

Hemispheric Asymmetries for Different Components of Global/Local Attention Occur in Distinct Temporo-parietal Loci

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Data from brain-damaged and neurologically intact populations indicate hemispheric asymmetries in the temporo-parietal cortex for discriminating an object's global form (e.g. the overall shape of a bicycle) versus its local parts (e.g. the spokes in a bicycle tire). However, it is not yet clear whether such asymmetries reflect processes that (i) bias attention toward upcoming global versus local stimuli and/or (ii) attend/identify global versus local stimuli after they are presented. To investigate these possibilities, we asked sixteen healthy participants to perform a cued global/local attention task while their brain activity was recorded using event-related functional magnetic resonance imaging (fMRI). The results indicated a novel double dissociation. Hemispheric asymmetries for deploying attention toward expected global versus local object features were specific to the intraparietal sulcus (iPs). However, hemispheric asymmetries for identifying global versus local features after they were presented were specific to the inferior parietal lobe/superior temporal gyrus (IPL/STG). This double dissociation provides the first direct evidence that hemispheric asymmetries associated with different components of global/local attention occur in distinct temporo-parietal loci. Furthermore, it parallels an analogous dissociation reported in a recent fMRI study of spatial orienting, suggesting that global/local attention and spatial attention might rely on similar cognitive/neural mechanisms.

Keywords: attention, fMRI, hemispheric asymmetries, hierarchical stimuli, parieto-temporal cortex

Introduction

Recognizing common objects such as faces, words and animals depends critically on the identification of both global and local stimulus features (Rumelhart and McClelland, 1982; Kimchi, 1992; Davidoff and Robertson, 2002). Thus, determining how the brain attends, identifies and ultimately integrates global and local object features is crucial for developing adequate models of object recognition (Navon, 1977). Data from behavioral, patient and functional neuroimaging studies indicate distinct brain mechanisms, lateralized to different cerebral hemispheres of the brain, play asymmetric roles in attending to global versus local aspects of an object's shape (Robertson *et al.*, 1988, 1993a; Kimchi and Merhav, 1991; Fink *et al.*, 1997b; Martinez *et al.*, 1997; Weissman and Banich, 1999; Yamaguchi *et al.*, 2000). For example, findings from human patients indicate that damage to right temporo-parietal regions of the brain impairs the identification of an object's global overall form (e.g. an airplane's overall shape) while damage to left temporo-parietal regions adversely affects the identification of an object's local parts (e.g. an airplane's propeller) (Robertson *et al.*, 1988).

Nonetheless, the precise cognitive operations and neural loci underlying hemispheric asymmetries associated with iden-

tifying global versus local object features remain unclear. For instance, numerous studies have distinguished between preparatory control processes that deploy attention to expected stimuli and feature identification mechanisms that attend and/or identify those stimuli after they are presented (Kastner *et al.*, 1999; Shulman *et al.*, 1999; Corbetta *et al.*, 2000; Hopfinger *et al.*, 2000; MacDonald *et al.*, 2000; Yamaguchi *et al.*, 2000; Weissman *et al.*, 2002a). Data from one of these studies have revealed roles for the intraparietal sulcus (iPs) and inferior parietal lobe /superior temporal gyrus (IPL/STG) in preparatory control and feature identification processes, respectively (Corbetta *et al.*, 2000). Consistent with such data, findings from event-related potentials (ERPs) suggest hemispheric asymmetries in temporo-parietal regions for both preparatory control and feature identification mechanisms associated with identifying global versus local object features (Yamaguchi *et al.*, 2000). Moreover, data from a patient study suggests dorsal regions of temporo-parietal cortex regulate the allocation of attention to global versus local object features while ventral regions identify those features (Robertson *et al.*, 1988). However, both the ERP and the patient study above lacked the spatial resolution necessary to infer precise neural loci.

Therefore, the goal of the present functional magnetic resonance imaging (fMRI) investigation was to investigate the precise neural loci of hemispheric asymmetries for preparatory control and feature identification mechanisms associated with identifying global versus local object features. We asked participants to perform a fast-rate, cued version of the global/local selective attention task (Navon, 1977; Weissman *et al.*, 2002a) while their brain activity was recorded using a recently developed event-related fMRI approach (Shulman *et al.*, 1999; Corbetta *et al.*, 2000; Weissman *et al.*, 2002a; Woldorff *et al.*, 2004). In each trial (Fig. 1), an attention-directing cue instructed participants to attend to and identify either the global letter or the local letters of an upcoming hierarchical stimulus (e.g. a large, global H made up of small, local Ss). Preparatory control mechanisms that differed for the global and local tasks were indexed by differential activity for global versus local cues. Feature identification mechanisms that differed for the global and local tasks were indexed by differential activity for global versus local targets.

In line with the suggestive findings from patient and ERP studies of global/local attention discussed earlier (Robertson *et al.*, 1988; Yamaguchi *et al.*, 2000), we predicted hemispheric asymmetries for preparatory control and feature identification mechanisms that differed for the global and local tasks in dorsal versus ventral regions of the temporo-parietal cortex, respectively. Specifically, we predicted a significant interaction between Task (global, local) and Hemisphere (right, left) in dorsal

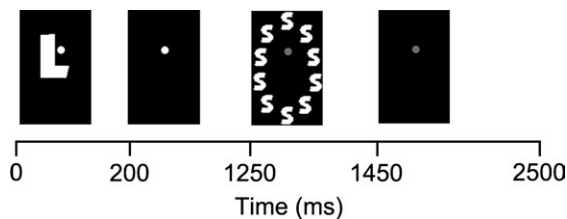


Figure 1. Timing and sequence of events in a sample trial of the experimental task. In each 2.5 s trial, an attention-directing cue instructed participants to attend to and identify either the large, global letter or the small, local letters of an upcoming hierarchical stimulus.

temporo-parietal regions during cue processing and in ventral temporo-parietal regions during target processing. We note that in studies of global/local attention, the simple effects of significant Task by Hemisphere interactions are not always significant, either in neurologically-intact (Weissman and Banich, 1999) or in brain-damaged populations (Robertson *et al.*, 1988). In other words, it is not always the case that the right hemisphere exhibits significantly greater involvement in global versus local processing while the left hemisphere exhibits significantly greater involvement in local versus global processing. Thus, our predictions focused on the presence of Task by Hemisphere interactions, which are generally accepted as the ‘gold standard’ measure of hemispheric asymmetries (Hellige, 1983; Robertson *et al.*, 1993a; Weissman and Banich, 1999). Other data from the present study, which did not include analyses of hemispheric asymmetries, have also recently been accepted for publication (Weissman *et al.*, 2004).

Materials and Methods

Participants

Sixteen healthy participants (six male, ten female; aged 18–29 years) were recruited from the Duke University community. All were right-handed, had normal or corrected-to-normal vision, and had no history of serious neurological trauma or disorders. Informed consent was obtained from each participant prior to the experiment in accordance with the local internal review board. Before the MR session, each participant practiced one or two blocks of the experimental task. Participants were paid \$20 per h for their participation, which lasted ~2 h.

Task

In each 2.5 s trial, an attention-directing cue (G or L; $1.6^\circ \times 1.0^\circ$ of visual angle; duration = 200 ms) instructed participants to attend to and identify either the global letter ($3.3^\circ \times 2.1^\circ$) or the local letters ($0.6^\circ \times 0.4^\circ$) of an upcoming hierarchical stimulus (e.g. a large, global H made up of small, local Ss; abbreviated ‘Hs’; duration = 200 ms). Note that cue stimuli were sized midway between the global and local forms to prevent reflexive orienting to either stimulus dimension. Participants were told to press one button if the cued target letter was either an H or an S and a different button if it was either an X or an O, using the index and middle fingers of the right hand. They were also instructed to maintain fixation at all times.

Two categories of trials allowed us to isolate neural activity associated with preparatory control and feature identification mechanisms. In cue-plus-target trials (75%), a hierarchical target stimulus appeared 1.25 s after cue onset. The global and local letters in each hierarchical stimulus were always perceptually distinct. The letter at the irrelevant stimulus dimension was mapped to a different response as the letter at the cued dimension (33%; incongruent trials), to the same response (33%; congruent trials), or to no response (33%; neutral trials). The specific hierarchical stimuli used in congruent, incongruent, and neutral trials were as follows: congruent (Hs, Sh, Xo, Ox), incongruent (Hx, Os, Xh, Oh) and neutral (global task: Hd, Sf, Od, Xf; local task: Dh, Fs, Do, Fx).

In cue-only trials (25%), the cue was not followed by a hierarchical stimulus.

The fixation dot turned red 1.25 s after cue onset in all trials (coincident with target presentation in cue-plus-target trials and to signal no target would occur in cue-only trials). This procedure equated the duration of cue-triggered attention-focusing processes in cue-plus-target and cue-only trials (Corbetta *et al.*, 2000). Comparisons of neural activity in global cue-only versus local cue-only trials allowed isolation of brain areas differentially involved in deploying attention to expected global versus local object features. Contrasting neural activity in cue-plus-target versus cue-only trials, separately for each task, isolated neural activity associated with global and local targets (Shulman *et al.*, 1999). Subsequent comparisons of neural activity associated with global versus local targets revealed brain areas differentially involved in attending and/or identifying global versus local object features.

Data Acquisition and Analysis

A PC was used to present stimuli and to record participants’ responses. Stimuli were projected onto a screen at the back of the magnet’s bore that participants viewed through a mirror. Responses were made using the index and middle fingers of the right hand and recorded with an MR-compatible response box.

The blood oxygenation level-dependent (BOLD) signal was measured with a spiral imaging sequence ($T_R = 1.25$ s, $T_E = 40$ ms, flip angle = 90° , 17 contiguous 7.5-mm-thick slices, in plane resolution = 3.75 mm \times 3.75 mm) during the collection of functional images on a 1.5 T GE whole-body scanner. Each participant completed six runs. During each run, 282 brain volumes were collected. The first six functional images of each run contained no trials and were discarded. Structural images for each participant were collected using a T1-weighted spin echo sequence ($T_R = 500$ ms, $T_E = 14$ ms, flip angle = 90° , 17 contiguous 7.5-mm-thick slices, in plane resolution = 0.94 mm \times 0.94 mm).

SPM’99 (Friston *et al.*, 1995) was used to correct functional images for head motion, normalize functional images to standard space, and spatially smooth the functional data with a three-dimensional Gaussian filter (full-width half-maximum = 8 mm). The time series for each functional run was analyzed using the general linear model without making an assumption about the shape of the BOLD response (Ollinger *et al.*, 2001a,b). For each of the two cue-only and six cue-plus-target trial types, we modelled 12 T_{RS} (16 s) of the BOLD response. This approach was optimized by varying the inter-trial-interval (ITI) from zero to five T_{RS} using a nearly exponential distribution that favored short ITIs. Within the design matrix, we also included six motion regressors (i.e. SPM’99 motion estimates) and regressors for the linear trend and γ -intercept term. Parameter estimates for each run were converted to units of percent change from baseline (i.e. the γ -intercept term for that run) and then averaged across runs for each participant separately. In every participant, this procedure yielded eight regression-estimated time courses, one for each trial type in the design. We note that our method of using the general linear model to estimate hemodynamic responses to cue-only and cue-plus-target trials has been described and validated in greater detail elsewhere (Shulman *et al.*, 1999; Ollinger *et al.*, 2001a,b).

ROI Analyses

We functionally defined ROIs in the iPs in the following way. First, we averaged the regression-estimated BOLD responses to global cue-only and local cue-only trials. Then, we entered the averaged cue-only response into a voxelwise one-way, repeated-measures (random effects) analysis of variance (ANOVA) to identify cue-related activity. The resulting F-map was then height and extent thresholded ($P < 0.01$, five contiguous voxels), after which peak cue-related activations were identified bilaterally in the iPs. We created 27-voxel left and right iPs ROIs by drawing a three-dimensional cube around each peak.

An analogous ANOVA on the average BOLD response to global and local targets was used to isolate peak target activity. For this analysis, the average regression-estimated BOLD response to global targets was calculated by subtracting the estimated response to global cue-only trials from the average estimated response to the three types of global cue-plus-target trials. The average estimated BOLD response to local targets was calculated by subtracting the estimated BOLD response to

local cue-only trials from the average estimated BOLD response to the three types of local cue-plus-target trials. We then averaged the estimated responses to global and local targets to produce an average target response at each voxel. A one-way, repeated-measures (random effects) ANOVA on this average target response identified a peak in the left IPL/STG. An ROI centered in an analogous part of the right IPL/STG was also created, although no peaks associated with target activity were found in this region.

In each of our four ROIs (left and right iPs, left and right IPL/STG), we computed the average time course (across all 27 voxels) for global cues, local cues, global targets, and local targets, separately for each participant. All subsequent ROI analyses were performed using these averaged time courses from each participant. Specifically, random-effects, one-tailed *t*-tests on peak cue- and peak target-activity (3.75–5 or 5–6.25 s after stimulus onset) were conducted to investigate directional hypotheses about hemispheric asymmetries for global/local attention in the iPs and the IPL/STG. Importantly, all contrasts performed during the ROI analyses were statistically orthogonal to the contrasts used to create the ROIs. Thus, the results of the ROI analyses were not biased by our method of creating ROIs. As we only considered four ROIs in the entire brain, *P*-values less than 0.05 were considered to be significant. Conversion from MNI to Talarach (Talarach and Tournoux, 1988) coordinates was implemented with two non-linear transformations (<http://www.mrc-cbu.cam.ac.uk/Imaging/mnispac.html>).

Finally, we note two reasons why we used functionally-defined ROIs rather than Talarach coordinates defined by previous fMRI, ERP and Positron Emission Tomography (PET) studies. First, prior patient and ERP studies lacked the spatial resolution to identify precise Talarach coordinates. Second, prior PET and fMRI studies of global/local attention have not distinguished between cue-related and target-related activity. Therefore, using Talarach coordinates from these prior PET and fMRI studies might limit our ability to localize spatially separable neural loci underlying hemispheric asymmetries for preparatory control (i.e. cue-related) versus feature identification (i.e. target-related) mechanisms.

Results

Behavior

Analyses of mean reaction times (RT) and mean percent error rates (ER) were conducted in separate repeated-measures analyses of variance with Task (Global, Local) as a within-participants factor. As expected (Kimchi, 1992; Navon, 1977), performance was both significantly faster [$F(1,15) = 29.847, P < 0.001$] and significantly more accurate [$F(1,15) = 23.131, P < 0.001$] for the global task (RT = 668 ms, ER = 4.23%) than for the local task (RT = 728 ms; ER = 6.92%).

fMRI

Hemispheric Asymmetries in Temporo-parietal Regions

Consistent with predictions, ROI analyses of fMRI data revealed significant hemispheric asymmetries for global versus local cues in the iPs and for global versus local targets in the IPL/STG (Fig. 2*a,b*).

In support of hemispheric asymmetries for preparatory control mechanisms, there was a significant Task (global, local) by Hemisphere (left, right) interaction across bilateral regions of the iPs during the cue period [$t(15) = 1.89, P < 0.04$; left hemisphere Talarach coordinates: $x = -30, y = -67, z = 45$; right hemisphere coordinates: $x = 30, y = -67, z = 45$]. Tests of simple effects revealed that local cues evoked significantly greater peak activity than global cues in the left iPs [$t(15) = 2.27, P < 0.02$; Fig. 2*b*, top left]. In the right iPs, however, peak responses to local and global cues did not significantly differ [$t(15) = 0.325, P > 0.35$]. These simple effects indicate the significant Task by Hemisphere interaction for preparatory control mechanisms across

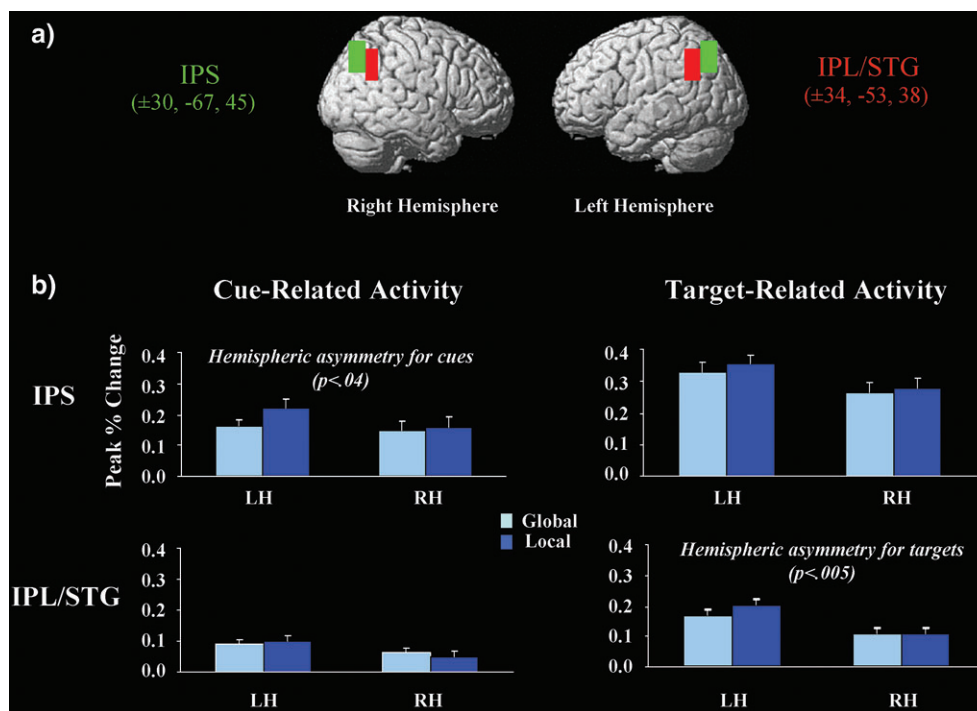


Figure 2. Hemispheric asymmetries for identifying global versus local object features. (a) Regions of interest in the intraparietal sulcus (iPs) in green and the inferior parietal lobe/superior temporal gyrus (IPL/STG) in red. Regions of interest are rendered on the three-dimensional SPM'99 template brain. (b) Peak event-related activity in the iPs (top row) and the IPL/STG (bottom row) associated with cues (left column) and targets (right column) in the global and local tasks. Each plot depicts peak percent signal change from baseline for the global task (light blue bars) and for the local task (dark blue bars), separately for the left and right hemispheres. Error bars indicate the standard error of the mean for each condition.

bilateral regions of the iPs was driven mainly by differential cue activity in the left iPs.

In support of hemispheric asymmetries for feature identification mechanisms, there was a significant Task by Hemisphere interaction across bilateral regions of the IPL/STG during the target period $t(15) = 2.95, P < 0.005$ (left hemisphere Talarach coordinates: $x = -34, y = -53, z = 38$; right hemisphere coordinates, $x = 34, y = -53, z = 38$). Tests of simple effects indicated that local targets produced significantly greater peak activity than global targets in the left IPL/STG [$t(15) = 1.88, P < 0.04$; Fig. 2*b*, bottom right]. In the right IPL/STG, though, there was no significant difference in peak activity for local versus global targets [$t(15) = -0.17, P > 0.40$]. This pattern of simple effects indicates the significant Task by Hemisphere interaction across bilateral regions of the IPL/STG was driven mainly by differential target activity in the left IPL/STG.

Additional analyses revealed that hemispheric asymmetries for cues were specific to the iPs while those for targets were specific to the IPL/STG. First, the Task by Hemisphere interaction in the iPs did not achieve significance for global versus local targets ($P > 0.23$; Fig. 2*b*, top right), in contrast to what we found for global versus local cues. Second, the Task by Hemisphere interaction in the IPL/STG did not reach significance for global versus local cues ($P > 0.10$; Fig. 2*b*, bottom left), in contrast to what we found for global versus local targets. As suggested by the two findings above, the tendency for hemispheric asymmetries to be stronger for differential cue activity in the iPs, but stronger for differential target activity in the IPL/STG achieved marginal significance [$t(15) = 1.67, P < 0.058$], as indexed by the four-way interaction between Period (Cue, Target), Task (Global, Local), Region (iPs, IPL/STG) and Hemisphere (right, left). This four-way interaction indicates a double dissociation in which hemispheric asymmetries for (i) preparatory control mechanisms that differ for the global and local tasks (indexed by differential cue activity) and (ii) feature identification mechanisms that differ for the global and local tasks (indexed by differential target activity) occur in distinct neurological loci.

As mentioned earlier, although there were significant Task by Hemisphere interactions in both the iPs and the IPL/STG, only in the left hemisphere did neural activity significantly differ for local versus global processing, consistent with some (though not all) findings from behavioral studies of global versus local processing (Hopkins, 1997; Robertson *et al.*, 1993a; Weissman and Banich, 1999). To more formally determine whether the hemispheric asymmetries we observed were driven mainly by the left hemisphere, we analyzed the simple effects of hemisphere for the four-way interaction described above. That is, we analyzed the three-way interaction between Period (Cue, Target), Task (Global, Local) and Region (iPs, IPL/STG) separately for the left versus right hemisphere ROIs. Indicating that our results were driven mainly by the left hemisphere ROIs, differential cue activity and differential target activity selectively activated the left iPs versus the left IPL/STG, respectively [$t(15) = 1.92, P < 0.035$], but did not selectively activate the right iPs versus the right IPL/STG, respectively ($P > 0.40$).

Hemispheric Asymmetries in Visual Cortex

There is growing controversy about whether hemispheric asymmetries for global/local attention also occur in extrastriate visual cortices (Fink *et al.*, 1997b, 1999; Proverbio *et al.*, 1998; Mangun *et al.*, 2000; Sasaki *et al.*, 2001; Han *et al.*, 2002; Weissman *et al.*, 2002a; Lux *et al.*, 2004). Therefore, we next

determined whether, and for which component(s) of processing (i.e. cue versus target), hemispheric asymmetries in visual cortex occurred in the present study. First, we contrasted peak activity for global versus local cue-only trials using a voxelwise t -test. Second, we contrasted peak activity for global versus local targets using an analogous t -test. No significant differential activity was observed in visual cortex in either analysis ($t = 3.72, P < 0.001$, three contiguous voxels).

Discussion

Behavioral, ERP and functional neuroimaging studies have provided converging support for the view that left temporo-parietal regions of the brain attend to local aspects of an object's shape while right temporo-parietal regions attend to global aspects (Fink *et al.*, 1997a; Kimchi and Merhav, 1991; Martinez *et al.*, 1997; Proverbio *et al.*, 1998; Weissman and Banich, 1999). However, the precise cognitive and neural loci of these asymmetries have been difficult to determine. Recent fMRI studies have identified separable neural loci for cue-related processes that bias attention toward upcoming task-relevant stimuli versus target-related processes that identify those stimuli after they are presented (Kastner *et al.*, 1999; Shulman *et al.*, 1999; Corbetta *et al.*, 2000; Hopfinger *et al.*, 2000; MacDonald *et al.*, 2000; Yamaguchi *et al.*, 2000; Weissman *et al.*, 2002a). Although patient and ERP studies of global/local attention have also attempted to distinguish between such processes (Robertson *et al.*, 1988; Yamaguchi *et al.*, 2000), they lacked the spatial resolution necessary to determine precise neural loci.

In the present study, we therefore used fMRI to investigate hemispheric asymmetries for preparatory control and feature identification mechanisms that enable global versus local attention. Critically, we found a double dissociation for hemispheric asymmetries related to preparatory control and feature identification mechanisms. Hemispheric asymmetries for preparatory control mechanisms that differ for the global and local tasks (indexed by differential cue activity) were specific to the iPs. This result is consistent with other data indicating the iPs plays a crucial role in orienting attention (Corbetta *et al.*, 2000; Kanwisher and Wojciulik, 2000). Hemispheric asymmetries for feature identification mechanisms that differ for the global and local tasks (indexed by differential target activity) were specific to the IPL/STG. This finding is consistent with target-processing deficits observed in human patients with damage to ventral temporo-parietal regions (Robertson *et al.*, 1988). To our knowledge, the present data are the first to demonstrate a double dissociation in temporo-parietal regions for preparatory control and feature identification mechanisms that differ for global versus local attention.

These significant hemispheric asymmetries in temporo-parietal regions are highly consistent with various neurological models of global/local attention. Global features are represented by relatively low spatial frequencies while local features are represented by relatively high spatial frequencies (Sergent, 1982, 1983; Fink *et al.*, 1999). Therefore, the hemispheric asymmetries we have observed fit with the view that right and left temporo-parietal regions are biased to attend to relatively low versus relatively high spatial frequencies, respectively (Sergent, 1982; Kitterle *et al.*, 1990; Ivry and Robertson, 1998; Proverbio *et al.*, 1998). Other data suggest that attention to global features relies on adopting a wide attentional spotlight while attention to local features is enabled by adopting a narrow attentional spotlight (Robertson *et al.*, 1993b; Sasaki *et al.*, 2001).

From this perspective, our results suggest roles for right and left temporo-parietal regions in adopting wide versus narrow attentional spotlights, respectively. Careful studies will be needed to distinguish between these differing hypotheses of global/local attention, however, since varying the diameter of the attentional spotlight also results in varying attention to low versus high spatial frequencies (Robertson *et al.*, 1993b; Sasaki *et al.*, 2001).

Given the discussion of spatial attention above, it is interesting to compare our results with findings from a recent fMRI study of spatial orienting (Corbetta *et al.*, 2000). Analogous to the present study, the results indicated that the right iP and right IPL/STG make distinct contributions to cue- and target-related spatial attentional processes. We noted earlier that certain models posit that global/local attention is enabled by varying the diameter of an attentional spotlight to focus either on global or local object features (Robertson *et al.*, 1993b; Sasaki *et al.*, 2001). Such models suggest the possibility that global/local attention and spatial attention rely on common attentional processes.

Evidence consistent with this view comes from studies of hemineglect, a syndrome in which damage to unilateral temporo-parietal regions leads human patients to ignore stimuli on the contralesional side of space. Hemineglect is much more common after right than after left-sided lesions. It has been proposed that this asymmetry might occur because right-sided lesions disrupt the ability to attend to global aspects of a display, leading to hyper-attention to local features (Rafal and Robertson, 1995). Spatial orienting and global attention may therefore both rely on common right temporo-parietal mechanisms that create a relatively wide attentional spotlight. Future studies investigating whether global/local attention and spatial attention rely on common cognitive/neural substrates may therefore advance our understanding of both normal and disrupted attentional functioning.

Interestingly, the significant Task by Hemisphere interactions in temporo-parietal regions were driven mainly by differential activity in the left hemisphere. Specifically, we observed greater activity for local than for global processing in the left hemisphere, but did not observe greater activity for global than for local processing in the right hemisphere. The lack of differential activity in the right temporo-parietal cortex does not appear to be a power problem, given the significant differential activity we observed in corresponding areas of the left hemisphere. Moreover, the presence of a significant Task by Hemisphere interaction is sufficient to support a claim of hemispheric asymmetries, even in the absence of differential processing in one cerebral hemisphere (Hellige, 1983; Van Kleeck, 1989; Weissman and Banich, 1999). However, it is still important to consider why we might not have observed greater activity for global than for local processing in right temporo-parietal regions.

First, demands on attentional control processes appear to be an important determinant of whether hemispheric asymmetries for global versus local processing are observed in temporo-parietal regions. Specifically, greater demands on attentional control processes often lead to more pronounced hemispheric asymmetries. For example, greater asymmetric temporo-parietal activity for global versus local processing is observed during blocks of trials in which participants switch between the global and local levels than during blocks in which they do not switch (Fink *et al.*, 1996, 1997a). Additionally, recent behavioural findings indicate that practice, which reduces demands on

attentional control processes (Norman and Shallice, 1986; Weissman *et al.*, 2002b), reduces hemispheric asymmetries for global versus local processing (Weissman and Compton, 2003). Thus, relatively low demands on attentional control processes enabling global processing might have produced the lack of greater right temporo-parietal activity for global versus local processing.

Second, varying the spatial frequency composition of hierarchical stimuli also appears to affect hemispheric asymmetries for global/local processing. For example, presenting stimuli unilaterally (which filters high spatial frequencies relative to central presentation), increases right temporo-parietal activity more for global than for local processing (Han *et al.*, 2002). In addition, contrast balancing a set of hierarchical stimuli, which filters low spatial frequencies, increases left temporo-parietal activity more for local than for global processing (Han *et al.*, 2002). Thus, the spatial frequency content of our stimuli may also have been suboptimal for observing greater right temporo-parietal activation for global versus local processing.

Our findings also add to a growing controversy about the roles of extrastriate cortices in global/local attention (Fink *et al.*, 1997b, 1999; Proverbio *et al.*, 1998; Mangun *et al.*, 2000; Sasaki *et al.*, 2001; Han *et al.*, 2002; Lux *et al.*, 2004; Weissman *et al.*, 2002a). Specifically, we did not observe hemispheric asymmetries for global versus local processing in occipital regions. On the one hand, this result fits well with claims that hemispheric asymmetries in visual cortices index eye movements (Mangun *et al.*, 2000; Sasaki *et al.*, 2001) and findings that such asymmetries do not occur when eye movements are absent (Sasaki *et al.*, 2001). The present findings also fit nicely with data indicating that attention in visual cortices follows the retinotopic organization of visual cortex, which is bilaterally symmetric (Tootell *et al.*, 1998; Brefczynski and DeYoe, 1999).

On the other hand, our data conflict with findings suggesting that hemispheric asymmetries in visual cortices reflect top-down enhancement of sensory processing in the hemisphere specialized for local or global processing. For example, in contrast to earlier results (Sasaki *et al.*, 2001), one recent study has shown that the expected pattern of hemispheric asymmetries for global versus local processing can occur in visual cortices, even when trials with eye movements are not included in the analysis (Lux *et al.*, 2004). Moreover, using contrast balanced hierarchical stimuli (i.e. filtering low spatial frequencies from hierarchical stimuli) appears to strengthen hemispheric asymmetries for global versus local attention in extrastriate cortices (Han *et al.*, 2002). These results suggest that hemispheric asymmetries for global versus local attention in visual cortices may reflect reentrant effects of attention on sensory representations of global versus local stimulus features (Lux *et al.*, 2004). Future studies will clearly be necessary to resolve the role of extrastriate cortices in global/local processing.

The lack of differential activity for global versus local processing in right temporo-parietal and extrastriate cortices might appear to contradict findings that attention leads to greater activity in neural regions that process goal-relevant stimuli (Corbetta *et al.*, 1991; Kastner *et al.*, 1998; Chawla, 1999; Hopfinger *et al.*, 2000; Woldorff *et al.*, 2004). However, attention-related enhancements of activity are not universally observed (Corbetta *et al.*, 2000; Shulman *et al.*, 2002). As we discussed earlier, demands on attentional control processes (Fink *et al.*, 1996, 1997a; Weissman and Compton, 2003), the spatial frequency content of hierarchical stimuli (Fink *et al.*,

1999; Han *et al.*, 2002), and the difficulty of an upcoming target discrimination (Handy *et al.*, 2001) all likely influence the exact pattern of attention-related activity that is observed in any particular study. Most important for present purposes, even when certain aspects of attention-related biasing activity are not observed, it is still possible to draw meaningful conclusions about the neural correlates of attentional control (Corbetta *et al.*, 2000; Shulman *et al.*, 2002).

Given the aforementioned issues, it is important to consider whether other factors, rather than demands on global/local attention processes, could have produced the patterns of data we observed in temporo-parietal regions. For example, one might wonder whether the asymmetries we observed could have been produced by differential demands on various motor preparation/execution processes. This possibility is unlikely for three reasons. First, the significant hemispheric asymmetries we observed are unlikely to have been produced by unequal demands on motor processes imposed by the global versus the local task, since the global and local tasks had identical response requirements. Second, our finding of greater local than global cue activity in the left iPs is unlikely to have been produced by either making or suppressing eye movements. The iPs is known to play a role in regulating eye movements (Snyder *et al.*, 2000). Our global and local cue stimuli, however, were individual letters presented at fixation that could be easily discriminated without making any eye movements. Third, the greater left IPL/STG activity that we observed for local versus global targets was also unlikely due to either making or suppressing eye movements. Since the neural mechanisms regulating eye movements are bilaterally distributed (Corbetta *et al.*, 1998; Luna *et al.*, 1998; Petit *et al.*, 1997), an eye movement/suppression account would posit greater bilateral activity in temporo-parietal regions for local versus global processing, rather than greater unilateral activity, as we observed. These considerations weigh against an account of the differential cue and/or differential target activity we observed as stemming from unequal demands on motor and/or eye movement/suppression processes.

Finally, our finding of significant hemispheric asymmetries for local, but not global, processing raises the possibility that local processing in our study simply raised demands on left hemisphere letter recognition processes. However, we did not observe greater activity for local versus global targets in occipital cortices, contrary to findings indicating specialized letter recognition circuitry in the left visual cortex (Polk *et al.*, 2002). We therefore conclude that the significant hemispheric asymmetries for global versus local processing that we observed in temporo-parietal regions are much more likely to reflect unequal demands on global versus local attentional processes than on letter recognition processes.

In summary, the present findings make several important contributions to our understanding of hemispheric asymmetries for global/local attention. First, they indicate hemispheric asymmetries for global versus local attention occur for at least two distinct processing components: (i) a preparatory control component that deploys attention to upcoming task-relevant stimuli and (ii) a feature identification component that attends to and/or identifies those stimuli after they are presented. Second, they indicate a double dissociation wherein the two types of hemispheric asymmetries above occur in distinct temporo-parietal regions. Third, they converge with other recent data indicating the iPs and IPL/STG make distinct contributions to attention (Corbetta *et al.*, 2000), suggesting

possible interactions between global/local attention and spatial attention in temporo-parietal regions.

Notes

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