver, J. Inattentional blindness versus inattentional amnesia for fixated but ignored words. *Science* **286**, 2504–2507 (1999).
13. Luck, S. J. & Girelli, M. in *The Attentive Brain* (ed. Parasuraman, R.) 71–94 (MIT Press, Boston, 1998).
14. Moran, J. & Desimone, R. Selective attention gates visual processing in the extrastriate cortex. *Science* **229**, 782–784 (1985).
15. Maunsell, J. H. R. The brain's visual world: representation of visual targets in cerebral cortex. *Science* **270**, 764–769 (1995).
16. Roelfsema, P. R., Lamme, V. A. & Spekreijse, H. The implementation of visual routines. *Vision Res.* **40**, 1385–1411 (2000).
17. Ito, M. & Gilbert, C. D. Attention modulates contextual influences in the primary visual cortex of alert monkeys. *Neuron* **22**, 593–604 (1999).
18. Mehta, A. D., Ulbert, I. & Schroeder, C. E. Intermodal selective attention in monkeys. I: distribution and timing of effects across visual areas. *Cereb. Cortex* **10**, 343–358 (2000).
19. Luck, S. J., Chelazzi, L., Hillyard, S. A. & Desimone, R. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.* **77**, 24–42 (1997).
20. Motter, B. C. Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* **70**, 909–919 (1993).
21. Gandhi, S. P., Heeger, D. J. & Boynton, G. M. Spatial attention affects brain activity in human primary visual cortex. *Proc. Natl Acad. Sci. USA* **96**, 3314–3319 (1999).
22. Brefczynski, J. A. & DeYoe, E. A. A physiological correlate of the 'spotlight' of visual attention. *Nature Neurosci.* **4**, 370–374 (1999).
    This study used fMRI to show the neural correlates of the attentional 'spotlight' in human retinotopic visual cortex. As subjects' attention moved from one location to the next with the stimulus held constant, cortical activity varied in a fashion similar to that observed when an actual stimulus moves over the same locations.
23. Somers, D. C., Dale, A. M., Seiffert, A. E. & Tootell, R. B. Functional MRI reveals spatially specific attentional modulation in human primary visual cortex. *Proc. Natl Acad. Sci. USA* **96**, 1663–1668 (1999).
24. Watanabe, T. *et al.* Task-dependent influences of attention on the activation of human primary visual cortex. *Proc. Natl Acad. Sci. USA* **95**, 11489–11492 (1998).
25. Martinez, A. *et al.* Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neurosci.* **2**, 364–369 (1999).
    An elegant study in which both ERPs and fMRI experiments were run on the same attentional paradigm; although the earliest cortical response to visual stimuli was not modulated by attention as measured by ERPs, attentional modulation was nonetheless found in the primary visual cortex, as measured with fMRI. The authors hypothesize that the attentional effects found with fMRI may represent a delayed, re-entrant feedback from higher visual areas or a sustained biasing of striate cortical neurons during attention.
26. Kastner, S., Pinsk, M., De Weerd, P., Desimone, R. & Ungerleider, L. Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron* **22**, 751–761 (1999).
    This is the first study to report attentional modulation of activity in retinotopic cortex in the absence of visual stimulation (a baseline shift). This effect was stronger in frontal and parietal areas, indicating that they provide the source of top-down control signals that bias neural activity in the visual cortex.
27. Lavie, N. Perceptual load as a necessary condition for selective attention. *J. Exp. Psychol. Hum. Percept. Perform*. **21**, 451–468 (1995).
28. Rees, G., Frith, C. D. & Lavie, N. Modulating irrelevant motion perception by varying attentional load in an related task. *Science* **28**, 1616–1619 (1997).
    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.
29. Handy, T. C. & Mangun, G. R. Attention and spatial selection: electrophysiological evidence for modulation by perceptual load. *Percept. Psychophys.* **62**, 175–186 (2000).
30. Pardo, J. V., Pardo, P. J., Janer, K. W. & Raichle, M. E. The anterior cingulate cortex mediates processing selection in the Stroop attentional conflict paradigm. *Proc. Natl Acad. Sci. USA* **87**, 256–259 (1990).
31. Casey, B. J. *et al.* Dissociation of response conflict, attentional selection, and expectancy with functional magnetic resonance imaging. *Proc. Natl Acad. Sci. USA* **97**, 8728–8733 (2000).
32. Eriksen, B. A. & Eriksen, C. W. Effects of noise letters upon the identification of a target letter in a non-search task. *Percept. Psychophys.* **16**, 143–149 (1974).
33. Connor, C. E., Preddie, D. C., Gallant, J. L. & Van Essen, D. C. Spatial attention effects in macaque area V4. *J. Neurosci.* **17**, 3201–3214 (1997).
34. Chaudhuri, A. Modulation of the motion aftereffect by selective attention. *Nature* **344**, 60–62 (1990).
35. Treue, S. & Trujillo, J. C. M. Feature-based attention influences motion processing in macaque visual cortex. *Nature* **399**, 575–579 (1999).
36. Duncan, J. Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* **113**, 501–517 (1984).
37. Blaser, E., Pylyshyn, Z. & Holcombe, A. Tracking an object through feature-space. *Nature* (in the press).
38. Downing, P. & Kanwisher, N. fMRI evidence for location-based attentional selection. (Paper to be presented at the Society for Neuroscience, New Orleans, 2000.)
39. Anllo-Vento, L., Luck, S. J. & Hillyard, S. A. Spatio-temporal dynamics of attention to color: evidence from human electrophysiology. *Hum. Brain Mapp*. **6**, 216–238 (1998).
40. Torriente, I., Valdes-Sosa, M., Ramirez, D. & Bobes, M. A. Visual evoked potentials related to motion-onset are modulated by attention. *Vision Res*. **39**, 4122–4139 (1999).
41. Eimer, M. Attentional modulations of event-related brain potentials sensitive to faces. *Cogn. Neuropsychol.* **17**, 103–116 (2000).
42. O'Craven, K., Downing, P. & Kanwisher, N. fMRI evidence for objects as the units of attentional selection. *Nature* **401**, 584–587 (1999).
    Subjects viewed stimuli consisting of a face transparently superimposed on a house, with one moving and the other stationary. Consistent with object-based models of attention, attention to one attribute of the stimulus (for example, the motion) produced not only enhancement in the cortical region coding that attribute (for example, MT), but also enhancement in the cortical region coding the other attribute of the same object (for example, the fusiform face area, when it was the face that was moving).
43. O'Craven, K. M. & Kanwisher, N. Visual imagery of moving stimuli activates area MT/MST. (Paper presented at the Society for Neuroscience, New Orleans,1997).
44. Kanwisher, N., McDermott, J. & Chun, M. The fusiform face area: a module in human extrastriate cortex specialized for the perception of faces. *J. Neurosci.* **17**, 4302–4311 (1997).
45. Epstein, R. & Kanwisher, N. A cortical representation of the local visual environment. *Nature*, **392**, 598–601 (1998).
46. McAdams, C. J. & Maunsell, J. H. Effects of attention on the reliability of individual neurons in monkey visual cortex. *Neuron* **23**, 765–773 (1999).
47. Reynolds, J., Pasternak, T. & Desimone, R. Attention increases sensitivity of V4 neurons. *Neuron* **26**, 703–714 (2000).
48. Smith, A. T., Singh, K. D. & Greenlee, M. W. Attentional suppression of activity in the human visual cortex. *Neuroreport* **7**, 271–277 (2000).
49. Ress, D, Backus, B. & Heeger, D. Activity in primary visual cortex predicts performance in a visual detection task. *Nature Neurosci.* **3**, 940–945 (2000).
    When subjects were cued by a tone to look for a dim annulus grating, activity in human V1 increased almost as much when no annulus was actually presented as when it was. This large stimulus-independent 'baseline shift' in V1 predicted accuracy at the annulus detection task, showing that attentional effects in V1 are large and are predictive of task performance.
50. Shulman, G. L. *et al.* Areas involved in encoding and applying directional expectations to moving objects. *J. Neurosci*. **19**, 9480–9496 (1999).
51. Chawla, D., Rees, G. & Friston, K. J. The physiological basis of attentional modulation in extrastriate visual areas. *Nature Neurosci*. **2**, 671–676 (1999).
52. Goebel, R., Khorram–Sefat, D., Muckli, L., Hacker, H. & Singer, W. The constructive nature of vision: direct evidence from functional magnetic resonance imaging studies of apparent motion and motion imagery. *Eur. J. Neurosci*. **10**, 1563–1573 (1998).
    An fMRI study showing that mental imagery of motion activates cortical area MT; this activation was also observed in earlier areas, and increased with the synaptic distance of an area from V1 along the dorsal processing stream.
53. Kourtzi, Z. & Kanwisher, N. Activation in human MT/MST for static images with implied motion. *J. Cogn. Neurosci.* **12**, 48–55 (2000).
54. O'Craven, K. & Kanwisher, N. Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *J. Cogn. Neurosci.* (in the press).
55. Posner, M. I., Snyder, C. R. R. & Davidson, B. J. Attention and the detection of signals. *J. Exp. Psychol. Gen*. **109**, 160–174 (1980).
56. Hillyard, S. A. & Anllo-Vento, L. Event-related brain potentials in the study of visual selective attention. *Proc. Natl Acad. Sci. USA* **95**, 781–787 (1998).
57. Mesulam, M. M. A cortical network for directed attention and unilateral neglect. *Ann. Neurol*. **10**, 309–325 (1981).
58. Vallar, G. & Perani, D. The anatomy of unilateral neglect after right-hemisphere stroke lesions. A clinical/CT-scan correlation study in man. *Neuropsychologia* **24**, 609–622 (1986).
59. Posner, M. I., Walker, J. A., Friedrich, F. J. & Rafal, R. D. Effects of parietal lobe injury on covert orienting of visual attention. *J. Neurosci.* **4**, 1863–1874 (1984).
60. Robinson, D. L., Goldberg, M. E. & Stanton, G. B. Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. *J. Neurophysiol*. **41**, 910–932 (1978).
61. Wurtz, R. H. & Mohler, C. W. Enhancement of visual responses in monkey striate cortex and frontal eye fields. *J. Neurophysiol*. **39**, 766–772 (1976).
62. Posner, M. I. & Petersen, S. E. The attention system of the human brain. *Annu. Rev. Neurosci.* **13**, 25–42 (1990).
63. Corbetta, M., Miezin, F. M., Shulman, G. L. & Petersen, S. E. A PET study of visuospatial attention. *J. Neurosci.* **13**, 1202–1226 (1993).
64. Nobre, A. C. *et al.* Functional localization of the system for visuospatial attention using positron emission tomography. *Brain* **120**, 515–533 (1997).
65. Vandenberghe, R. *et al.* Attention to one or two features in left or right visual field: A positron emission tomography study. *J. Neurosci.* **17**, 3739–3750 (1997).
66. Shulman, G. L. *et al.* Areas involved in encoding and applying directional expectations to moving objects. *J. Neurosci*. **19**, 9480–9496 (1999).
    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).
67. 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).
68. Coull, J. T., Frith, C. D., Buchel, C. & Nobre, A. C. Orienting attention in time: behavioural and neuroanatomical distinction between exogenous and endogenous shifts. *Neuropsychologia* **38**, 808–819 (2000).
69. Hopfinger, J. B., Buonocore, M. H. & Mangun, G. R. The neural mechanisms of top-down attentional control. *Nature Neurosci*. **3**, 284–291 (2000).
70. Colby, C. L. in *Attention and Performance XVI* (ed. Inui, T. & McClelland, J. L.) 157–177 (MIT Press, Cambridge, Massachusetts, 1996).
71. Andersen, R. A. Encoding of intention and spatial location in the posterior parietal cortex. *Cereb. Cortex* **5**, 457–469 (1995).
72. Rizzolatti, G., Riggio, L., Dascola, I. & Umilta, C. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* **25**, 31–40 (1987).
73. Sweeney, J. A. *et al.* Positron emission tomography study of voluntary saccadic eye movements and spatial working memory. *J. Neurophysiol*. **75**, 454–468 (1996).
74. Paus, T. Location and function of the human frontal eye-field: a selective review. *Neuropsychologia* **34**, 475–483 (1996).
75. Coull, J. T. & Nobre, A. C. Where and when to pay attention: the neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *J. Neurosci*. **18**, 7426–7435 (1998).
76. 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).
77. Corbetta, M. *et al.* A common network of functional areas for attention and eye movements. *Neuron* **21**, 761–773 (1998).

78. Culham, J. C. *et al.* Cortical fMRI activation produced by attentive tracking of moving targets. *J. Neurophysiol.* **80**, 2657–2670 (1998).
79. 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).
80. 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).
81. Wojciulik, E. & Kanwisher, N. The generality of parietal involvement in visual attention. *Neuron* **23**, 747–764 (1999). **This study found that several spatial and nonspatial 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.**
82. Lynch, J. C., Mountcastle, V. B., Talbot, W. H. & Yin, T. C. Parietal lobe mechanisms for directed visual attention. *J. Neurophysiol.* **40**, 362–389 (1977).
83. Culham, J., Cavanagh, P., Kanwisher, N., Intriligator, J. & Nakayama, K. Varying attentional load produces different fMRI task response functions in occipitoparietal cortex and frontal eye fields. (Paper presented at the annual meeting of the Society of Neuroscience, New Orleans, LA, October, 1997).
84. Ungerleider, L. G. & Mishkin, M. in *Analysis of Visual Behavior* (ed. Ingle, D. J., Goodale, M. A. D. & Mansfield, R. J. W.) 549–586 (MIT Press, Cambridge, Massachusetts, 1982).
85. 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). **This PET study investigated feature binding. Conjunction but not feature search activated superior parietal cortex, in a region previously shown (reference 63) to support spatial shifts of attention, consistent with the hypothesis that binding relies on a serial spatial attention mechanism.**
86. Treisman, A. M. & Gelade, G. A feature-integration theory of attention. *Cogn. Psychol.* **12**, 97–136 (1980).
87. Duncan, J. *et al.* Systematic analysis of deficits in visual attention. *J. Exp. Psychol. Gen.* **128**, 450–478 (1999).
88. Husain, M., Shapiro, K., Martin, J. & Kennard, C. Abnormal temporal dynamics of visual attention in spatial neglect patients. *Nature* **385**, 154–156 (1997).
89. 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).
90. Milner, A. D. & Goodale, M. A. *The Visual Brain in Action* (Oxford Univ. Press, Oxford, 1995).
91. Jonides, J. *et al.* Spatial working memory in humans as revealed by PET. *Nature* **363**, 623–625 (1993).
92. Jonides, J. *et al.* The role of parietal cortex in verbal working memory. *J. Neurosci.* **18**, 5026–5034 (1998).
93. Dehaene, S., Spelke, E., Pinel, P., Stanescu, R. & Tsivkin, S. Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science* **284**, 970–974 (1999).
94. Platt, M. L. & Glimcher, P. W. Neural correlates of decision variables in parietal cortex. *Nature* **400**, 233–238 (1999).
95. Duncan, J. *et al.* A neural basis for general intelligence. *Science* **289**, 457–460 (2000).
96. Raichle, M. E. Behind the scenes of function brain imaging: A historical and physiological perspective. *Proc. Natl Acad. Sci. USA* **95**, 765–772 (1998).
97. Chen, M. S. & Bookheimer, S. Y. Localization of brain function using magnetic resonance imaging. *Trends Neurosci.* **17**, 268–277 (1994).
98. Buckner, R. L. *et al.* Detection of cortical activation during averaged single trials of a cognitive task using functional magnetic resonance imaging. *Proc. Natl Acad. Sci. USA* **93**, 14878–14883 (1996).
99. Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18**, 193–222 (1995).
100. Duncan, J. Converging levels of analysis in the cognitive neuroscience of visual attention. *Phil. Trans. R. Soc. Lond. B* **353**, 1307–1317 (1998).
101. Treisman, A. Features and objects: the fourteenth Bartlett memorial lecture. *Q. J. Exp. Psychol.* **40A**, 201–237 (1988).
102. Friedman–Hill, S. R., Robertson, L. C. & Treisman, A. Parietal contributions to feature binding: evidence from a patient with bilateral lesions. *Science* **269**, 853–855 (1995).
103. Wojciulik, E. & Kanwisher, N. Implicit but not explicit feature binding in a Balint's patient. *Vis. Cogn.* **5**, 157–181 (1998).
104. Pugh, K. R. *et al.* Auditory selective attention: an fMRI investigation. *Neuroimage* **4**, 159–173 (1996).
105. Linden, D. E. *et al.* The functional neuroanatomy of target detection: an fMRI study of visual and auditory oddball tasks. *Cereb. Cortex* **9**, 815–823 (1999).
106. Kawashima, R. *et al.* Selective visual and auditory attention toward utterances — a PET study. *Neuroimage* **10**, 209–215 (1999).
107. Klingberg, T. Concurrent performance of two working memory tasks: potential mechanisms of interference. *Cereb. Cortex* **8**, 593–601 (1998).
108. Tzourio, N. *et al.* Functional anatomy of human auditory attention studied with PET. *Neuroimage* **5**, 63–77 (1997).
109. Burton, H. *et al.* Tactile attention tasks enhance activation in somatosensory regions of parietal cortex: a positron emission tomography study. *Cereb. Cortex* **9**, 662–674 (1999).
110. Hadjikhani, N. & Roland, P. E. Cross-modal transfer of information between the tactile and the visual representations in the human brain: A positron emission tomographic study. *J. Neurosci.* **18**, 1072–1084 (1998).
111. Banati, R. B., Goerres, G. W., Tjoa, C., Aggleton, J. P. & Grasby, P. The functional anatomy of visual-tactile integration in man: a study using positron emission tomography. *Neuropsychologia* **38**, 115–124 (2000).
112. Macaluso, E., Frith, C. & Driver, J. Selective spatial attention in vision and touch: unimodal and multimodal mechanisms revealed by PET. *J. Neurophysiol.* **83**, 3062–3075 (2000).
113. 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). **This paper reported that detection of changes in visual, auditory or tactile stimuli activates a right-lateralized multimodal network, including temporo-parietal junction and several frontal areas.**
114. Duncan, J. & Owen, A. M. Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci.* **23**, 475–483 (2000).
115. Luck, S. J. & Hillyard, S. A. in *The New Cognitive Neurosciences* (ed. Gazzaniga, M.) 687–700 (MIT Press, Cambridge, Massachusetts, 2000).

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.