Anatomical Physiology of Spatial Extinction

Neurologically intact volunteers participated in a functional magnetic resonance imaging experiment that simulated the unilateral (focal) and bilateral (global) stimulations used to elicit extinction in patients with hemispatial neglect. In peristriate areas, attentional modulations were selectively sensitive to contralaterally directed attention. A higher level of mapping was observed in the intraparietal sulcus (IPS), inferior parietal lobule (IPL), and inferior frontal gyrus (IFG). In these areas, there was no distinction between contralateral and ipsilateral focal attention, and the need to distribute attention globally led to greater activity than either focal condition. These physiological characteristics were symmetrically distributed in the IPS and IFG, suggesting that the effects of unilateral lesions in these 2 areas can be compensated by the contralateral hemisphere. In the IPL, the greater activation by the bilateral attentional mode was seen only in the right hemisphere. Its contralateral counterpart displayed equivalent activations when attention was distributed to the right, to the left, or bilaterally. Within the context of this experiment, the IPL of the right hemisphere emerged as the one area where unilateral lesions can cause the most uncompensated and selective impairment of global attention (without interfering with unilateral attention to either side), giving rise to the phenomenon of extinction.

Keywords: attention, hemispheric specialization, neglect, neural networks, parietal cortex

Introduction

Damage to the right side of the brain can trigger a debilitating impairment known as the left hemineglect syndrome. Patients with this syndrome minimize the salience of events in the contralateral side of the environment, display a reluctance to shift attention to a leftward direction, and cannot effectively search for targets embedded within the left hemispace. The left hemineglect syndrome is assumed to reflect damage to a large-scale frontoparietal network that normally sustains the adaptive distribution of spatial attention (Mesulam 1981; Heilman et al. 1985; Mort et al. 2003; Corbetta et al. 2005; Peers et al. 2005; Schotten et al. 2005). Marked dissociations can exist among individual manifestations of this syndrome, raising the possibility that components of this network display differential specializations for specific aspects of spatial attention (Stone et al. 1998).

Sensory extinction is one of the most distinctive manifestations of left hemispatial neglect. It is identified when a left-sided visual stimulation that is recognized upon unilateral presentation becomes ignored when paired with a simultaneously presented right-sided stimulus (Mesulam 2000; Karnath et al. 2003). As is the case for all other manifestations of the contralateral neglect syndrome, extinction tends to be more frequent, severe, and lasting when caused by right hemisphere damage (Stone et al. 1993). Furthermore, in patients who receive intracarotid amytal injections (the Wada test), reversible inactivation of the right hemisphere causes more prominent contralateral extinction (Meador et al. 1988).

Multiple experiments, many of which have been reviewed by Driver and Vuilleumier (2001), show that the extinguished stimulus gains access to the central nervous system where it exerts a covert influence on behavior (Kobayashi et al. 2005). For example, patients with extinction are slower in detecting right-sided stimuli during simultaneously presented bilateral stimulation compared with unilateral stimulation although both are reported as unilateral right-sided stimulation (Di Pellegrino and De Renzi 1995). Furthermore, extinguished stimuli have been shown to influence semantic priming of objects shown on the intact side (Berti and Rizzolatti 1992), and extinguished letters can influence the speed of identifying centrally presented target letters (Audet et al. 1991).

The detection of the unilaterally presented left stimulus shows that the patient can access sensory information from both sides of space and that extinction may reflect a high-order distortion in mapping the extrapersonal space as a whole. Numerous explanations have been advanced to explain the mechanisms underlying extinction. Perceptual rivalry (Denny-Brown et al. 1952), difficulty in disengaging attention from the right-sided stimulus (Posner et al. 1984), and an exaggeration of the normal difficulty in distributing attention to multiple targets (Driver and Vuilleumier 2001) have been invoked. An alternative possibility is to conceptualize extinction as a selective impairment of global but not focal attention. Dissociations of these 2 modes and a greater impairment of the global mode of attentional distribution after right hemisphere lesions have been described in patients with brain lesions (Robertson et al. 1988; Marshall and Halligan 1995). A right hemisphere specialization for global attention has been reported in normal subjects but has been based on tasks that emphasize focal versus global features of a complex stimulus rather than the bilaterality versus unilaterality of the attention span (Fink et al. 1996). Although a few functional imaging experiments have compared unilateral with bilateral stimulation, they have used tasks where attention is intentionally directed to one side or the other even during the bilateral stimulation period (Fink et al. 2000; Vandenbergh et al. 2005).

The purpose of this investigation was to explore the functional anatomy of unilateral versus bilateral attention with an experimental paradigm simulating the conditions that elicit extinction in patients with brain damage. The hypothesis was that parts of parietal cortex would display a differential participation in focal versus global attention and that these relationships would display hemispheric asymmetry.
Materials and Methods

Task
Twelve right-handed subjects (mean age 30.6 years; 9 males) were given a task of covert spatial attention during an event-related functional magnetic resonance imaging (fMRI) experiment. One of 4 foveal cue types, presented for 200 ms, initiated each trial (Fig. 1). The cue was either spatially uninformative (neutral) or signaled that the target would be presented on the left, on the right, or bilaterally, as indicated by the pattern of thick (bolded) lines in the foveally presented diamond. Targets were placed at 7.5 degrees eccentricity on either side of the fixation point along the horizontal meridian. Targets were presented inside squares (1.5°), which stayed on the screen throughout the trial. The interval between cue and target was 3.8, 4, or 4.2 s. In the unilateral trials, the cue pointed to the left or right, and the subject was asked to press a button as rapidly as possible upon the appearance of the target (×) but not foil (+) at the designated location. In the bilateral trials, the cue pointed in both directions, and the subject was asked to press the button only if both locations contained a ×. In the neutral trials (signaled by a diamond with no thick sides), a button was pressed if the × appeared either on the right, on the left, or bilaterally (but not if one side contained the × and the other the +). In the unilateral conditions, foils always appeared in the same location as targets. Either type of stimulus always appeared in the locations signaled by the central cue. The proportion of Y/N trials was 50% for all conditions. In 27.3% of trials, no target followed the cue. These catch trials minimized the influence of target appearance upon the hemodynamic response triggered by the cue (Ollinger et al. 2001a, 2001b). Subjects completed 8 fMRI runs, each containing 11 randomly intermixed trials of each of the 4 conditions. Trial-to-trial intervals varied from 8.4 to 12.6 s. An eye tracker (Applied Science Laboratories, Bedford, MA) was used to monitor visual fixation in the scanner. Participants practiced the task outside the scanner before the functional imaging.

Neuroimaging
A 3-Tesla Siemens Trio whole-body MRI system with a birdcage head coil was used. The head was immobilized with calipers built into the head coil. A nonmagnetic response button was used for responses. A vitamin E capsule was taped to the left temporal region to mark laterality for image processing. Stimuli were back projected with an LCD projector onto a translucent screen viewed through a mirror. Anatomical scans were obtained using a sagittal magnetization prepared rapid gradient echo sequence (repetition time/echo time [TR/TE]: 2300/2.91 ms, flip angle: 9°, field of view [FOV]: 256 × 256, slice thickness: 1 mm). Functional scans were acquired using 34 slices (3 mm) with 1 mm gap using an ascending echoplanar sequence (TR/TE: 2100/30, flip angle: 80°, FOV: 220, matrix: 64 × 64). The orientation of the functional scans was aligned with the anterior commissure–posterior commissure line. For all functional runs, the first 4 scans were excluded from the analyses to allow signal equilibration.

Image Processing and Analysis
Analyses of the data were performed using SPM5 software (Wellcome Department of Cognitive Neurology, London, UK) running in a MATLAB 7 environment (Mathworks, Sherborn, MA). Functional images were realigned to correct for movement artifacts. High-resolution anatomical T1 images were coregistered with the realigned functional images to enable anatomical localization of the activations. Structural and functional images were spatially normalized into a standardized anatomical framework using the default echoplanar imaging template provided in SPM5, based on the averaged brain of the Montreal Neurological Institute and approximating the normalized probabilistic spatial reference frame.

Figure 1. Upper panel: Centrally placed diamond instructed the subject to attend to the left, to the right, or bilaterally. The instructions were to maintain central fixation and press a button as rapidly as possible upon appearance of the target (×) but not foil (+). A central diamond without thick lines denoted a neutral (spatially uninformative) cue, which could be followed by stimuli on either side or bilaterally. Some cues were not followed by peripheral stimuli in order to improve our ability to identify activity related to the cue-to-task interval, relatively uncontaminated by activity related to the sensory and motor aspects of the task. Trials lasted for 2 (for no target trials) or 3 (for full trials) TRs. Intertrial intervals randomly varied between 1 and 3 TRs. Lower panel: Average group RTs to left, right, and global targets after spatial (informative) and neutral cues. Subjects showed faster RTs for trials with informative cue (spatial) compared with neutral cue trials.
Functional data were spatially smoothed with a 7-mm isotropic Gaussian kernel. The resulting spatial resolution was about 10 mm³ full width at half maximum. Model estimation included a high-pass filter (128 s) and autoregressive (1) model for autocorrelations.

Our goal was to estimate event-related hemodynamic responses to cues. The inclusion of trials where cues were not followed by targets lessened the influence of target onset upon the modeled hemodynamic responses. The responses were estimated for a period of 9 TRs (18.9 s) with a finite impulse response (FIR) function, which does not assume a canonical shape for the hemodynamic response function. Each FIR period was equivalent to 1 TR or 2.1 s.

Areas significantly modulated by the task were assessed by a voxel-wise repeated-measures analysis of variance (ANOVA) with task conditions and time points (1–9 TRs) as within-subject factors. The interaction of condition with time point identified voxels affected by the experimental modulation. The resulting F statistics were corrected for multiple comparisons using Gaussian random field theory as implemented in SPM. Voxels were considered significant at a family-wise error of \( P < 0.05 \) corrected.

We were specifically interested in identifying brain areas that were specialized for processing of the bilateral frame-of-reference, over and above unilateral processing of either left or right visual stimuli. Regions fulfilling this criterion were identified by looking for a significant effect (voxel family-wise error, \( P < 0.05 \)) of bilateral attention within a masking image that included only those voxels where bilateral attention was greater than both unilateral attention conditions, see Figure 2a–c. The masking image was formed by thresholding each of the bilateral–unilateral contrasts at \( P < 0.05 \) uncorrected, and then the resulting t maps were set to binarizing and logical AND. The use of an uncorrected threshold when thresholding the masks is consistent with the standard method used in SPM as the masks are only being used to restrict the potential activation search space to voxels showing the desired effects, that is, bilateral–unilateral, but not for statistical inference. Thus, if many voxels were included in the mask, the correction for multiple comparisons on the main effect of bilateral attention would increase. At the limit in which the mask included all voxels in the image, the multiple comparisons correction would be the same as using no mask. As noted above, statistical inference for the main effect of bilateral attention was based on \( P < 0.05 \) using a stringent family-wise error correction for multiple comparisons at the voxel level.

To examine brain areas that were differentially sensitive to the lateralization of stimuli, we performed a 2 (left–right) × 9 (time points) ANOVA to reveal the effects of left and right focal attention conditions, Figure 2d. The direction of these effects was determined in follow-up regional analyses.

Time course of activity in the peak regions of activation resulting from these analyses was extracted from individual subject images and modeled to reflect the response to the cue, during the interval when the subject adjusted attentional expectancy to be focal or global. The inclusion of partial trials (27.3% of total) where cues were not followed by the target allowed us to focus on the response to the cue rather than the target, at a time prior to the manual response. Data were extracted from and averaged within an 8-mm diameter sphere around the peak activation. Repeated-measures ANOVAs were conducted to determine if different attention conditions (left, right, or bilateral) produced different time courses. When activations occurred over symmetrical areas across the hemisphere, the ANOVA also included the factor of hemisphere. Interactions involving condition and time course were followed up by subsidiary ANOVAs to determine the nature of the condition effects and their hemispheric distribution.

**Figure 2.** Group averaged significant voxel-wise ANOVA maps (F maps) using family-wise error corrected (for the whole brain) \( P < 0.05 \). F values are presented with a scale depicted in the right of the illustration. The main effect of global attention \( (a, b, c) \) inclusively masked with global–left and global–right attention maps showed an asymmetric right IPL activation, as well as bilateral activations in the IPS, and IFG. CS, collateral sulcus; IFS, inferior frontal sulcus; IPL, inferior parietal lobule; IPS, inferior parietal sulcus; LPS, lateral peristriate cortex. The comparison of left and right attention \( (d) \) showed activations along the CS and more posterior LPS cortex (not shown in this picture).
Results

Behavioral and Eye Movement Data
Accuracy was very high (100%) and there were no differences between conditions. A 2-way ANOVA was performed to investigate the effects of cue predictability (spatial or neutral) and the type of target array (left, right, or bilateral) upon reaction times (RTs). Cue predictability exerted a significant main effect on RT ($F_{(1,11)} = 10.86$, $P < 0.01$, see Fig. 1). Informative spatial cues successfully triggered a shift of attention in the prescribed direction, resulting in significantly faster RTs when participants could anticipate the type of target array to be discriminated. The type of target array did not influence RTs significantly and did not interact with cue predictability ($P > 0.39$). Overall, participants responded to bilateral, left, and right stimulus arrays with equivalent speed.

We were able to record eye movements of 4 subjects reliably, during the entire experiment. Using the subjects’ point of gaze, the time spent after cue presentation within a 1° radius of the fixation point was calculated (Gitelman 2002). There were no differences for the time spent in the vicinity of the fixation cross for the 4 conditions (unilateral left, 95 ± 3%; unilateral right, 95 ± 4%; bilateral, 96 ± 3%; neutral, 95 ± 3%).

fMRI Data
The main effect of bilateral attention inclusively masked by the bilateral–right and bilateral–left contrasts revealed significant activities in the inferior parietal lobule (IPL) of the right hemisphere, intraparietal sulcus (IPS) bilaterally, posterior part of inferior frontal gyrus (IFG) bilaterally, lateral peristriate (LPS) region in the right hemisphere, sensorimotor cortex, and cerebellum (see Fig. 2a-c and Table 1). The left–right contrast showed bilateral activations within the tempo-occipital region and around the collateral sulcus (CS) (see Fig. 2d and Table 2). Time course analyses focused on these regions.

Bilateral versus Unilateral Activations
Modulation by the global versus local framework was tested in 4 brain areas—IPL, IPS, IFG, and LPS. The time courses of the blood oxygen level–dependent signal elicited by each type of cue (bilateral, left, and right) were compared for each of the regions of interest extracted around the peak of the activation. Figure 3 shows the time courses extracted from these regions.

| Table 1 |
| Activations in the main effect of global attention map inclusively masked with global–left and global–right contrasts |
| Brain area | X | Y | Z | Z score |
| R IPL* (59) | 36 | −42 | 45 | 5.37 |
| 45 | −48 | 51 | 4.65 |
| R IPS* (48) | 30 | −63 | 51 | 5.36 |
| R sensory cortex (59) | 45 | −36 | 42 | 4.31 |
| L IPS* (12) | −24 | −60 | 42 | 4.83 |
| −24 | −66 | 33 | 4.58 |
| L IPS* (12) | 39 | 9 | 27 | 5.72 |
| 51 | 9 | 18 | 4.78 |
| L IFG* (66) | −42 | 3 | 33 | 5.42 |
| 45 | −60 | −9 | 5.42 |
| L sensory cortex (14) | −45 | −36 | 42 | 4.99 |
| −9 | −48 | −36 | 4.42 |

Note: R, right; L, left. Table includes peak as well as local maxima 8 mm apart. Cluster sizes are indicated in parentheses.

*Peak coordinates are the locations for region of interest (ROI)-based time courses shown in Figure 3.

Most of the differential activations were bilateral, but one region of the posterior parietal cortex, located in the IPL, was differentially activated only in the right hemisphere (Fig. 3b). There was a significant cue by time-point interaction in this region ($F_{(16,176)} = 3.1, P = 0.011$). Follow-up analyses showed that the response to the bilateral cue was greater than the response to the left cue ($F_{(39,388)} = 2.9, P = 0.012$) and to the right cue ($F_{(39,388)} = 4.7, P = 0.009$). As a further test of the asymmetry for this effect, the time courses were also extracted from the mirror symmetric region as compared between cue conditions. No cue-related modulation occurred in the equivalent left hemisphere region (Fig. 3a).

The differential activation of the IPS in the bilateral condition was approximately symmetrical (Fig. 3c and d). Analyses showed an interaction between cue and time points ($F_{(16,176)} = 3.0, P = 0.002$), which did not differ significantly depending on hemisphere. Subsidiary analyses of cue activations within each hemisphere were also performed. There were significant cue-related modulations in the right hemisphere ($F_{(16,176)} = 2.9, P = 0.003$) and the left hemisphere ($F_{(16,176)} = 2.6, P = 0.012$). The response to the bilateral cue was significantly greater than the response to the left ($F_{(39,388)} = 2.9, P = 0.006$ for right hemisphere; $F_{(39,388)} = 11.0, P < 0.001$ for left hemisphere) and right ($F_{(39,388)} = 4.7, P = 0.002$ for right hemisphere; $F_{(39,388)} = 4.0, P = 0.002$ for left hemisphere) cues.

The cue-related differential modulation was significant at the right LPS region ($F_{(16,176)} = 4.4, P = 0.001$) (Fig. 3b). Subsidiary analyses within this region showed that bilateral ($F_{(39,388)} = 6.4, P < 0.001$) and left cues ($F_{(39,388)} = 5.4, P < 0.001$) elicited greater responses than right cues. Though the response for bilateral cues also appeared greater than the response for left cues, this was not significant ($P > 0.14$). The mirror symmetric area on the left hemisphere did not show any cue-related differences ($P > 0.29$) (Fig. 3g).

Left versus Right Activations
Activations that were sensitive to the side indicated by unilateral cues occurred only in dorsal and ventral peristriate areas (see Fig. 2 and Table 2). In the left and right ventral peristriate areas around the CS, the time courses showed highly significant cue by time-point interactions (left: $F_{(16,176)} = 7.71, P < 0.001$; right: $F_{(16,176)} = 8.75, P < 0.001$), confirming the contralateral specialization for visual areas (see Fig. 3). Subsidiary follow-up ANOVAs showed that at the left CS, bilateral cues ($F_{(39,388)} = 10.89, P < 0.001$) and right cues ($F_{(39,388)} = 9.70, P < 0.001$) elicited greater activation than left cues. Bilateral and right cues elicited a similar degree of activation ($P > 0.70$). The complementary pattern was revealed for the right CS, where bilateral
cues ($F_{8,88} = 11.32, P < 0.001$) and right cues ($F_{8,88} = 13.11, P < 0.001$) elicited greater activation than right cues. Bilateral and left cues elicited similar activations ($P > 0.72$).

**Discussion and Conclusions**

We altered the spatial distribution of attention by presenting a cue that signaled the location of an upcoming target. In some trials, the cue focused expectant attention on a peripheral segment of the left or right hemispace, and in others it distributed attention more globally to encompass both sides of space simultaneously. These 3 conditions simulated the bedside examination for extinction. The longer RTs in trials preceded by spatially uninformative neutral cues confirmed that the cue-induced shifts of attention had taken place. The insertion of cues not followed by targets helped to identify the cue-related activity during the period of expectant attention, prior to the sensory and motor events related to task performance (Ollinger et al. 2001a, 2001b).

A primary goal of this experiment was to identify areas differentially engaged by global (bilateral) versus focal (unilateral) attention. The relevant analysis identified dorsal parietal, LPS, and IFG areas where activations were greater for the global (bilateral) than for the focal (unilateral) distribution of expectant attention. Greater parietal and frontal activations for bilateral than unilateral stimulation has also been reported by Geng et al. and attributed to target selection during spatially directed attention (Pinsk et al. 2004; Geng et al. 2006).
dorsal parietal areas with greater activations in the bilateral condition could further be subdivided into a posterior IPS and a more anterior IPL component. With the exception of LPS, all of these areas displayed signal changes of significantly greater magnitude in response to the bilateral than to each of the 2 unilateral conditions.

Hemispheric asymmetry of 2 kinds was observed in the set of areas with greater responsiveness to the bilateral distribution of attention. In the IPS and IFG, the preferential responses to bilateral attention were present in both hemispheres. In the IPL, however, the asymmetry was of a different kind. First, the area preferentially responsive to bilateral attention was present only in the right hemisphere. Secondly, its contralateral homologue in the left hemisphere displayed signal changes of equal magnitude in all 3 attentional conditions. Within the context of this analysis, the IPL region is the only one where damage to the right hemisphere could potentially cause a greater disruption of bilateral attention than equivalent damage to the left. The intact left IPL would maintain the capacity for unilateral attention to either side of space as shown by its responses to the 2 unilateral cues. Under conditions of bilateral stimulation, competitive interactions and a winner-take-all rule in the left IPL could potentially cause the right-sided stimulus to become dominant and left-sided one to be ignored. In the IPS and IFG, where the greater response to the bilateral versus unilateral mapping was represented bilaterally, the attentional consequences of damage to either side could presumably be compensated by the homologous area in the contralateral hemisphere.

Although the location of critical lesions in patients with extinction is not yet settled, many reports point to the parietal lobe and temporoparietal junction as the most commonly encountered site of damage (Driver et al. 1997; Karnath et al. 2003). In keeping with this clinicopathological correlation, a case study reported a patient with 2 sequential right hemisphere strokes in whom the first, in the frontal eye fields (FEFs), caused neglect without extinction, whereas the second, in dorsal parietal cortex, elicited extinction (Daffner et al. 1990). In normal subjects, extinction-like phenomena are obtained after transcranial magnetic stimulation of the parietal lobe but not of the occipital or temporal lobes (Pascual-Leone et al. 1994).

Several competing models have been proposed to account for the greater incidence and severity of contralateral neglect after damage to the right hemisphere (Heilman and Van Den Abell 1980; Mesulam 1981; Kinsbourne 1993; Corbetta et al. 2005). The results shown in Figures 2 and 3 raise the possibility that at least one source of this asymmetry is based on specialized neurons, concentrated within the right IPL, that are selectively tuned to a global mode of attention. Depending on the extent of the lesion, damage to these neurons or to their interconnections could participate in the emergence of extinction in some circumstances and the more dramatic manifestations of neglect in others.

In a second set of analyses, we contrasted the 2 unilateral conditions to identify areas that were more active when directing attention to one side versus the other. Such areas were located along the CS (Bradmann area 19) and in the more posterior LPS cortex, close to the area shown in Figure 2a, but bilaterally. Responses in these areas were significantly greater for contralateral than ipsilateral unilateral attention (Fig. 3). The response to the global (bilateral) distribution of attention in these areas, and in the right LPS, was not significantly different than the contralateral condition, suggesting that the global condition was exerting its influence upon peristriate cortex predominantly through the contralateral component of the bilateral task. This pattern is consistent with the known retinotopic pattern of attentional modulation in visual pathways (Kastner et al. 1999).

The lack of significant differences in responsivity to ipsilateral versus contralateral attentional tasks in the IPS, IPL, and IFG reflect a higher stage of information processing than in peristriate cortex, probably because events are represented according to their attentional valence rather than according to retinotopic location. Whether the ipsilateral attentional responses in the IFG, IPL, and IPS originate from the contralateral hemisphere or the colliculo-pulvinar route remains to be determined. In the monkey, single-unit recordings in the IPL and IPS show an admixture of spatial attention neurons with contralateral, ipsilateral, or bilateral sensory fields (Robinson et al. 1995). The preponderance of contralateral neurons can be quite modest in some areas, and the relative proportion of each type of neuron can display hemispheric asymmetry (Mountcastle et al. 1975; Lynch et al. 1977). In contrast to the IPL/IPS region and the dorsally located FEFs, there is little evidence in the monkey to implicate inferior frontal areas in spatial attention. The role of the human IFG region in spatial attention remains to be clarified and some authors have attributed an important role to this region in hemispatial neglect (Husain and Kennard 1996; Corbetta and Shulman 2002; Corbetta et al. 2005).

Previous functional imaging work on global versus focal attention has concentrated on featural rather than spatial determinants of perceptual mapping. For example, when subjects were shown a large V made of small Ps, switching from the global to the focal mode was associated with activation of the temporoparietal junction. Furthermore, attention to the global feature led to stronger activations in the right peristriate cortex, whereas attention to the focal internal detail led to greater activation in the left (Fink et al. 1996, 1997). Our analyses did not identify a perisstriate area with a general preference for global over focal attention, almost certainly because our global condition emphasized the spatial extent of attention rather than its selectivity for featural properties of the whole. Another difference is that our task did not include the reciprocal interference of global and focal patterns or the need to integrate local information to perceive global form. However, our results do support the conclusion that the right hemisphere is more responsive to tasks requiring a global distribution of attention.

Functional imaging experiments in which unilateral visual stimulation has been compared with bilateral simultaneous stimulation are surprisingly rare although this is how extinction is detected at the bedside. In one experiment, subjects were briefly shown a vertical column of 3 letters on one or both sides. During the unilateral conditions, they were asked to read as many letters on the designated side as they could. In the bilateral conditions, they were directed to one side or the other for the initial reporting of letters but were also instructed to move onto the letters of the other side if they could. Although, there was no truly simultaneous condition where attention had to be evenly distributed to both sides of space, the bilateral conditions were found to cause greater activation in the IPL/IPS region bilaterally (Fink et al. 2000). In another experiment, the stimulus was relevant in one side and irrelevant in the other so that bilateral stimulation took the form of perceptual rivalry (Vandenberghhe et al. 2005). In keeping with our results, a region...
in the midportion of the right IPS was identified as being preferentially activated by bilateral stimulation.

In everyday life, interactions with the environment necessitate rapid shifts between global and focal modes of spatial attention. Our task provides a naturalistic simulation of this process as well as the testing procedures used to elicit extinction in patients with hemispatial neglect. We found that greater responsibility to global than focal attention is a widespread property of parietal and frontal neurons in both hemispheres. However, we also found asymmetries indicating that the right IPL may be more responsive to the global mode of attention. This asymmetry could explain why right parietal lesions are more likely to cause contralateral extinction.

Notes
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