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On-Line Attentional Selection From Competing Stimuli in Opposite Visual Fields: Effects on Human Visual Cortex and Control Processes

Joy J. Geng,[1,2] Evelyn Eger,[1,2] Christian C. Ruff,[1,2] Árni Kristjánsson,[1,3] Pia Rotshtein,[1,2] and Jon Driver[1,2]

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Geng, Joy J., Evelyn Eger, Christian C. Ruff, Árni Kristjánsson, Pia Rotshtein, and Jon Driver. On-line attentional selection from competing stimuli in opposite visual fields: effects on human visual cortex and control processes. *J Neurophysiol* 96: 2601–2612, 2006. First published July 19, 2006; 10.1152/jn.01245.2005. We used fMRI to investigate competition and on-line attentional selection between targets and distractors in opposite visual hemifields. Displays comprised a high-contrast square-wave grating, defined as target by its orientation, presented alone (unilateral) or with a similar distractor of orthogonal orientation in the opposite hemifield (bilateral displays). The target appeared unpredictably on the left or right, precluding anticipatory attention to one side. We found greater activation in target-contralateral superior occipital gyrus for unilateral than for bilateral displays, indicating suppression of the target's visual representation by distractor presence despite the competing distractor projecting to a different occipital hemisphere. Several frontal and parietal regions showed greater activation for bilateral than unilateral trials, suggesting involvement in on-line attentional selection. This was particularly pronounced for regions in bilateral intraparietal sulcus (IPS), which also showed greater functional coupling with occipital cortex specifically on bilateral trials that required selection plus some repetition-suppression effects when target side was repeated, but again only on bilateral trials requiring selection. Our results indicate that competition between visual stimuli in opposite hemifields can influence occipital cortex, and implicate IPS in resolution of this competition by selection.

INTRODUCTION

Neuroscience studies of selective attention have led to an emerging "biased-competition" framework (Desimone and Duncan 1995; Duncan et al. 1997) in which multiple stimuli may compete to drive neural responses but with this competition being biased by top-down signals to favor currently task-relevant stimuli. In addition to single-cell recording studies in awake behaving monkeys (e.g., Chelazzi et al. 2001; Connor et al. 1996; Desimone and Duncan 1995; Luck et al. 1997; Moran and Desimone 1985; Reynolds and Chelazzi 2004; Reynolds et al. 1999), some evidence in accord with this general framework has now been obtained from human neuroimaging studies (e.g., Brefczynski and DeYoe 1999; Gandhi et al. 1999; Kastner and Ungerleider 2000; McMains and Somers 2004; Noesselt et al. 2002; O'Craven et al. 1997; Somers et al. 1999). Within much of the physiological literature, an emphasis has been placed on attentional modulation of competition between concurrent stimuli within a single receptive field (RF) rather than for potentially competing stimuli that

fall into separate RFs (e.g., see Luck et al. 1997; Moran and Desimone 1985).

In contrast, studies of brain-damaged patients in the clinical, neuropsychological literature on attention have often invoked the notion of "competition" to describe behavioral interactions between widely separated visual inputs, typically in opposite visual hemifields that project to different occipital hemispheres (e.g., Bender 1952; Cohen et al. 1994; Duncan et al. 1997; Kastner and Ungerleider 2000; Kinsbourne 1993). For instance, in the phenomenon of "extinction" on double simultaneous stimulation, a patient with right-sided brain injury to parietal cortex or related structures may be able to detect a single stimulus in either visual field yet will characteristically miss a stimulus on the contralesional side if presented concurrently with a competitor on the ipsilesional side (e.g., di Pellegrino and de Renzi 1995; Driver and Vuilleumier 2001; Karnath et al. 2002; Mesulam 2002; Mort et al. 2004; Posner et al. 1984; Thiebaut de Schotten et al. 2005; Vuilleumier and Rafal 2000). This has often been attributed to pathological biases in "attentional competition" between opposite hemifields that may weaken the visual response for the affected side, resulting in a competitive disadvantage for the contralesional stimulus during double simultaneous stimulation (e.g., Cohen et al. 1994; Driver et al. 2001; Duncan et al. 1999; Geng and Behrmann 2005; Kinsbourne 1977; Marzi et al. 2001; Rees et al. 2000; Vuilleumier et al. 2001). Note, however, that the principle suggested from some neurophysiological studies of attentional modulation, whereby competition may arise only (or predominantly) *within* receptive fields (e.g., Luck 1997; Moran and Desimone 1985), might be taken to imply that stimuli in separate visual hemifields should not compete for visual processing within occipital cortex. Each RF is typically exclusively contralateral within occipital areas, raising the question of whether attentional competition between stimuli in opposite visual hemifields can ever affect such low-level visual regions or only higher-level brain regions where RFs may include some ipsilateral representations of visual space (e.g., Kastner et al. 2001; Pouget and Driver 2000; Schwartz et al. 2005; Smith et al. 2001; Tootell et al. 1998).

Human neuroimaging studies on the question of whether inter-hemispheric rivalry can arise within occipital visual cortex when processing competing stimuli from opposite hemifields have not as yet converged on one answer. In a PET study by Fink et al. (2000), participants were asked to report columns

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of three letters presented for 200 ms either unilaterally or bilaterally. Unilateral displays resulted in greater contralateral occipital activations than bilateral displays. This was taken as direct evidence that inter-hemispheric sensory competition can arise between stimuli in opposite visual hemifields, to affect occipital cortex. However, this result may have been a consequence of task demands because subjects were always instructed to report letters on one particular side first in the bilateral blocks, followed by the other side if possible. During unilateral blocks, subjects reported 88% of the letters correctly on the one stimulated side. During bilateral blocks, they reported 80% of letters from the side they had been told to report first but only 13% from the side that had lower priority for report, reflecting typical capacity limits as often found in such "whole-report" tasks (cf. Duncan et al. 1999; Sperling 1960). Because one side was always prioritized in advance for report during bilateral blocks, Fink et al.'s (2000) neuroimaging results for occipital cortex could in principle reflect anticipatory top-down allocation of attention to that prioritized side, which might then lead to the reduced activation observed for the lower-priority side (see Pinsk et al. 2004). The overall lower occipital activations in the bilateral blocks of Fink et al. (2000) might therefore reflect anticipatory attention to one side rather than stimulus-driven competition between hemifields as originally argued (see also Marzi et al. 2001 for critical discussion along these lines).

A more recent fMRI study that explicitly tested for stimulus-driven competition between visual hemifields required subjects to attend to a central stream of visual stimuli while presenting peripheral uni- or bilateral checkerboards that were always task irrelevant (Schwartz et al. 2005). This study reported that adding a second checkerboard concurrently in the other hemifield did not change activations in occipital cortex contralateral to the original checkerboard. That is, checkerboards in separate hemifields did not influence each other within occipital visual cortex in that study, interacting only at the higher level of parietal cortex where some suppression of the response to one hemifield by addition of a concurrent stimulus in the other hemifield was found. Schwartz et al. (2005) therefore suggested that attentional competition between stimuli in opposite hemifields does not affect activity at the level of occipital cortex due to the contralateral nature of receptive fields within it (see preceding text). However, because the peripheral checkerboards were always task irrelevant in Schwartz et al.'s (2005) paradigm, these may never have entered into competition for attention: neither peripheral checkerboard was ever a potential candidate for attentional selection during the central (foveal) task used throughout. Thus although Schwartz et al.'s (2005) results suggest that stimuli in opposite visual hemifields do not always instigate sensory competition at the level of occipital visual cortex, they still leave open the question of whether such competition can arise in visual cortex when both stimuli are potentially task relevant.

In the present study, we therefore sought to examine whether competition between stimuli in opposite hemifields can ever modulate occipital visual responses in a new paradigm devised so that target side was *not* known in advance of each display, hence preventing anticipatory top-down allocation of attention to a particular side (cf. Fink et al. 2000) prior to the display. The stimuli presented on each side could nevertheless still compete for on-line attentional selection because both loca-

tions were potentially task relevant prior to the display (cf. Schwartz et al. 2005). Note that here it was unknown, until the display appeared, which hemifield contained the target and which the distractor (when present). By precluding spatial anticipatory effects in this way, we could better examine effects of competition for attention on activations in visual cortex during on-line selection.

To do so, we compared unilateral target-alone trials for a particular target side against bilateral target-with-distractor trials for that target side. This was done separately for each target side to examine any impact of inter-hemifield distractor competition on the occipital response contralateral to each target. In this way, we could take advantage of the contralateral nature of occipital cortex (which we confirmed directly for the specific stimuli and occipital regions involved, see following text) to distinguish target responses from distractor responses.

Importantly, in the bilateral condition, stimuli in both visual hemifields were potentially task relevant at onset, thereby increasing potential competition and the need for selection. The "filtering" property that distinguished targets from distractors in the bilateral condition was the elementary visual feature of line orientation, which differed by 90° and should thus allow for efficient attentional selection (see Duncan and Humphreys 1989; Treisman and Gormican 1988). The reported target property for both uni- and bilateral conditions was whether the target lines were alternating black and white, or uniform (all black / all white) on a given frame (see Fig. 1). Thus the uni- and bilateral conditions differed in the need for target selection but not in the judgment on the target when selected, which was equivalent. This new paradigm was designed specifically to address the question of whether inter-hemispheric competition for attention can affect occipital visual activations, when targets and distractors appear in opposite hemifields and are distinguished by the elementary visual feature of line orientation, with target location unknown in advance.

We used fMRI to test for any reduction of blood-oxygen-level-dependent (BOLD) activation in occipital visual cortex contralateral to the target when a competing distractor was presented in the opposite hemifield as compared with the same target appearing on its own. In addition, we also assessed whether putative attentional-control structures for selective attention (e.g., in parietal and/or frontal cortex) (see Corbetta and Shulman 2002; Donner et al. 2002; Gitelman et al. 1999; Kincade et al. 2005; Pinsk et al. 2004; Posner et al. 1984; Vandenberghe et al. 2001; Yantis et al. 2002) may be involved in on-line target selection from bilateral displays when target side was unknown prior to the display as here.

METHODS

Participants and imaging

Sixteen volunteers (10 females, 15 right-handed) from 23 to 32 yr in age participated. All were screened for MRI compatibility and gave written informed consent in accord with local ethics clearance as approved by the Joint Ethics Committee of the National Hospital for Neurology and Neurosurgery (NHNN) and Institute of Neurology (ION), London, UK. All had normal or corrected visual acuity. Functional images were collected on a Sonata 1.5 Tesla Siemens MR system with standard head coil (Siemens, Erlangen, Germany), as T2*-weighted echoplanar image (EPI) whole-brain volumes every 2,880 ms. Each functional volume consisted of 32 tilted axial slices

with in-plane resolution of 3×3 mm, slice thickness of 2.5 mm plus 50% gap. The experiment involved three runs lasting 11.6 min each per participant.

Stimuli were presented via a video projector and rear projection screen mounted at the back of the magnet bore. The screen was viewed via a mirror system attached to the head coil. Manual responses were made using an MRI-compatible response box with the right hand.

Experimental design and stimuli

Unilateral displays contained only the target, whereas bilateral displays contained the oriented target on one side plus a distractor with orthogonal orientation in the opposite visual hemifield (see Fig. 1). In both conditions, the target appeared unpredictably on the left or right. All stimuli were created and presented with the MATLAB (The MathWorks, Nantick, MA) custom toolbox Cogent (http://www.vislab.ucl.ac.uk/Cogent). Each display was presented for 530 ms. Central fixation was required, and eye position was monitored on-line with an infra-red tracker inside the scanner (see following text). The inter-trial interval was randomly jittered between 3 and 5 s with an average of 4 s. To prevent anticipatory spatial attention, the side of the target was unpredictable in a random sequence with repetition or nonrepetition of target side equally likely across successive trials (we examined this aspect in the following text to test for any repetition-suppression effects) (cf. Grill-Spector and Malach 2001; Henson and Rugg 2003; Naccache and Dehaene 2001; Schachter et al. 2004; Wiggs and Martin 1998). Thus the visual field of the target, and whether or not this repeated across successive trials, varied in an event-related manner to make target side unpredictable as our experimental questions required. The unilateral/bilateral factor was blocked across 10 successive trials for efficiency. Although this resulted in some foreknowledge of whether a distractor would be present or not, it remained impossible to anticipate the location of the target prior to onset of each trial, and hence on-line attentional selection was always required on bilateral trials.

Each stimulus within a display (i.e., the target, plus a single distractor on the opposite side if present) consisted of high-contrast square-wave gratings (diagonal lines), tilted 45° clockwise or counterclockwise from vertical, within a square window; see Fig. 1. The least eccentric and most superior corner of the square was in the lower visual field, ~2° below the horizontal meridian and ~3.5° from the vertical meridian. The most eccentric and most inferior corner was ~8° below the horizontal meridian and ~10° from the vertical meridian. The exact locations of diagonal lines within the square window were offset from trial to trial such that the lines were nonoverlapping on successive trials. To produce robust BOLD acti-

vations in visual cortex, the diagonal lines within each stimulus flickered, reversing from black to white at a rate of 8 Hz. Within each single frame, these lines were either uniform (i.e., all black or all white on a gray background), or alternating (i.e., black lines interleaved with white, each separated by gray background). Whether the lines in the target and any distractor were uniform or alternating was randomly and independently assigned on each trial.

The task was to attend selectively to the stimulus with clockwise tilt (left example in Fig. 1) and report via button-press whether its lines were uniform or alternating, regardless of the presence or absence of a distractor on the other side. Target selection was thus based on line-orientation (which should be an efficient "filtering" property with the orthogonal orientations used here) (see Treisman and Gormican 1988), whereas report was always based on whether the target lines were uniform or alternating. All subjects practiced the behavioral task outside the scanner for a minimum of 20 trials, continuing further if necessary until they could perform the task accurately. They were repeatedly instructed not to move their gaze from central fixation during both practice and scanning.

Eye-tracking

Eye position was monitored during scanning, using an ASL 504 eye-tracking system (Applied Science Laboratories). Good eye-position signal was obtained for six participants (but not from the others due to technical constraints). These data were analyzed to determine if there was any systematic tendency for gaze to shift toward the target side. Eye data were excluded from consideration if there was any loss of pupil signal during a trial (14.4% of data, mainly due to occasional blinks). Trials with any single value exceeding 1° of visual angle from fixation were then inspected to determine if this reflected an eye movement, as indicated by an abrupt change in horizontal eye-position preceded and followed by plateaus (Fischer et al. 1993a,b). Less than 2% of the data revealed such eye-movements. Moreover, one-way ANOVAs confirmed no significant differences in eye position between conditions, neither for the stimulus period nor for an equivalent period after stimulus offset (all Ps > 0.2; Fig. 2). Note that the critical brain activations we found (see following text) cannot plausibly reflect eye movements, but nevertheless the eye-monitoring data confirm that eye position did not vary systematically with target side for the successfully monitored participants.

Data analysis and image processing

Behavioral data were analyzed using R software (http://www.r-project.org/). Imaging data were analyzed with SPM2 (http://www.fil.ion.ucl.ac.uk/spm2.html). Image preprocessing included realignment and unwarping; spatial normalization to the Montreal Neurological Institute (MNI) standard space and spatial smoothing using a 6-mm full width at half maximum Gaussian kernel. Hemodynamic responses to targets in the eight experimental conditions (given by crossing target side with bilateral/unilateral displays, and with repetition or nonrepetition of target side over successive pairs of trials) were modeled by delta functions convolved with a canonical hemodynamic response function (HRF) and its temporal derivative. The latter revealed no effects that qualify the main results for the standard HRF, and so its outcome is not reported further. In addition to the experimental conditions, the model also contained regressors representing a temporal high-pass filter at 128 s and an AR(1) process to account for temporal autocorrelations (Friston et al. 2002). Signal intensity in all voxels and scans was scaled to the global brain mean during the entire session (grand mean scaling, a default setting in SPM2). Thus the parameter estimates derived for the different experimental conditions are scaled to a numerically identical "baseline" value. This standard scaling procedure cannot confound comparisons of the different conditions that were contrasted here.

FIG. 1. Example of stimuli in a bilateral-display trial. The target was defined by orientation, as the square comprising 45° lines tilted clockwise from upright (left example here). The participant's task was to determine if the target lines were uniform (as for the left target here) or alternating (as for the right distractor in this example). In either case, each line flickered from black to white on the gray background at 8 Hz. For unilateral trials, the target appeared alone. Central fixation was maintained during the brief displays.
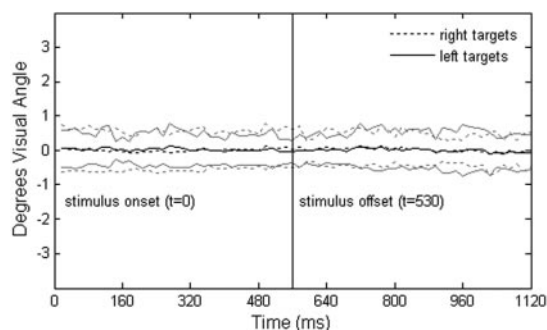
FIG. 2. Mean (black lines) ± SE (gray) of horizontal eye position for right (dotted) and left (solid) targets. The stimulus was on the screen for ~530 ms (left of dividing line). An equivalent period of time following stimulus offset is represented right of the dividing line.

Parameter estimates for all regressors were obtained by maximum-likelihood estimation. All statistical comparisons were performed as random-effects group analyses with 16 participants, using one-sample t-test on contrast images of HRF parameter estimates. Results for specific regions of interest (e.g., stimulus-responsive occipital cortex contralateral to the target, see following text) are reported at a threshold of $P < 0.001$ uncorrected, with a cluster size of ≥ 10 voxels (except where noted for completeness), and likewise for any tests that had to pass multiple independent contrasts and were therefore more stringent (e.g., with inclusive masking in the context of conjunction analyses) (see Nichols et al. 2005). Unconstrained whole-brain contrasts are reported at cluster-corrected $P < 0.05$ levels of significance.

In addition to the main SPM analyses, we also implemented analyses of "effective connectivity" or functional coupling using the established "psychophysiological interaction" (PPI) (e.g., Friston et al. 1997; Gitelman et al. 2003) approach, as explained later, to address whether coupling between parietal cortex (specifically, bilateral IPS) and visual cortex might differ for the bilateral versus unilateral conditions, given that only the former emphasized attentional selection.

SPM results were projected onto a mean structural image created from T1-weighted high-resolution anatomical scans from 15/16 of our participants. Behavioral errors were relatively few (see following text), and an additional SPM model in which errors were modeled separately did not change the overall pattern of fMRI results.

RESULTS

Behavioral results

Behavioral performance during the scanning session is plotted in Fig. 3. ANOVAs on reaction time (RT) and accuracy data revealed a main effect of display type with slower and less accurate performance for bilateral than unilateral displays overall as expected due to the additional requirement for attentional selection of the target from the competing distractor [for RT: $F(1,15) = 69.9$, $P < 0.001$. Means: unilateral = 746 ms, bilateral = 957 ms; for percent correct, $F(1,15) = 13$, $P < 0.005$. Means: unilateral = 94.5%, bilateral = 91.5%]. This effect of distractor competition did not interact with target visual field [for RT: $F(1,15) = 0.6$; for percent correct: $F(1,15) = 0.06$; mean percent correct: unilateral-right target = 94.8, unilateral-left target = 94.4, bilateral -right target = 91.1, bilateral-left target = 89.9]. This indicates that distractor competition had equivalently disruptive behavioral effects for a target on either side. Attentional selection of the targets was thus more demanding for the bilateral than the unilateral displays as anticipated.

A further behavioral issue concerned any effects of repeating target location in the unpredictable sequence. Previous behav-

ioral studies have shown that repeating target location can benefit performance in some attention tasks (e.g., Bravo and Nakayama 1992; Hillstrom 2000; Kristjánsson et al. 2005; Maljkovic and Nakayama 1996). Here we assessed whether such a benefit only arises when attentional selection of targets from distractors is required, as for the present bilateral but not unilateral trials. Repetition of target location did indeed benefit RT performance more for the bilateral trials that required attentional selection than for unilateral trials that did not, as confirmed by an interaction between display type and spatial repetition, $[F(1,15) = 7.2 \ P < 0.05]$. This effect did not depend on target side [no 3-way interaction, $F(1,15) = 2.0$]. The significant two-way interaction was not merely a consequence of overall slower RTs for bilateral targets as it was still found $[F(1,15) = 4.1, P = 0.05]$ when normalized by absolute RT [i.e., (unilateral nonrepeat − unilateral repeat)/(unilateral nonrepeat + unilateral repeat) and (bilateral nonrepeat − bilateral repeat)/(bilateral nonrepeat + bilateral repeat)]. Finally, location repetition did not produce any significant term in analysis of percentage correct (all Fs <1), perhaps as accuracy was already close to ceiling.

fMRI results

To demarcate regions of occipital cortex that responded to our particular stimuli, we first contrasted unilateral left targets with unilateral right targets and vice versa. As expected for unilateral stimuli in the lower visual field, this produced substantial and extensive activation of the contralateral superior occipital gyrus and cuneus (Fig. 4, A and B). This initial result of contralateral activation in occipital cortex, by unilateral displays, provides stimulus-defined regions of interests (ROIs) in contralateral visual cortex. These ROIs were used (via inclusive masking, see following text) to constrain further analyses to voxels that were clearly involved in contralateral, hemifield-specific visual processing of the stimuli used here.

As a further confirmation that these visual ROIs contained only *contralateral* visual representations (important for assessing whether any inter-hemifield competition within such occipital regions might extend beyond the local receptive fields, see INTRODUCTION), we also compared each of the unilateral conditions against ongoing baseline activation. Importantly, this did not reveal any significant *ipsilateral* voxels within the stimulus-defined ROI (Fig. 4C). This indicates that with the
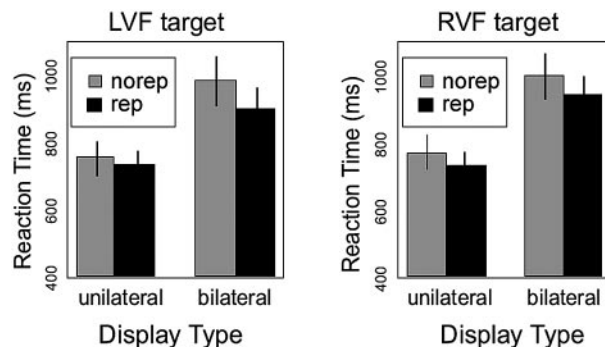

FIG. 3. Behavioral reaction times (RTs) showing the interaction between display type and spatial repetition of target location (bigger benefit of repeated location for bilateral than for unilateral displays), in addition to the main effect of slower RTs for bilateral than unilateral trials overall. Equivalent effects were found for either target side, shown separately here for clarity.
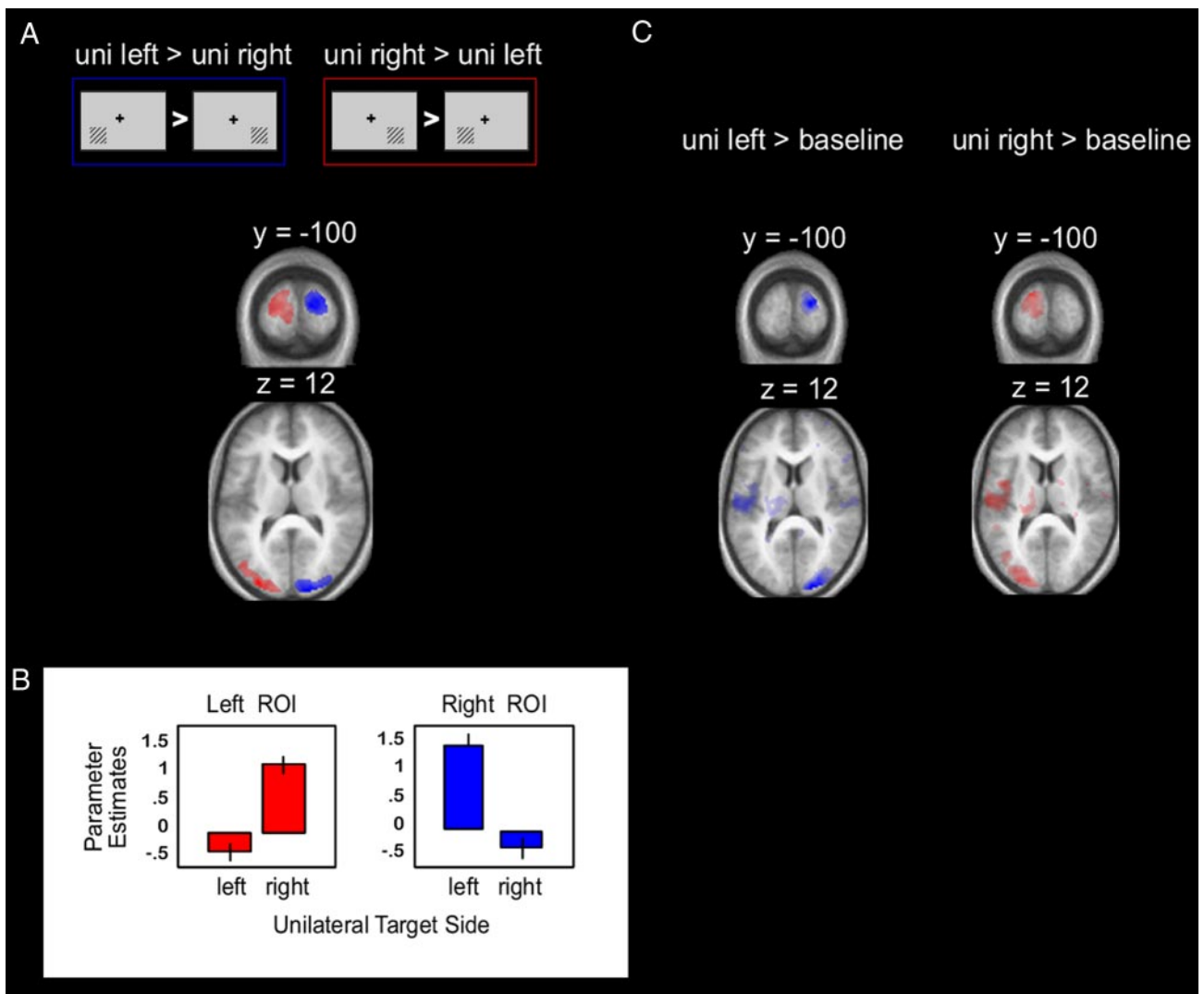
FIG. 4. *A*: contrasts of unilateral left minus unilateral right displays and the reverse, shown in blue and red, respectively. Activations are superimposed on the mean of T1-weighted anatomical images from15/16 of our subjects. These activations were used in subsequent analyses as stimulus-defined visual ROIs, to isolate regions involved in contralateral visual stimulus processing. *B*: average mean parameter estimates (proportional to percentage signal change) for all voxels within each stimulus-defined ROI, showing positive values for contralateral stimuli and no increase for ipsilateral stimuli. Bars are standard error of the mean. *C*: activation associated with each unilateral condition minus ongoing baseline. Note that there were no significant voxels activated ipsilateral to the unilateral stimulus (left in blue, right in red), indicating that the unilateral stimuli only produced contralateral activations here.

measures used here, our posterior occipital ROIs responded to contralateral stimulation but not to ipsilateral stimulation. Of course, this does not preclude the possibility that some ipsilateral representations may exist within higher visual cortex as might be revealed by different measures to those used here (e.g., see Kastner et al. 2001; Pouget and Driver 2000; Smith et al. 2001; Tootell et al. 1998).

Target suppression in occipital cortex by distractor competition from the other hemifield

Our main question of interest concerned possible effects of competition between stimuli in opposite visual hemifields on occipital visual cortex within contralateral target representations (see previous section). To assess this, we addressed the issue separately for each target side. The critical contrasts were: unilateral-left target minus bilateral-left target (any suppressive competition effect would then be

expected to occur in right occipital cortex, contralateral to the target) and separately, unilateral-right target minus bilateral-right target (any suppressive competition effect should now occur in left occipital cortex). In this way, we could test for any reduction in visual activation contralateral to a target on bilateral trials, as compared with the isolated target on unilateral trials. These contrasts yielded significant focal activations within the stimulus-defined occipital ROIs (Fig. 4*A*) in the superior occipital gyrus, contralateral to each target (Fig. 5*A*; Table 1).

No occipital voxels contralateral to the target showed the reverse pattern (i.e., of higher activation on the corresponding bilateral than unilateral trials); although naturally occipital voxels contralateral to the possible *distractor* showed higher response with a distractor present than absent (see later). These results show that adding a potentially task-relevant distractor to the hemifield opposite to the target results in reduced activity in occipital cortex corresponding to the target location, consis-
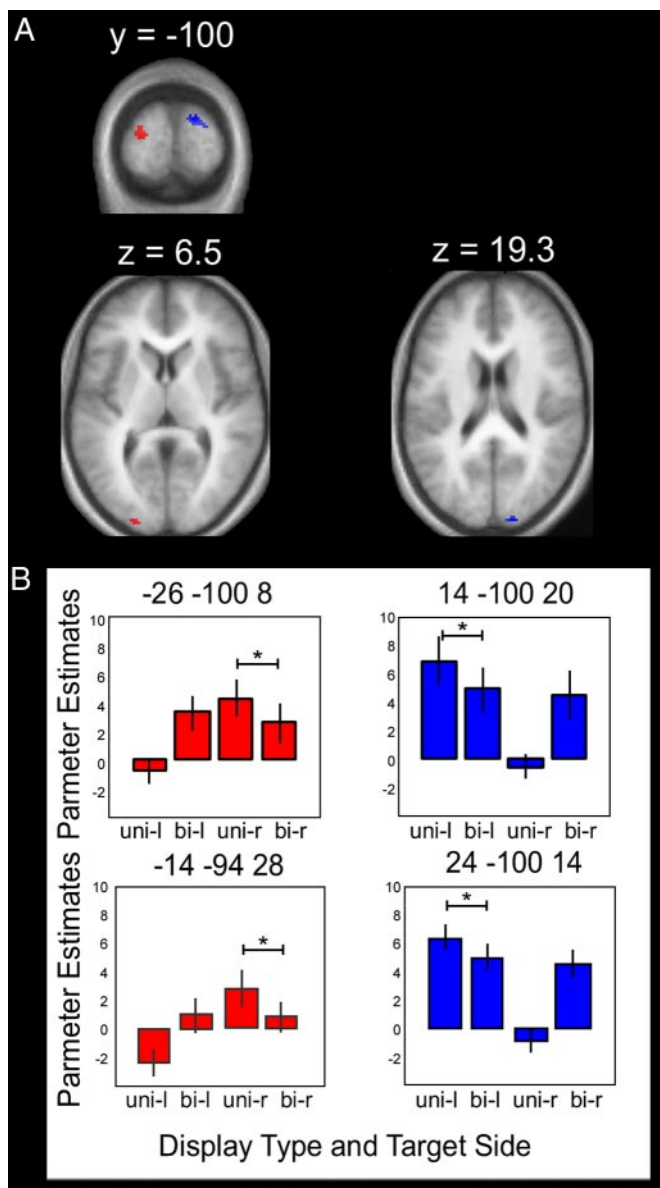
FIG. 5. *A*: occipital sites activated more strongly for a contralateral visual target when presented in unilateral rather than bilateral displays, shown for right-hemifield targets (red) and left-hemifield targets (blue), within the stimulus-defined visual ROIs from the contrasts in Fig. 4*A*. These results demonstrate reduced activation in occipital cortex for targets with a distractor in the opposite visual field, compared with targets appearing alone. (Peak MNI coordinates were as follows: left occipital, $xyz = -26 -100 8$ and $xyz = -14 -94 28$; right occipital, $xyz = 14 -100$ 20 and $xyz = 24 -100 14$). *B*: mean parameter estimates for the 2 peak occipital activations from the separate left- or right- target unilateral minus bilateral contrasts. Note the significantly stronger response to a contralateral unilateral target (uni-r for left occipital cortex; uni-l for right occipital cortex) than a bilateral target. (The opposite pattern for ipsilateral targets trivially reflects the presence of an added distractor stimulus contralateral to the relevant occipital hemisphere in the bilateral condition). SE also shown for each condition.

tent with the notion of suppressive interactions between the target and the distractor. Importantly, the critical decreases in target-related occipital activity were strictly contralateral to the target, making it quite implausible that these effects were related to more general factors, such as different behavioral latencies or habituation for uni- and bilateral trials. We never-

theless conducted further analyses to directly rule out such possibilities.

First, we ran a further model that included trial-specific RT as an additional parametric regressor for each condition, which should reveal any effect that specifically relates to response slowing (rather than stimulus competition, per se). This model produced equivalent results to the original model in occipital cortex contralateral to the target, for the simple contrasts of unilateral minus bilateral for each target side (peak effect for right target at $-22 -102 8$; for left target at $16 -100 20$, cf. Table 1, Fig. 5). Furthermore, activity in these occipital regions did not show any tendency for less activation with parametrically slower RTs. Hence our critical suppressive effect due to inter-hemifield competition, within occipital cortex contralateral to the target (see Fig. 5) cannot be explained by RT increases alone. Moreover, as previously mentioned, the same fMRI results were obtained regardless of whether error-trials were included or modeled separately, so the critical occipital effect cannot be attributed to errors per se either.

Second, we addressed whether occipital cortex might be affected by possible "habituation" effects during the unpredictable sequence of uni- and bilateral target trials. These analyses showed that visual cortex was unaffected by target location repetition factor, showing no main effects of repetition; no simple effect of this for left or right unilateral target trials nor for left or right bilateral trials alone; and no interaction between display type and repetition. We return later to consider repetition effects in regions beyond occipital cortex that did show an activation pattern that mirrored the spatial repetition effects found in behavior.

To summarize the critical effects thus far, we found reduced activation in visual cortex contralateral to the target when a competing distractor appeared in the opposite visual hemifield as compared with when the target appeared alone. These results clearly demonstrate that competition between stimuli in opposite visual fields can produce relative suppression in occipital visual cortex contralateral to the target (Fig. 5) within regions that respond selectively to contralateral but not ipsilateral stimulation (Fig. 4).

On-line attentional selection implicates parietal and frontal cortex

Thus far we have considered how inter-hemifield competition affects visual cortex, leading to reduced activation contralateral to the current target for bilateral as compared with unilateral displays. We next considered areas that may be involved in the on-line attentional selection required for bilateral but not unilateral displays, regardless of target side. If resolving attentional competition to select the target requires more attentional control, this should presumably lead to increased activation for attentional-control structures (e.g., in parietal and frontal cortex) on bilateral than on unilateral trials.

The main effect of bilateral-minus-unilateral conditions did indeed reveal activation of several areas thought to reflect attentional demand (Table 2), including bilateral IPS, supramarginal and angular gyri, bilateral posterior inferior temporal gyri, right middle frontal gyrus, and medial superior frontal gyrus. These areas were similar to those observed in many previous studies of attentional demand (e.g., Corbetta and

TABLE 1. *Left and right unilateral minus bilateral displays*

Contrast	Region (Within Occipital Lobe Stimulus-Defined Visual ROI)	Voxel Cluster Size	T Value	Z Score	MNI Coordinates
L: Unilateral > bilateral	R superior occipital gyrus	42	7.10	4.63	14 −100 20
			4.02	3.26	24 −100 14
R: Unilateral > bilateral	L superior occipital gyrus	21	4.53	3.55	−26 −100 8
		18	4.26	3.39	−14 −94 28

ROI, region of interest

Shulman 2002; Donner et al. 2002; Hopfinger et al. 2000; Kincade et al. 2005; Nobre 2001; Pinsk et al. 2004; Schwartz et al. 2005; Wojciulik and Kanwisher 1999; Yantis et al. 2002). There was also some activation of occipital cortex (Table 2) but now due trivially to the added distractor stimulus on bilateral trials. This was confirmed by simple contrasts of left (or right) bilateral displays, minus left (or right) unilateral displays, respectively, which showed that any increased occipital activation on bilateral trials was always contralateral to the distractor.

The main effect of bilateral-minus-unilateral collapses over target side but does not directly test whether any activation applies reliably for both target sides (rather than being mainly related to one particular target side). We assessed this with a form of conjunction analysis (inclusive masking) that reveals regions that show greater activation during bilateral than unilateral trials, for both left- and right-target trials (Nichols et al. 2005). This resulted in significant activations only in bilateral IPS and right middle temporal gyrus (Table 2).

As might be expected, as the corollary of the attention network being activated by the main effect of bilateral minus unilateral, the reverse contrast of unilateral minus bilateral resulted in significant activations in regions described as form-ing parts of a "resting state" or default, network (e.g., Greicius et al. 2003; Gusnard and Raichle 2001; Raichle et al. 2001) (see Table 2). The conjunction of the left and right simple effects of unilateral minus bilateral similarly produced similar activations in the anterior and posterior cingulate, left angular gyrus, and left superior frontal gyrus (Table 2).

In summary, as expected the bilateral-minus-unilateral main effect (and its conjunction over target side) highlighted regions in the well-known "attention network" (e.g., Corbetta and Shulman 2002; Yantis et al. 2002), consistent with the increased attentional demand when selection of the target from a distractor was required on bilateral trials. This was particularly marked for bilateral IPS (see conjunction results in Table 2 and Fig. 6A). Analogously, those regions that were more active overall in the unilateral than bilateral trials, regardless of target side, were consistent with the reduced attentional demand on such trials.

Enhanced functional coupling of parietal cortex with visual cortex when attentional selection is required

It has previously been proposed that parietal cortex may become more functionally coupled with visual cortex as de-

TABLE 2. *Bilateral vs. unilateral displays*

| Contrast	Region	Voxel Cluster Size	T Value	Z Score	MNI Coordinates
Conjunction of L and R Bilateral - Unilateral	R intraparietal sulcus	14	5.10	3.83	34 −50 50
	L intraparietal sulcus	24	4.71	3.64	−30 −54 44
	R middle temporal gyrus	19	5.00	3.78	48 −62 −10
Bilateral > Unilateral	R middle occipital gyrus	339	7.38	4.73	20 −98 4
	L middle occipital gyrus (including L Intraparietal sulcus)	1566	7.20	4.67	−34 −96 4
	R inferior temporal gyrus	278	6.14	4.28	48 −68 −12
		218	5.7	4.1	32 −74 −6
	R middle frontal gyrus	124	5.94	4.2	46 12 32
	L inferior temporal gyrus	222	5.52	4.02	−50 −66 −14
	R intraparietal sulcus	586	5.84	4.16	36 −52 52
	Medial superior frontal gyrus	102	4.51	3.53	−2 8 54
Conjunction of L and R Unilateral - Bilateral	Bilateral anterior cingulate	484	6.89	4.56	2 50 0
	L superior frontal gyrus	27	6.22	4.31	−18 60 16
	L angular gyrus	61	5.24	3.89	−50 −72 34
	L posterior cingulate	13	5.22	3.88	−6 −50 26
	R posterior cingulate	17	4.54	3.55	8 −62 16
Unilateral > Bilateral	Bilateral anterior cingulate	4939	9.35	5.29	2 48 0
	Bilateral posterior cingulate	2923	9.17	5.25	−6 −56 32
	L angular gyrus	814	7.11	4.63	−52 −68 32
	R anterior middle temporal gyrus	115	6.57	4.44	60 4 −20
	L anterior middle temporal gyrus	331	6.56	4.44	−56 −16 −20
	R precentral gyrus	226	5.77	4.13	56 −10 24
	R cingulate	113	5.12	3.83	16 −28 36
	L paracentral lobule	233	5.1	3.82	−8 −30 68
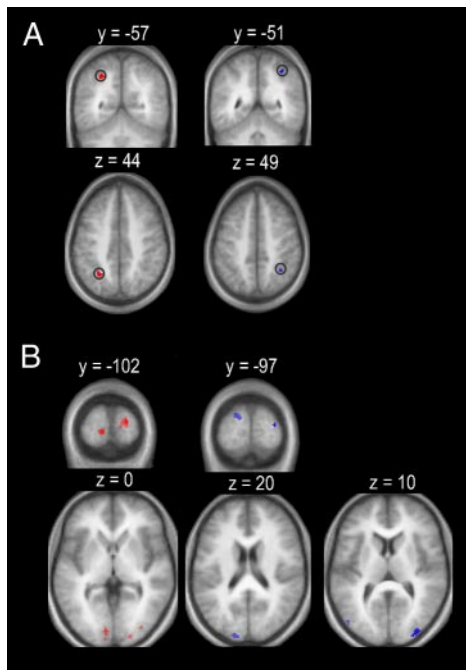
FIG. 6. *A*: Left (red) and right (blue) IPS sites that showed greater activation for bilateral than unilateral displays for *both* left and right hemifield targets, as confirmed by separate statistical tests for each, that were then combined to form a "conjunction" via inclusive masking. A spherical volume of interest, centered on the peak voxel with 6 mm radius (black circles) from either of these sites was used as a seed for functional coupling PPI analyses (see main text), which tested for brain regions that showed stronger functional coupling with the seed IPS site during bilateral than unilateral displays. *B*: occipital sites showing condition-specific coupling with left IPS (red) and right IPS (blue).

mands on visual attention are increased (Büchel and Friston 1997, 1998; Friston et al. 1997). To test this idea for our paradigm, we applied the "psychophysiological interactions" (PPI) approach (Friston et al. 1997) to assess whether trial-by-trial functional coupling of IPS with other areas might vary as a consequence of attentional demand (manipulated here by comparing bi- with unilateral trials). The PPI approach tests for condition-dependent covariation in activity between a "seed" region and any other brain area, after the mean effects of experimental factors in the model have been accounted for.

We seeded our PPI analyses in left or right IPS regions (left IPS centered at 34 −50 50; right IPS at −30 −54 44) that had shown bilateral greater than unilateral effects reliably for both left and right targets (see conjunction effects in previous section, see also Table 2; Fig. 6*A*). For each subject, mean-adjusted data were extracted from all voxels within a sphere (6-mm radius) centered at these left or right IPS sites. The PPI procedure in SPM2 was then used to create regressors representing the time course of activation in each seed region and their interaction with the bi- versus unilateral condition, i.e., with our manipulation of attentional demand (see Gitelman et al. 2003). These regressors were added to the existing subject-specific models, and two new random-effects models were calculated to identify any regions showing increased coupling with either IPS site for bilateral versus unilateral conditions.

To assess whether occipital areas involved in stimulus processing may become more strongly coupled with IPS during the bilateral trials, we first examined those areas in the occipital stimulus-defined ROIs (Fig. 4). Such coupling was indeed found between bilateral occipital cortex and the left IPS seed (see Fig. 6*B*; Table 3), at $P < 0.001$. Coupling between the right IPS seed and bilateral occipital cortex was also found but only at $P < 0.05$, which we report for completeness (Fig. 6*B*; Table 3).

The PPIs for left and right IPS also both independently revealed more coupling with an overlapping area within the left middle frontal gyrus (see also Hopfinger et al. 2000; Huettel and McCarthy 2004) as a function of attentional demand (i.e., again more coupling for bilateral than unilateral conditions). In addition, right IPS showed some condition-specific coupling with further structures (Table 3). These coupling results highlight the interactive nature of attentional processing between the IPS and visual cortex and other control regions when selective attention is necessary as for the bilateral but not the unilateral trials here.

fMRI effects of target-side repetition for bilateral but not unilateral trials

Recall that behaviorally (see Fig. 3) we had found greater priming effects from repeating target location over successive trials for the bilateral displays that require attentional selection

TABLE 3. *Psychophysiological interaction analyses*

Seed Site	Region (Within Occipital Lobe Stimulus-Defined Visual ROIs)	Voxel Cluster Size	T Value	Z Score	MNI Coordinates
L intraparietal sulcus	L occipital	101	4.83	3.69	−10 −100 −4
		46	2.67	2.38	−46 −74 −8
		40	2.51	2.26	−14 −100 22
		40	2.39	2.16	−30 −76 −6
			2.3	2.10	−26 −78 −14
	R occipital	167	5.70	4.10	20 −100 8
		14	3.23	2.77	34 −86 2
R intraparietal sulcus	L occipital	30	2.38	2.16	−16 −98 20
		13	2.29	2.09	−46 −70 −14
		12	2.05	1.90	−48 −80 12
	R occipital	36	2.63	2.35	30 −98 10
	Extra occipital whole brain analysis				
L intraparietal sulcus	L middle frontal gyrus	23	4.95	3.75	−30 30 48
R intraparietal sulcus	L middle frontal gyrus	32	7.75	4.84	−26 34 48
	R central sulcus	34	6.43	4.39	32 −24 58
	L anterior cingulate	41	4.97	3.77	−10 16 52

than for unilateral displays where there was no distractor. Although there were no effects of such repetition within our visual ROIs (see preceding text), we tested the whole-brain fMRI data for any "repetition-suppression" effects (Grill-Spector and Malach 2001; Henson and Rugg 2003; Schachter et al. 2004; Wiggs and Martin 1998) showing an analogous pattern to the behavioral spatial repetition effects. Similar to the visual ROIs, there was no overall main effect of repeating target side over successive trials in the random sequence (i.e., nonrepetition > repetition) in whole-brain analysis. Similarly, there were no significant voxels within the conjunction of nonrepetition minus repetition for both left and right targets. However, the analogous fMRI pattern to the behavioral interaction [of the form (bilateral nonrepetition > repetition) > (unilateral nonrepetition > repetition)] did arise within the putative attentional control structures (i.e., those activated by bilateral minus unilateral), specifically for a region in right IPS (Fig. 7; $xyz = 26\ -64\ 40$). A similar cluster on the left, but more anterior, also showed this interaction ($xyz = -40\ -48\ 40$; note only 6 voxels of a larger cluster lay within the masked area).

These results indicate that parietal regions associated with attentional selection can show repetition suppression when target location is repeated in the unpredictable sequence (see also Kristjánsson et al. 2006) but do so significantly more for the bilateral trials that required attentional selection than for the unilateral trials that did not (thus mirroring the behavioral effects in Fig. 3). These new fMRI repetition-suppression results, as a function of unpredictable repetition of target locations, support the general idea that parietal cortex plays a critical role in both attentional selection (as on the bilateral trials here in particular) *and* in the spatial representation of stimuli (consistent with the present sensitivity to repeating target location, when selection was required).

DISCUSSION

Here we studied how presenting a distractor stimulus in one hemifield changed visual activations elicited by a lateralized target in the other hemifield. Target side was not known in advance so that anticipatory attention to one side was precluded. Hence targets had to be selected from distractors on-line here based on the basic visual feature of orientation. We found that bilateral trials, on which the target was presented concurrently with a competing distractor in the opposite hemifield, produced reduced activation in the superior occipital gyrus contralateral to the target in comparison to the same target presented alone. We ruled out general difficulty or mere habituation as the cause of these effects, concluding that the reduced activation in visual cortex contralateral to the bilateral target reflects competition for attention between two stimuli that were both potentially task relevant at initial onset (unlike Schwartz et al. 2005) because target-side could not be anticipated (unlike Fink et al. 2000).

Although it was not possible to implement detailed retinotopic mapping in the present random-effects group study, comparison of the coordinates for the present competition effects with the published normalized coordinates of visual areas in other studies (e.g., see Amunts et al. 2000; Dougherty et al. 2003) appears broadly consistent with these effects arising in V2/V3. But such attribution to specific retinotopic areas is not crucial for our present purposes. The most critical
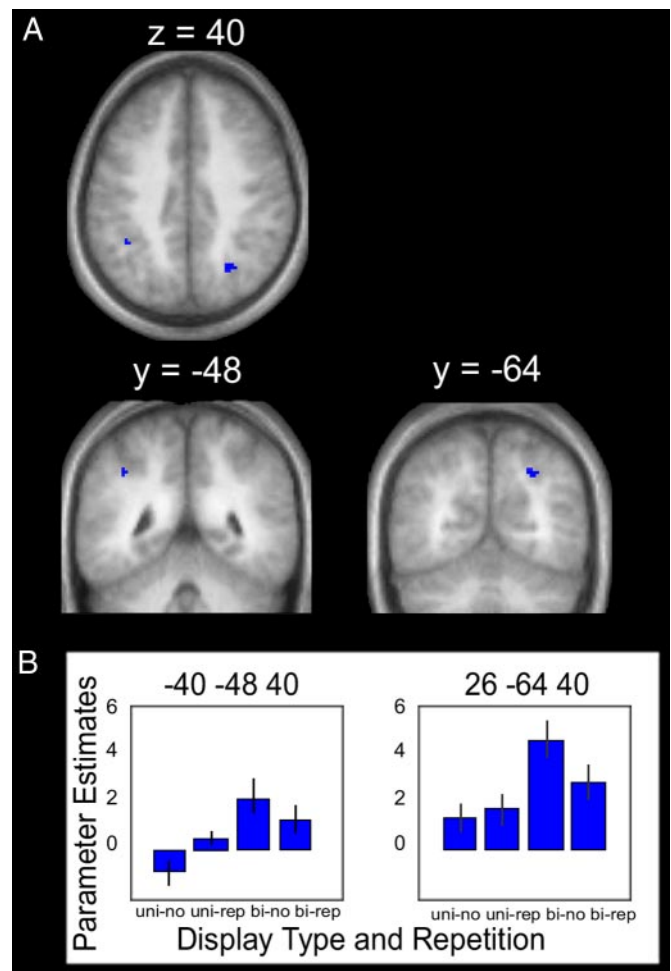

FIG. 7. *A*: left and right IPS regions that showed greater repetition suppression when the target location was repeated for bilateral displays than for unilateral displays. *B*: plots of parameter estimates from the left and right IPS peaks (MNI coordinates: $-40\ -48\ 40$; $26\ -64\ 40$) for each condition. Note the reduced response for location repetition ('rep') than for nonrepetitions ('no') specifically for the bilateral ('bi') displays but not for the unilateral ('uni') displays.

point is that inter-hemifield competition affected posterior occipital cortex in regions that responded contralaterally to the target and showed no ipsilateral visual response (at least none that could be detected with the fMRI methods used here, which did reveal a strong contralateral response; see Fig. 4). Thus inter-hemifield competition evidently can affect visual regions in which RFs for the two separate stimuli should not overlap (see also Kastner et al. 2001). This suggests that attentional competition can sometimes affect visual processing at a level where the competing stimuli are represented in distinct RFs (indeed, in distinct occipital hemispheres). This aspect of our results seems consistent with the clinical evidence for attentional competition between hemifields affecting visual processing in pathological conditions such as extinction (di Pellegrino and de Renzi 1995; Driver and Vuilleumier 2001; Driver et al. 2001; Geng and Behrmann 2005; Kinsbourne 1977; Marzi et al. 2001; Posner et al. 1984) (see INTRODUCTION), and also with the general principle of selective attention involving interactions between multiple brain areas that together resolve competition between spatially or temporally separate stimuli (Co-

hen et al. 1994; Duncan et al. 1997; Macaluso et al. 2000; Serences and Yantis 2006).

Although our occipital results may initially appear discrepant with those of Schwartz et al. (2005), the fact that all of our stimuli were potentially *task relevant* at onset may resolve this. In Schwartz et al. (2005), the lateralized peripheral stimuli were known to be task-irrelevant throughout the entire experiment with attention always directed to stimuli at central fixation. It thus appears that potential task relevance may be necessary for competition between separate visual hemifields to affect occipital visual cortex as here. The fact that Schwartz et al. (2005) did not find stimulus competition within visual cortex further suggests that the present effects do not merely reflect unilateral stimuli acting like an exogenous cue to their location (cf. Posner 1980) as otherwise a similar outcome should have been found.

The present results accord with the findings of Fink et al. (2000), in which the peripheral stimuli were also task relevant; but here we were able to exclude potential confounds from anticipatory spatial attention to one side prior to each display, which might have applied to the Fink et al. (2000) study, and has been shown to modulate occipital activation (e.g., Brefczynski and DeYoe 1999; Gandhi et al. 1999; Gitelman et al. 1999; Hopfinger et al. 2000; Kastner and Ungerleider 2000; McMains and Somers 2004; Somers et al. 1999). Furthermore, although Fink at al. (2000) suggested that competition between hemifields in visual cortex might reflect purely bottom-up factors, the absence of such an effect in Schwartz et al. (2005) suggests not. Moreover, the present data provided evidence that when inter-hemispheric competition does affect occipital cortex, this may be mediated via higher-level attentional control structures (see also Pinsk et al. 2004), such as spatial representations in the IPS.

A number of structures related to attentional control were activated in the overall contrast between bi- and unilateral trials here (see also Corbetta and Shulman 2002; Donner et al. 2002; Kincade et al. 2005; Pinsk et al. 2004; Posner et al. 1984; Vandenberghe et al. 2001; Wojciulik and Kanwisher 1999; Yantis et al. 2002). The IPS in particular was activated in both hemispheres for bilateral displays compared with unilateral displays, regardless of target side as confirmed by conjunction analysis (see Fig. 6A). Moreover, the IPS showed stronger effective connectivity (or functional coupling) with occipital cortex and with the middle frontal gyrus, specifically in the context of attentional selection during bilateral displays. Note that the occipital sites showing such greater coupling with IPS were located within the stimulus-defined visual ROIs and thus within occipital representations of the visual stimulus location.

These results reinforce the general idea that attentional modulation of visual cortex may involve interactions with higher-level control structures, including regions of the parietal lobe (e.g., Büchel et al. 1998; Hopfinger et al. 2000; Pinsk et al. 2004; Ruff and Driver 2006), but they further suggest that IPS may be involved in on-line adjudication of competition between stimuli in opposite visual hemifields. This may accord with the clinical data on pathological competition between hemifields after parietal damage (e.g., Cohen et al. 1994; di Pellegrino and de Renzi 1995; Driver and Vuilleumier 2001; Driver et al. 2001; Duncan et al. 1999; Geng and Behrmann 2005; Karnath et al. 2002; Kinsbourne 1977; Marzi et al. 2001; Mesulam 2002; Mort et al. 2004; Posner et al. 1984; Rees et al.

2000; Thiebaut de Schotten et al. 2005; Vuilleumier and Rafal 2000; Vuilleumier et al. 2001). Future work might address whether similar competitive effects within occipital cortex to those here can arise when target and distractor appear within the same hemifield but in different quadrants (see Kastner et al. 2001), although there is some initial evidence for greater competition between rather than within hemifields (Awh and Pashler 2000; McMains and Somers 2004; Sereno and Kosslyn 1991). Here we focused specifically on the inter-hemifield situation because this is analogous to the situations typically studied in clinical studies of extinction.

In the present study, on-line attentional selection from the bilateral displays involved determining which stimulus was the target (defined by orientation) and then making a feature judgment on it (uniform/alternating). Behaviorally, we found that repeating target location across successive trials led to enhanced performance but more so for the bilateral trials (where attentional selection from a distractor was required) than for the unilateral trials (where no selection was needed; see Fig. 3). Although several previous studies have shown some benefits of repeating target location in selective attention tasks (e.g., Bravo and Nakayama 1992; Hillstrom 2000; Maljkovic and Nakayama 1996, 2000; for review, see e.g., Kristjánsson 2006), this is the first to demonstrate that such benefits are specific to conditions with distractors, being absent for isolated targets.

Turning to the fMRI data, we used the general logic of BOLD repetition suppression (Grill-Spector and Malach 2001; Henson and Rugg 2003; Schachter et al. 2004; Wiggs and Martin 1998), to determine if any areas within the putative "attentional-control" network (defined here as those areas activated by bilateral more than unilateral trials overall) showed an analogous fMRI pattern for spatial repetition to that observed in behavior. IPS regions showed exactly such a pattern (see also Kristjánsson et al. 2006), with such repetition suppression being found only for the bilateral displays where spatial selection was necessary. This suggests that parietal regions involved in attentional selection can be primed by target-location repetition only when selection is required, then leading to BOLD-suppression effects that may be analogous to those found for repetition of attended object properties in other brain regions (e.g., ventral visual cortex for repeated object identity, see Eger et al. 2004; Murray and Wojciulik 2004).

Although the IPS peaks for the repetition-suppression interaction (Fig. 7) were at some distance from the IPS seeds for the functional-coupling results (see Fig. 6), both fell within the bilateral minus unilateral contrast that functionally defined the attentional network here. Taken together, these results indicate that bilateral IPS forms part of an attention-related network that interacts with occipital cortex (as shown by the PPI result) and that represents the location of selected targets (as shown by the repetition-suppression interaction), specifically when distractor competition must be resolved via attentional selection.

In conclusion, the present results demonstrate that inter-hemispheric competition between potentially task-relevant stimuli in opposite visual hemifields can affect activation in occipital cortex. In particular, reduced activation contralateral to the target was found in the superior occipital gyrus when a competing distractor was presented in the opposite hemifield (as in the situations of double simultaneous stimulation that can lead to pathological attentional competition in parietal pa-

tients). These effects on occipital cortex may reflect interplay with higher-level regions, such as IPS, which showed greater functional coupling with occipital cortex specifically in the context of attentional selection (i.e., for the bilateral displays). Moreover, regions in the IPS showed repetition-suppression effects when target side was repeated, but again only for displays that required attentional selection (i.e., the bilateral displays), analogous to the behavioral pattern found. These results demonstrate that inter-hemifield competition can affect visual cortex, while also suggesting that higher regions representing task-relevant spatial locations (as in IPS) may mediate such attentional competition.

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