Cortical mechanisms of space-based and object-based attentional control

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Visual attention, the mechanism by which observers select relevant or important information from scenes, can be deployed to locations in space or to spatially invariant object representations. Studies have examined both the modulatory effects of attention on the strength of extrastriate cortical representations, and the control of attention by parietal and frontal cortical circuits. Subregions of parietal and frontal cortex are transiently active when attention is voluntarily shifted between spatial locations or object representations. This transient activity may reflect an abrupt shift in the attentional set of the observer, complementing sustained signals that are thought to maintain a given attentive state.

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Abbreviations

BOLD	blood-oxygenation-level-dependent
fMRI	functional magnetic resonance imaging
IPS	intraparietal sulcus
LIP	lateral intraparietal
PrCes	precentral sulcus
SFS	superior frontal sulcus
SPL	superior parietal lobule

Introduction

Visual attention is an expression of cognitive control over perception. To attend is to select from what William James called the ‘‘blooming, buzzing confusion’’ of the sensorium that which is required for behavior. The deployment of attention can be either goal-directed and voluntary, or stimulus-driven and involuntary. Here we consider only the former; stimulus-driven attentional capture has been recently reviewed elsewhere [1,2•].

Attention may be viewed as a mechanism for biasing the competitive interactions among mutually inhibitory sensory representations in cortex, so that an attended object ‘wins’ the competition and thereby comes to enter awareness [3]. Attended objects thus produce more robust cortical activity than unattended objects. We review recent evidence concerning both the sources of attentional control signals and their modulatory effects on extrastriate cortical activity in two distinct representational domains: the domain of spatial locations and the domain of perceptual objects.

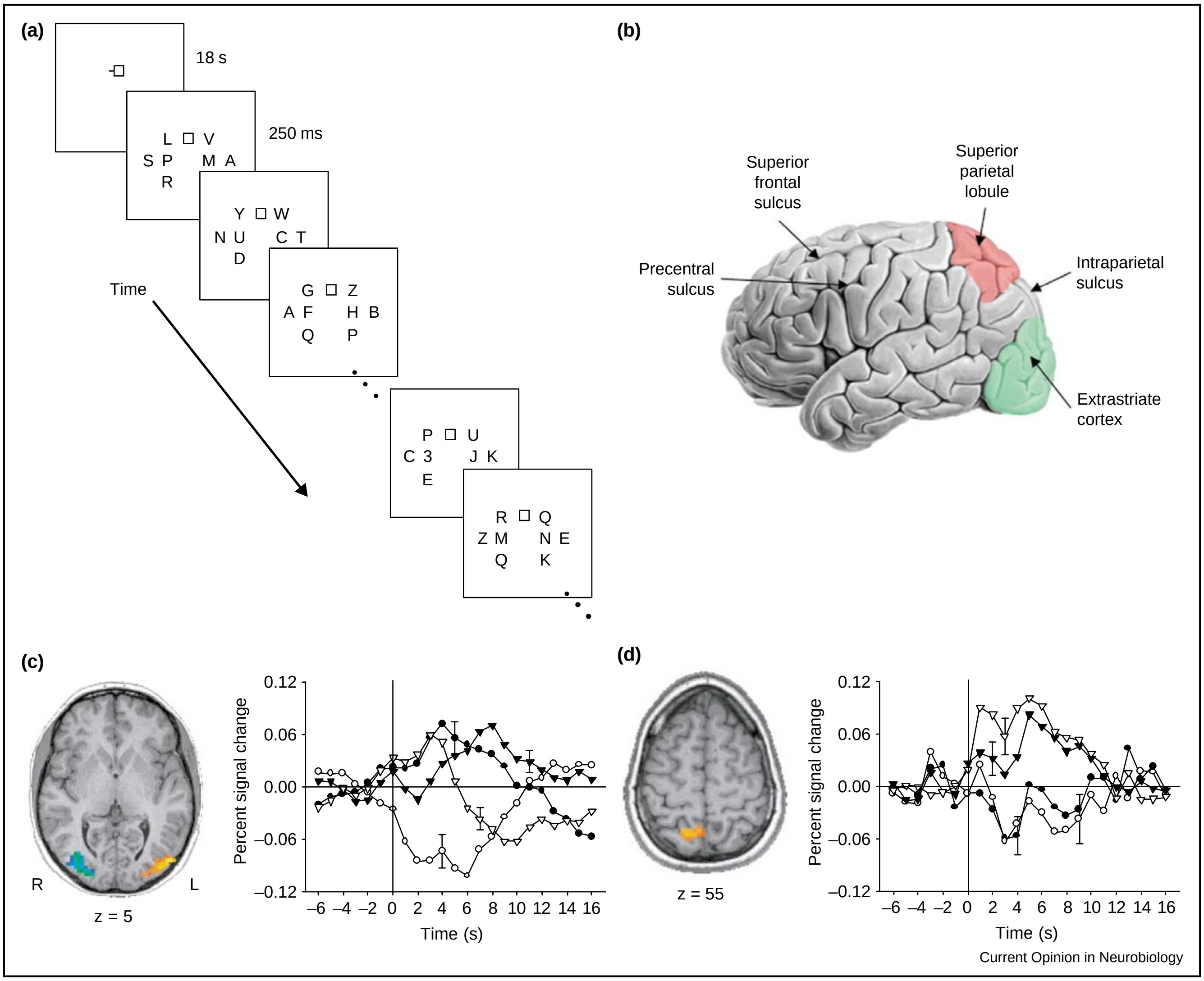
Space-based attention

Much evidence has shown that the cortical response to an object appearing in an attended location is stronger than that to objects in unattended locations [3, 4•,5–16]. For example, the firing rate of individual neurons and spiking synchrony in neural populations increases when their driving stimulus is attended, and the magnitude of blood-oxygenation-level-dependent (BOLD) functional magnetic resonance imaging (fMRI) signals is greater for attended locations than for unattended locations in both visual cortex and lateral geniculate nucleus [17•]. In the past decade, investigators have attempted to identify the source of the control signals that lead to competitive advantages for attended locations in visual cortex [18–24].

Starting with their pioneering work in the early 1990s, Corbetta *et al.* [2•,25–28,29•] have used positron emission tomography and fMRI to investigate the neural substrates of the control of spatial attention. In their recent study using fMRI [29•], subjects shifted attention to a location on the left or right of the display (while continuously fixating the center with their eyes) in response to a centrally presented arrow cue. The object of the task was to detect the onset of a target, which was in the attended location in most of the trials and in the unattended location in the remaining trials. Regions of parietal cortex (intraparietal sulcus [IPS]) and frontal cortex (superior frontal sulcus and precentral sulcus [SFS–PrCes], which is near what is thought to be the human homologue of the frontal eye field) showed an increased BOLD response after the attention cue (Figure 1b). In addition, ventral IPS and SFS–PrCes regions produced a sustained increase in BOLD response when attention was directed to the contralateral side of space, suggesting that these areas may be involved in tonically maintaining a specific locus of attention.

In a study by Beauchamp *et al.* [30•], regions of IPS and PrCes showed sustained increases in activity when subjects attentively tracked (without eye movements) a small dot that was successively displaced in the visual periphery. Together with several other studies of the control of spatial attention, these results reveal the presence of tonic

Figure 1



Control of spatial attention shifts. **(a)** The rapid serial visual presentation task. In this task, participants fixate on the central square throughout each run and begin by attending to the central stream of letters on one side (left in this example). Letters change identity simultaneously four times per second. Hold and shift target digits (e.g. 3 and 7) instruct the observer to maintain attention on the currently attended side and to shift attention to the other side, respectively. **(b)** Lateral view of a human brain showing the relevant cortical areas. The lateral intraparietal area (LIP; not visible here) is located within the lateral bank of the intraparietal sulcus in monkeys and possibly in humans. **(c)** Attentional modulation of right and left extrastriate cortex detected by contrasting ‘attend right’ with ‘attend left’ conditions, and the mean event-related BOLD response time courses from the activated region of right extrastriate cortex. Filled circles represent hold left; filled triangles, shift right to left; open circles, hold right; open triangles, shift left to right. Error bars indicate standard error of the mean. The baseline (0% signal change) for each target type is the mean BOLD signal for that target type during the 6 s preceding the onset of the event. **(d)** A transverse slice through parietal cortex showing an activated region of right SPL identified by contrasting shift and hold events, and the mean BOLD response time course from this activated region after shift and hold events. Data are taken from [35••].

increases in the BOLD signal in subregions of parietal and frontal cortex when subjects deploy spatial attention [31,32,33••,34].

We and our co-workers [35••] recently investigated the functional role of parietal cortex in the control of spatial attention using rapid event-related fMRI. Observers viewed a display in which letters appeared in rapid succession (four per second) in eight locations on the screen (Figure 1a). They were to attend to either the left or the right central (target) stream (without moving their eyes from a central fixation square) to detect an occasional digit target in the attended stream. If the target digit was (say) a ‘3’, they were to maintain attention at the same location; if it was a ‘7’, they were to shift attention to the other location (targets were separated by 3–5 s).

This task allowed us to assess the effects of attention by contrasting brain activity during epochs of attention to the left and the right sides of space. In addition, it could reveal the time course of cortical activity after shift targets as compared with hold targets, and thus it could provide insights about the dynamics of attentional control signals. The presence of spatially adjacent distractors maximized cortical competition and thereby increased the potential for attentional modulation; the continuous visual stream permitted us to assess the control of attention without contamination from isolated sensory transients to cue attention.

Attentional modulation of sensory representations was observed in extrastriate cortex (Figure 1b): the BOLD signal was greater when attention was directed to the contralateral than to the ipsilateral side of space. In addition, a crossover in the BOLD time course after switch targets was observed that mirrored similar observations in extrastriate single unit recording [11]. A very different pattern of activity was observed in right superior parietal lobule (SPL), an area that is putatively involved in attentional control (Figure 1b). Here, shift targets evoked a transient increase in the BOLD signal (the direction of the shift did not matter) but hold targets did not (Figure 1c). More tellingly, activity in SPL was more transient when a shift target was followed by two hold targets than when it was followed by another shift target.

These results suggest that the SPL issues a transient attentional control signal when a change in the locus of attention is required. It corroborates a similar conclusion from an experiment in which observers' attention was directed to a sequence of abrupt onset targets appearing in different locations [33••]. As in previous studies [29•,30•,33••], sustained activity was also observed in IPS, which might reflect its role in continuously maintaining the locus of attention.

Object-based attention

The investigation of visual attention has focused primarily on the deployment of attention to spatial locations. Growing behavioral and neurophysiological evidence has shown, however, that selective attention frequently operates on an object-based representational medium in which the boundaries of segmented objects, and not just spatial position, determine what is selected and how attention is deployed [36–42]. This reflects the fact that the visual system is optimized for segmenting complex three-dimensional scenes into representations of (often partly occluded) objects for recognition and action, because perceivers must interact with objects in the world and not with disembodied locations.

For example, attention to one part of an object confers an attentional advantage to other parts of that object [43]. Similarly, attention to one aspect of an object (say, its shape) enhances the cortical response to other aspects of that object (say, its color or motion); thus, all the attributes of an attended object seem to be bound together into a unitary package. This concept holds even when the attended and ignored objects are spatially superimposed.

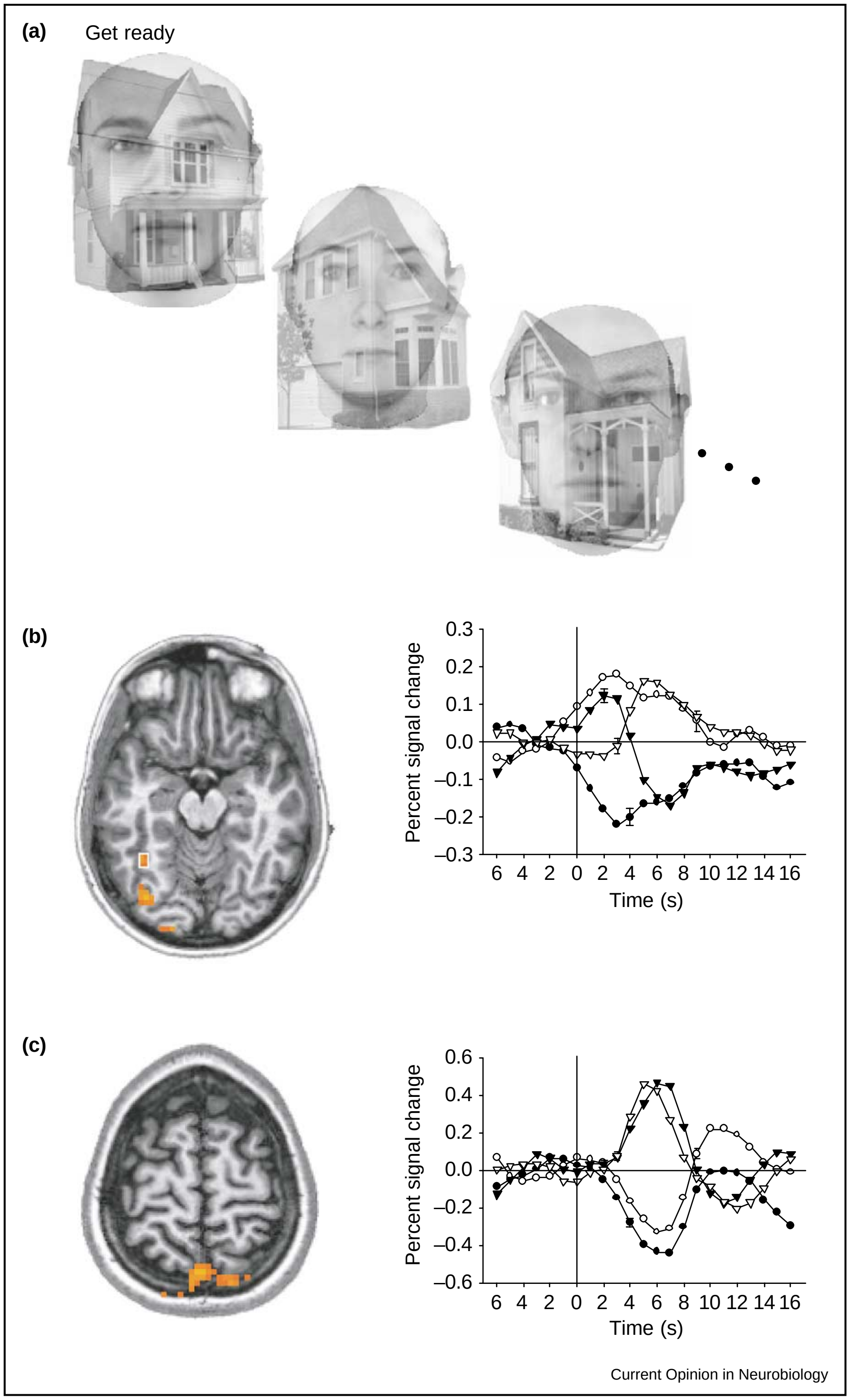
O'Craven *et al.* [44] have observed the effects of object-based attention using fMRI. In this study, observers viewed a display containing a sequence of semitransparent grayscale images of spatially superimposed faces and houses (Figure 2a shows similar stimuli). At any given moment, either the house or the face showed oscillatory motion. The task required observers to decide whether the currently visible house (or face) matched the one immediately preceding it, which required them to attend closely to the relevant object type. A spatial 'spotlight of attention' could not select one of the two superimposed objects; it would necessarily select both or neither.

The researchers found that activity in face- and house-selective cortical regions mirrored the subject's state of attention (despite the fact that both a house and a face were present in the scene at all times), indicating that object-based selection was possible in this task. The key observation was that neural activity in MT+ (a motion-selective brain region) depended on whether the motion was carried or not by the currently attended object, despite the fact that motion was always present and irrelevant to the task. As predicted by an object-based account, all of the features of the attended object (including its motion) were selected, and the features of the ignored object were (relatively) suppressed.

To investigate the control of object-based attention, we and our co-workers (Serences *et al.*, personal communication) recently carried out an fMRI-based study using object stimuli modeled after the task of O'Craven *et al.* [44] and an experimental design inspired by our spatial attention study described above [35••]. Observers viewed a continuous stream of superimposed houses and faces (Figure 2a). Each face spatially morphed into another face every second, in synchrony with house-to-house morphing. Attention was directed to either the house stream or the face stream at any given moment as the observer monitored for one of four targets (two faces, two houses) that had been memorized before the experiment began. One face target and one house target signaled that attention should remain on the face or house stream, respectively; the other face and house targets signaled that attention should be shifted to the other stream. A separate scan was conducted to locate cortex regions that were more active during the presentation of houses and faces, respectively [45,46].

We observed modulation of the BOLD signal in house-selective and face-selective regions according to the

Figure 2



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Control of object-based attention shifts in a single subject. **(a)** Examples of superimposed face/house pairs used in the study. The subject first heard a verbal command to attend to either houses or faces. Each face spatially morphed into the next face, and (simultaneously) each house morphed into the next house, at a rate of 1 morph per second. The subject was instructed to maintain attention on the currently attended object stream until they detected a previously memorized face or house that instructed them to switch to the other object stream. **(b)** Object-based attentional modulation in right lateral fusiform cortex [45,46], and the event-related BOLD timecourses for each of four target types in the attention task. Hold house: ● (closed circle), shift face to house: ▼ (closed triangle), hold face: ○ (open circle), and shift house to face: ▽ (open triangle). **(c)** Region of medial SPL that exhibited greater increases in the BOLD response following shift compared to hold targets and the BOLD timecourse from the medial SPL cluster following shift and hold events.

current locus of object-based attention (Figure 2b). To examine the control of object-based attention, the effects of switch and hold targets were contrasted. As in our previous study [35••], we observed transient switch-related activity in SPL after switch targets but not after hold targets (Figure 2c). The similarity of the transient increase in BOLD response in SPL during shifts of object-based attention to that observed in the spatial attention study was striking; a direct comparison of the anatomical locus of the space-based and object-based shift-related activity awaits further study.

Neural mechanisms of attentional control

Above, we have reviewed evidence for two distinct mechanisms of attentional control that seem to underlie shifts of spatial and object-based attention. The time course of the BOLD signal after an instruction to shift attention produces a rapid, transient increase in SPL activation [33••,35••]. The transient nature of this attentional control signal makes it unsuitable for maintaining a particular attentive state for an extended period of time. One possibility is that the transient top-down signal synchronizes the spiking activity in targeted populations of extrastriate neurons that represent the attended object or location, and such synchronous activity drives activity more effectively in the next stage of visual representation [4•,47,48].

In contrast to these transient effects, several studies have found evidence for a sustained BOLD response in IPS and frontal areas after a cue to shift and hold attention in the periphery [16,28,29•,30•,31,32,33••,34]. The sustained activity in IPS observed during the delay period of spatial cueing tasks might be responsible for maintaining a given attentive state. Recent studies of monkey lateral intraparietal (LIP) area suggest that this region may have such a role in the deployment of attention. For example, when a monkey attends to a peripheral location in anticipation of a perceptual discrimination at that location, there is a tonic increase in the firing rate of LIP neurons throughout the delay period [49••].

Conclusions

These results suggest a twofold role for parietal and frontal regions in attentional control. Extrastriate sensory regions are subject to competitive interactions among cortical representations when several objects are simultaneously present in the visual scene [50]. A top-down signal that originates in the prefrontal cortex and reflects current behavioral goals arrives at the SPL, which responds by transiently increasing its activity. The transient switch signal is received both by extrastriate neural populations and by IPS and perhaps other structures, which then continuously maintain the new attentive state by providing a constant biasing signal to extrastriate cortical regions. Although many details of this model await empirical confirmation, it captures the key results discussed here. Taken together, these findings suggest a unified functional system of attentional control that initiates (through a transient signal) and maintains (through a sustained signal) the desired attentive state.

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In this review, the authors propose that two functionally distinct cortical circuits in humans mediate the control of voluntary and involuntary attentional control. A dorsal system that includes posterior parietal cortex and dorsal frontal cortex controls the voluntary deployment of attention. A ventral system that includes the temporoparietal junction and inferior frontal cortex is specialized for detecting unexpected salient stimuli and then interrupting ongoing voluntary attention, allowing ‘automatic’ redeployment of attention to salient events.

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In this study, human observers direct their attention to the left or right of a visual display while continuously fixating a central point. fMRI reveals attentional modulation of responses in the lateral geniculate nucleus of the thalamus, including enhancement of responses to attended stimuli, suppression of responses to ignored stimuli and increased baseline activity in the absence of stimulation. This is one of the first studies to find attentional modulation at this very early subcortical level, one synapse from the retina.

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A central arrow cue directs attention to a box in the left or right visual field where (in most trials) a target that requires a detection response appears. Sustained increases in event-related fMRI activity are observed in IPS and SFS–PrCes after the cue, suggesting that these areas provide a continuous biasing signal for maintaining spatial attention.

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A bright square appears in 1 of 10 horizontally arrayed positions, and every 2.3 s it abruptly changes its location. Observers covertly attend to the square to detect a brief dimming. Thus, both stimulus-driven attentional capture (by the abrupt onset of the square) and goal-directed attentional deployment are probably recruited by this task. SPL shows a transient increase in event-related fMRI activity after spatial shifts of attention. The magnitude of the increases in SPL activity are proportional to the size of the attention shift. In a second experiment, sustained peripheral attention is contrasted with passive fixation; this identifies a network of frontal and inferior parietal areas that are active during the maintenance of attention. This study reveals the distinct patterns of cortical activity in shifting and maintaining attention.

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Observers alternately maintain or shift attention between continuous streams of letters in the left and right visual field. Occasional digit targets in the letter streams instruct them either to maintain attention on the currently attended stream or to shift attention to the other stream. The locus of attention modulates the strength of fMRI activity in extrastriate cortical regions corresponding to the left and right attended regions. In addition, SPL shows transient increases in activity that are time-locked to the spatial attention shifts.

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