Attentional Preparation for a Lateralized Visual Distractor: Behavioral and fMRI Evidence

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Abstract

■ Attending to the location of an expected visual target can lead to anticipatory activations in spatiotopic occipital cortex, emerging before target onset. But less is known about how the brain may prepare for a *distractor* at a known location remote from the target. In a psychophysical experiment, we found that trial-to-trial advance knowledge about the presence of a distractor in the target-opposite hemifield significantly reduced its behavioral cost. In a subsequent functional magnetic resonance imaging experiment with similar task and stimuli, we found anticipatory activations in the occipital cortex contralateral to the expected distractor, but no additional target modulation, when participants were given advance information about a distractor's subsequent presence and location. Several attention-related control structures (frontal eye fields and superior parietal cortex) were active during attentional preparation for all trials, whereas the left superior prefrontal and right angular gyri were additionally activated when a distractor was anticipated. The right temporoparietal junction showed stronger functional coupling with occipital regions during preparation for trials with an isolated target than for trials with a distractor expected. These results show that anticipation of a visual distractor at a known location, remote from the target, can lead to (1) a reduction in the behavioral cost of that distractor, (2) preparatory modulation of the occipital cortex contralateral to the location of the expected distractor, and (3) anticipatory activation of distinct parietal and frontal brain structures. These findings indicate that specific components of preparatory visual attention may be devoted to minimizing the impact of distractors, not just to enhancements of target processing. ■

INTRODUCTION

Only a fraction of the information entering our senses at any given time is relevant for ongoing behavior. Perception and action depend on selective attention, a set of mechanisms that allows us to process the currently important aspects of our environment ("targets") in the face of potential distraction by irrelevant stimuli ("distractors"). Several recent functional magnetic resonance imaging (fMRI) studies (e.g., Macaluso, Eimer, Frith, & Driver, 2003; Hopfinger, Buonocore, & Mangun, 2000; Ress, Backus, & Heeger, 2000; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999) have focused on top-down contributions to visual selective attention by examining neuronal activations during attentional *preparation* for particular stimuli and judgments, prior to the actual presentation of the stimuli, and thus in the absence of changes in sensory input. Such studies have revealed not only anticipatory activation of putative attentional control structures (e.g., in frontal–parietal circuits), but also some spatiotopic modulations of the visual cortex in advance of stimulus presentation. These typically take the form of increased activations in those parts of the visual cortex representing the hemifield, quadrant, or retinotopic location in which a visual *target* is anticipated (e.g., see Macaluso et al., 2003; Hopfinger et al., 2000; Ress et al., 2000; Kastner et al., 1999). Such anticipatory effects in the visual cortex, termed "baseline shifts" by some authors (e.g., Kastner & Ungerleider, 2000; Chawla, Rees, & Friston, 1999), provide direct empirical support for the notion that visual selective attention operates in part by means of top-down signals that can modulate activity in the occipital cortex in a preparatory fashion. A common interpretation of these anticipatory modulations is that they bias processing (or "competition" between multiple incoming stimuli) in favor of target stimuli or locations, at the expense of processing for distractor stimuli in the scene (Kastner & Ungerleider, 2001; Duncan, Humphreys, & Ward, 1997).

In psychophysical studies of selective visual attention, it has been debated whether selective attention mainly operates by enhancing target-related signals (e.g., Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Hawkins et al., 1990) by suppressing signals from surrounding distractors (e.g., see Awh, Matsukura, & Serences, 2003; Lu, Lesmes, & Dosher, 2002) or by a combination of both mechanisms

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(e.g., Dosher & Lu, 2000; Cheal & Gregory, 1997). However, most previous neuroimaging studies on anticipatory top-down modulations of the visual cortex have focused mainly on an upcoming expected target (e.g., by manipulating the location of this), rather than seeking to isolate any anticipatory modulations that might relate to expectation of a *distractor* at a particular location. Kastner et al. (1999) did vary whether a target at a known upcoming location would subsequently be presented with or without concurrent distractors, but the focus was nevertheless on how this might affect activation in the visual cortex corresponding to the target quadrant. More recently, Serences, Yantis, Culberson, and Awh (2004) began to examine whether anticipatory modulations of the visual cortex may relate to the anticipation of distractors surrounding the target stimuli. We will discuss their study in more detail later, but note for now that distractor arrays in that study, when present, were tightly packed into the same retinal quadrant as the target (see also Awh et al., 2003). This means that any modulation of spatiotopic visual cortex corresponding exclusively to the location of an expected distractor, rather than the target, could not be isolated. Hence, it is unclear at present whether anticipatory selective attention can be employed to prepare for a single distractor stimulus that is spatially remote from a target, and whether any such distractor anticipation may involve modulation of occipital representations for that part of the visual field that would subsequently contain the distractor rather than the target.

In the present study, we therefore focused on any behavioral and fMRI effects specific to expecting a distractor at a known location that was distinct and remote from the expected target location. Specifically, we employed a single distractor stimulus in the *opposite hemifield* to a target, hence projecting to a different cortical hemisphere. In an initial behavioral experiment, we manipulated on a trial-by-trial basis any advance information about whether or not such a distractor would appear on the opposite side to the cued target location. To anticipate, we found that such advance knowledge about distractor presence reduced the behavioral cost of that distractor, relative to no foreknowledge about distractor presence/absence, even when advance knowledge about target location was held constant. Advance knowledge about distractor *absence* had no behavioral effect relative to no foreknowledge. This behavioral pattern of results thus indicates that participants can prepare beneficially for the presence of a single distractor at a particular location remote from the anticipated target.

In a subsequent fMRI experiment with a similar paradigm, we then examined the neural activations associated with such attentional preparation for a single distractor at a known location on the opposite side to the target. Using opposite hemifields for the target and distractor in this way allowed us to test whether anticipation of a visual distractor would modulate activity in the occipital hemisphere representing the distractor location, or in the (other) occipital hemisphere representing the target location (as might be expected if participants simply attended more strongly, or with a different strategy, to the target location when expecting a distractor), or whether both types of modulation exist when anticipating a distractor.
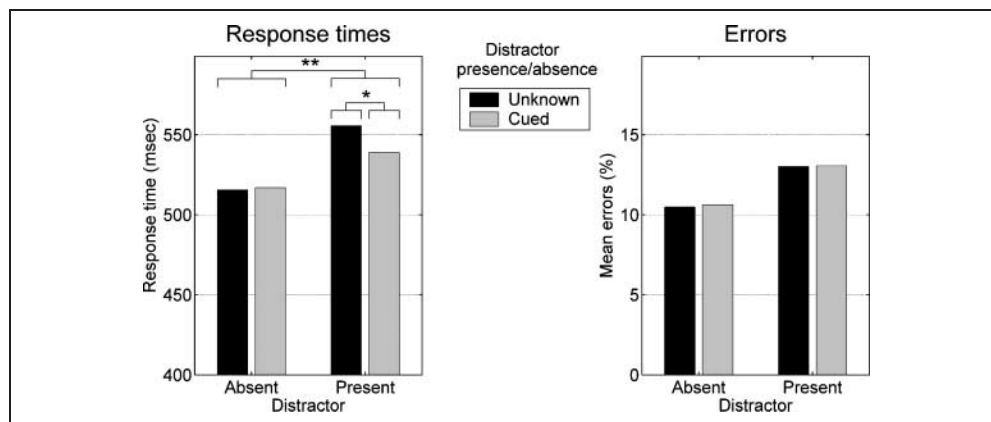
RESULTS

Experiment 1: Behavioral Study Outside Scanner

We examined whether trial-by-trial advance knowledge about the presence or absence of a distractor at a specific location could reduce the cost of this distractor for processing of a target in the opposite hemifield. On every trial, participants were randomly cued by a small central arrow to either the left or the right hemifield and performed a speeded discrimination task on the target appearing there (100% valid cuing of target side, which was held constant across all conditions; see Methods). These targets were either presented alone (*D-absent*), or with a distractor present in the other hemifield (*D-present*), in a randomly intermingled fashion. The cost of distractor presence versus absence on target processing speed (i.e., latencies for D-present minus D-absent trials) was measured in two types of blocks that differed in whether participants could or could not anticipate, on a trial-by-trial basis, the presence or absence of a distractor in the target-opposite hemifield.

In those blocks *with* foreknowledge about distractor presence or absence (*D-cued*, as in the subsequent fMRI study also), the color of the central cue (red or green) was 100% informative as to whether the following display would contain a distractor or not (respectively) on the opposite side to the target. In control blocks providing a behavioral baseline (implemented only in the behavioral Experiment 1, not during the subsequent fMRI study of Experiment 2), participants were given no foreknowledge about distractor presence or absence (*D-unknown*); that is, the color of the central cues (now always blue) no longer gave any information about the possible presence or absence of a distractor. By comparing the behavioral distractor cost in the D-cued and the D-unknown blocks, we could examine whether advance foreknowledge about the presence or absence of a distractor in a particular location allowed participants to minimize the behavioral impact of this distractor.

The results for Experiment 1 (see Figure 1) pool over left and right targets, as these led to similar outcomes for all conditions (see Methods). In both types of blocks (D-cued and D-unknown), distractor presence led to a significant slowing of response times; Friedman analysis

Figure 1. Advance knowledge
about distractor presence
on a known side reduces
the behavioral cost of the
distractor. Left, mean response
times; right, mean error rates
in behavioral Experiment 1,
with $n = 17$. Significant
differences are marked by
the top horizontal brackets
(**$p < .001$, *$p < .05$).
Responses were faster to
trials with single targets (left
two bars in each panel) than
to trials with targets and
distractors (right two bars
in each panel). However, the

latency cost of adding a distractor was significantly reduced on trials with advance knowledge about distractor *presence* (gray bar in right pair) as compared to no such foreknowledge (black bar in right pair). Note that cueing of distractor *absence* had no such effect on response times (gray vs. black bars in left pair) and that error rates (right) did not differ significantly between the distractor cueing conditions.

of variance, $\chi^2(1,16) = 17$, $p < .0001$; same result also significant by parametric t test, and likewise for further effects below. Critically, this behavioral cost due to the distractor was smaller when participants were given foreknowledge that a distractor would be presented opposite to the target side (i.e., smaller distractor cost in the D-cued blocks than in the D-unknown blocks). This was confirmed by a significant interaction between the presence/absence of a distractor and distractor foreknowledge, $\chi^2(1,16) = 13.24$, $p < .001$, and by the significant reduction in response times for D-present trials when the appearance of the distractor on that side was foreknown, as compared to D-present trials without distractor foreknowledge, $\chi^2(1,16) = 2.88$, $p < .05$.

In contrast, advance knowledge about distractor *absence* (as compared to D-absent trials from the other blocks without distractor foreknowledge) had no impact on trials where only a target was presented, $\chi^2(1,16) = 0.06$, $p = .81$. This lack of any difference in performance for D-absent trials in the D-cued versus D-unknown condition (i.e., with distractor-absence known or unknown) indicates that participants were not just more alert in general when given some foreknowledge about the distractor. Instead they could specifically counteract the impact of a subsequent distractor at a known location when given foreknowledge of distractor presence there. Our next experiment used fMRI to examine the possible neural mechanisms for such distractor anticipation on a particular side.
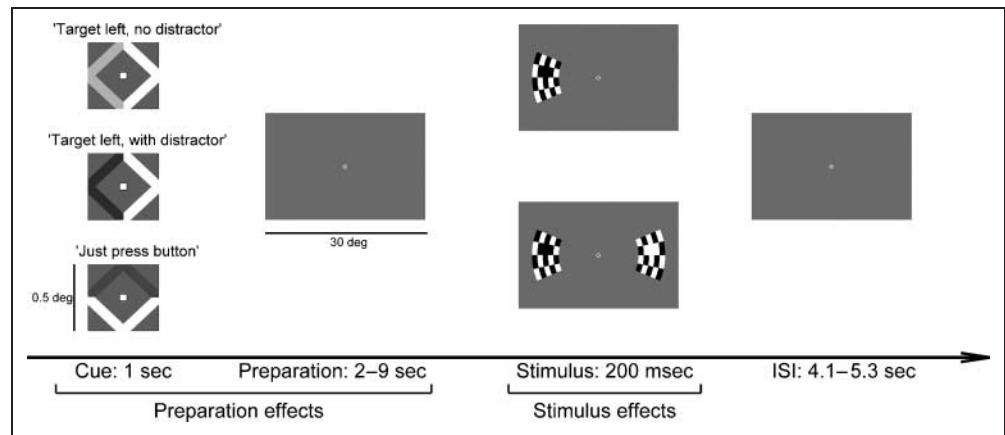
Experiment 2: fMRI Study

This study used the same task and stimuli, but now presented only D-cued blocks, which contain the critical comparisons of expecting a distractor to appear on a particular side versus expecting no distractor there. Note that presenting targets and distractors to opposite hemi-

fields (thereby projecting initially to different occipital hemispheres) allowed us to disambiguate whether any preparatory activity changes in the occipital cortex concerned the location of the expected target, or of the expected distractor, or both. More important, our design also entailed that the cued target side was held constant when comparing preparation for the presence versus absence of a distractor on the *other* side. Moreover, this particular comparison nicely equates for the information and interpretative demands conveyed by the central cue. This cue now always provided two bits of information (both with 100% validity), namely, target side plus presence/absence of a distractor on the other side, exactly as in the D-cued blocks of behavioral Experiment 1. Thus, by comparing preparation for trials with anticipated distractor presence versus absence on a particular side, we could isolate neural mechanisms specifically involved in preparing for distractor presence at a known location and separate these from any effects of cued target side.

Figure 2 shows a schematic timeline for the paradigm as implemented in the scanner. Target side was again cued by a central arrow on each trial, and the stimuli, instructions, and task were as for the previous behavioral experiment. However, as explained above, in the fMRI experiment we now only employed central cues that were 100% informative with respect to both target side and distractor presence/absence (i.e., just as in the D-cued blocks of the behavioral experiment). This strategy led to a simple 2×2 design, with factors of side (T-left and T-right; distractor side opposite to the target, if present) and distractor presence (D-present and D-absent). In addition, we ran a low-level control condition with similar sensory inputs and motor outputs, but no attentional preparation, to use as a baseline for testing for any general activity changes elicited by attentional preparation for all kinds of active trials. In this control condition, the task was simply to re-

Figure 2. Schematic time course of trials in the neuroimaging experiment. Each active trial began with the presentation of one of the three possible types of central arrow symbols. On active trials, a central arrow validly cued participants for target side, and its color also indicated with 100% validity the presence (red, here shown in dark gray) or absence (green, here shown in light gray) of a distractor in the hemifield opposite to the target. On sensorimotor control trials, a blue central arrow pointing upward was not informative with respect to any aspect of the subsequent stimuli, but instructed participants to simply press one button whenever any subsequent stimulus appeared. The cue was followed by a preparation interval, during which only a central fixation symbol was displayed. Note that all reported preparatory activations were attributable to this period and were thus not related to the presence of peripheral stimuli (see Methods and Figures 3 and 4 plus their legends). A single target, or a target with a distractor on the other side, were presented after the preparation interval and responded to by button press to discriminate the deviant check (making a small black or white "cross") in the target checkerboard.

spond to any peripheral visual stimulation with a button press.

Crucially, for all types of trials, the interval between cue and subsequent stimulation was now varied over an extended interval (see Methods) to allow separation of the hemodynamic response elicited by *attentional preparation* from that related to the subsequent peripheral visual *stimulation* (for a similar methodology, see Sakai & Passingham, 2003). Given our concern with preparatory attentional processes, we focus here on activations associated with this cue period rather than the subsequent stimulus period, as explained further below.

Behavioral Results Inside the Scanner

Table 1 summarizes the behavioral data acquired inside the scanner. As in the behavioral study (Experiment 1) described above, data were pooled across target side, as no response time or error rate differences were found between trials with targets on the left (586 msec and

Table 1. Behavioral Data Inside the Scanner

Distractor Expected	Target Expected On	
	Left	Right
Absent	572 msec (75 msec)	564 msec (86 msec)
	5.9% (5.5%)	8.0% (6.0%)
Present	600 msec (86 msec)	590 msec (86 msec)
	8.9% (4.3%)	6.6% (4.2%)

Mean reaction time (in milliseconds, top of each cell) and the mean percentage errors (bottom of each cell) for the four types of active trials. Standard deviations in brackets. Note that the four types of trials listed correspond to the four types of trials in the D-cued blocks of the purely behavioral Experiment 1.

7.4%, respectively) or right (577 msec and 7.3%, respectively), both $\chi^2(1,15) = 0$, *ns*. Participants were again slower for trials on which distractors were present (595 msec) than for trials with single targets (568 msec), $\chi^2(1,15) = 16$, $p < .0001$, with similar error rates in both conditions: 7.7% vs. 7.3%; $\chi^2(1,15) = 0, p = 1$. There was also no interaction of target side and distractor presence behaviorally, $\chi^2(1,15) = 0.25$, $p = .62$. Finally, and unsurprisingly, participants responded faster to the sensorimotor baseline that did not require perceptual discrimination (354 msec) than to trials with single targets, $\chi^2(1,15) = 16$, $p < .0001$, or to trials with a target plus a distractor, $\chi^2(1,15) = 16, p < .0001$.

The behavioral pattern found inside the scanner thus corresponded to that found for the equivalent trial types within the D-cued blocks of Experiment 1 (recall that inside the scanner, participants were always provided with foreknowledge about both target side and distractor presence/absence, as in the D-cued blocks of Experiment 1, for reasons explained above). We confirmed this similarity of behavior for equivalent trial types inside and outside the scanner by a direct comparison of the distractor cost elicited in the corresponding conditions in the behavioral and the neuroimaging experiment. This revealed no significant differences in the distractor-elicited cost between both experiments, neither in terms of slowing (22 msec vs. 27 msec; rank–sum test, $z = .88, p = .38$) nor in terms of accuracy changes (2.43% vs. 0.72%; rank–sum test, $z = .59, p = .55$).

Anticipatory fMRI Activations Related to the Expectation of a Target on a Particular Side
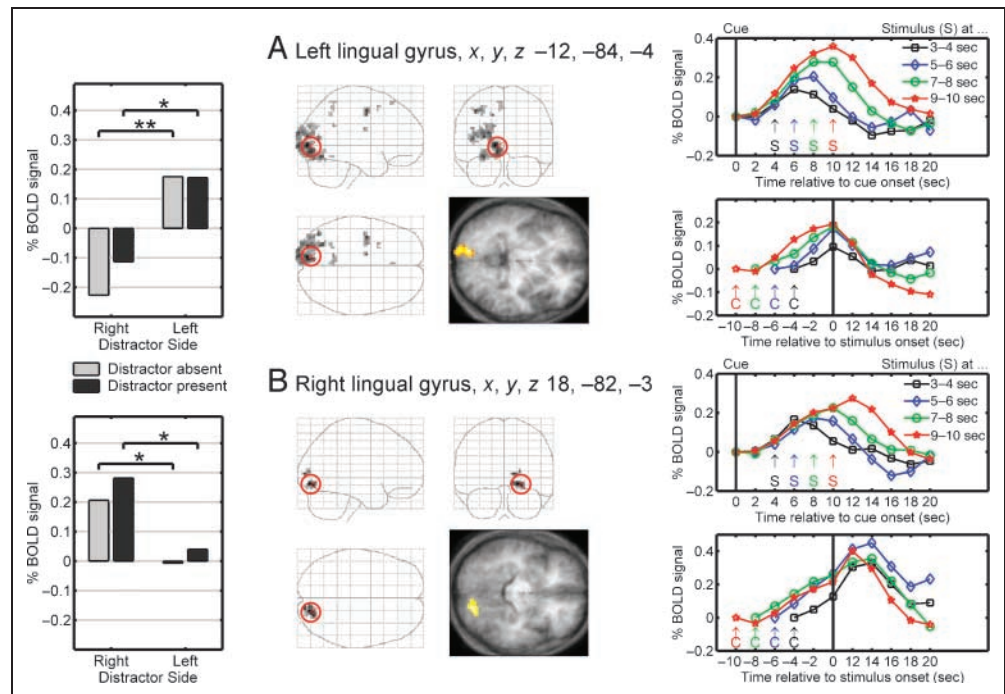
These results are depicted in Figure 3 and listed in Table 2. When comparing preparation for targets in

Figure 3. Target expectation on a particular side leads to anticipatory baseline shifts in the contralateral occipital cortex. Middle, shows the activations elicited by (A) preparation for right targets > left targets and (B) preparation for left targets > right targets, as standard glass-brain renderings of the whole-brain SPM(T), thresholded at $p <$ .001 and $k > 4$ voxels. Note that the peaks for preparation for left and right targets were located in a symmetric fashion in the target-contralateral lingual gyri, as circled in the glass-brain renderings, with coordinates given above. Left, plots of the mean-adjusted signal for all four preparation conditions, extracted from both activation peaks indicated. These plots show that expectation of a contralateral target always

led to stronger activation of lingual gyri than expectation of an ipsilateral target, regardless of whether a distractor was expected on the other side (dark gray bars) or not (light gray bars). Significant differences are marked by the top horizontal brackets (**$p <$ .001, *$p <$ .05). Finally, the time course plots (right) confirm that the increased BOLD signal extracted from the lingual gyri peaks, for trials with contralateral minus ipsilateral targets, did indeed involve *preparatory* processes: It clearly started at the typical hemodynamic delay of 4 sec after the *cue* onset, and thus before the onset of the peripheral stimuli at longer cue–target intervals. These time course plots show the activation increase in the best-fitted adjusted data for trials with contralateral targets, relative to the corresponding periods for trials with ipsilateral targets, plotted over time (*X* axis) separately for trials with different preparation durations (in different colors). The first and third plots show this temporally aligned to the *cue* onset (with stimulus onset marked by the colored arrows), whereas the second and fourth plots show the same data now realigned to the *stimulus* onset (with cue onset marked by the colored arrows). Note that effects are also seen for processing of the subsequent peripheral stimuli (positive values later than 4 sec poststimulus), as would be expected for a visual region of the brain, but the critical cue-locked activations start too early to reflect only stimulus modulation.

the right hemifield versus left hemifield, regardless of anticipated distractor presence or absence, all differences were as expected in the left hemisphere, contralateral to the anticipated (right) target. Most of these activations were located in the occipital gyri, with a peak in the left lingual gyrus ($x, y, z = -12, -84, 4$), but smaller target-contralateral clusters were also found in several parietal and frontal regions (see Table 2). For the inverse comparison (prepare T-left minus prepare T-right), we again found differences only in the hemisphere contralateral to the anticipated target (i.e., now in the right hemisphere), here restricted to occipital structures. Note that as when preparing for right minus left targets, the peak response was again located in lingual gyrus, but now in the right hemisphere ($x, y, z = 18, -82, -3$). Region-of-interest (ROI) extraction of mean blood oxygen level dependent (BOLD) signal during the different preparation conditions (see plots in Figure 3, left) confirmed that the lingual gyrus regions in each hemisphere always showed higher signal during preparation for contralateral than for ipsilateral targets, both when the targets were expected to be presented alone and when distractors were expected to be presented as well on the target-opposite side; Fried-

man analyses of variance: right lingual gyrus: D-absent trials, $\chi^2(1,16) = 4, p < .05$; D-present trials, $\chi^2(1,16) = 4, p < .05$; left lingual gyrus: D-absent trials, $\chi^2(1,16) = 12, p < .001$; D-present trials $\chi^2(1,16) = 9, p < .05$; same results also significant by parametric t tests, like all other ROI analyses presented below. Thus, the anticipation of a contralateral target elicited increased activity in these regions in a similar manner, regardless of anticipated distractor presence/absence. Finally, time course plots of the activation differences between trials with contralateral versus ipsilateral targets (see Figure 3, right) confirmed that these effects genuinely reflected *anticipatory* activations, rather than stimulus-related responses, as the effects of preparation for target side were clearly time-locked to cue onset, and thus began prior to presentation of the peripheral stimuli for trials with longer cue-target stimulus target asynchronies (SOAs; see Figure 3 legend).

Anticipatory Activations Related to the Expectation of a Distractor on a Particular Side

We examined this by comparing the neural activity during preparation for trials where distractors were

Table 2. Side-Specific Activations Elicited by Preparation for a Target or a Distractor in the Left or Right Hemifield

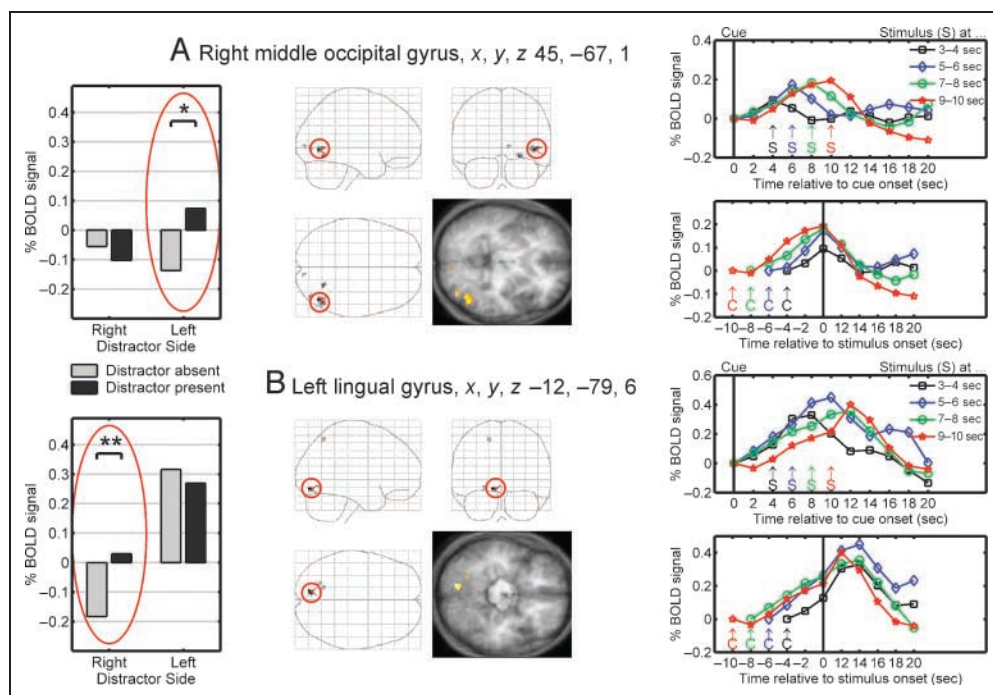| Location	Z Score	Size (No. of Voxels)	Talairach Coordinates		
			x	y	z
Preparation: Target right > left					
Occipital					
L lingual gyrus/cuneus	4.95	507	−12	−84	4
L precuneus (BA 7)	3.55	17	−6	−47	58
L middle occipital gyrus (BA 19)	3.53	6	−39	−78	9
Parietal					
L precuneus/cingulate gyrus	3.80	4	−15	−48	27
L inferior parietal lobule	3.54	4	−30	−50	41
Frontal					
L middle frontal gyrus (BA 6)	4.48	28	−39	−4	44
L superior frontal gyrus (BA 6)	3.54	7	−30	11	49
L cingulate gyrus (BA 6)	4.21	5	−15	−4	39
L precentral gyrus	3.74	5	−42	−8	22
L superior frontal gyrus (BA 6)	3.66	5	−3	−26	57
Cerebellum					
L declive	3.40	4	−24	−50	−10
Preparation: Target left > right					
Occipital					
R lingual gyrus (BA 18)	4.31	51	18	−82	−3
R cuneus/lingual gryus	3.91	14	12	−87	10
R lingual gyrus	3.32	4	24	−85	−6
Preparation: Right distractor present > absent					
Occipital					
L lingual gyrus (BA 18)	4.55	11	−12	−79	−6
L lingual/fusiform gyrus (BA 19)	3.51	5	−21	−67	−4
Parietal					
L precuneus (BA 7)	3.43	7	−18	−56	55
Preparation: Left distractor present > absent					
Occipital/Temporal					
R middle occipital/temporal gyrus	4.85	24	45	−67	1
R lingual/fusiform gyrus (BA 19)	4.34	8	24	−62	−7
R middle occipital gyrus	3.76	7	42	−78	4
R cuneus (BA 17)	3.65	4	9	−84	7

Note that the expectation of targets *and* of distractors exclusively activated regions in the hemisphere contralateral to the expected stimulus (target or distractor). SPM(T)s were thresholded for height at $p = .001$ and for spatial extent at $k > 4$ voxels. Location, Z score, and Talairach coordinates refer to the peak voxel of the cluster. The correspondence of this peak to a Brodmann's area (BA) is only listed when applicable. L = left, R = right.

expected to be *present* versus expected to be *absent* in a particular location of the visual field. In two separate analyses (i.e., for right or for left targets), we held expected target side constant by comparing D-present versus D-absent preparation periods separately for trials with the target expected on the right or on the left. Thus, a distractor was expected to be either present or absent in the corresponding fixed location in the target-opposite hemifield (i.e., on the left or right, respectively). In contrast to previous studies (e.g., Serences et al., 2004), this spatial separation of targets and distractors at particular locations made it possible to examine whether any preparatory activity changes in the occipital cortex spatially correspond to the anticipated location of the distractor, or of the target, or of both. That is, any preparatory influences of expected distractor presence versus absence may be found in visual regions contralateral to the expected distractor, signaling anticipatory modulation of representations for its location; or might be found in visual regions contralateral to the location of the expected target, indicating additional advance modulation for representations of the target location when a distractor was expected on the other side; or both target and distractor locations might be modulated conjointly.

The results of our analyses clearly support the first of these alternative hypotheses, as preparation for distractor presence versus absence elicited anticipatory activity increases exclusively in occipital cortices contralateral to the expected *distractor* location, with no distractor-expectancy modulations in the occipital cortex corresponding to the anticipated target location (neither increases nor decreases; see Figure 4 and Table 2). These distractor-expectation activations (Figure 4) were less extensive and not quite as symmetric as those found for expecting a target on one side versus the other, regardless of distractor expectancy (Figure 3), but they followed an analogous contralateral logic (albeit, importantly, now contralateral to the expected distractor). The activation peak when a distractor was expected (vs.

Figure 4. Distractor expectation leads to anticipatory baseline shifts in the occipital cortex contralateral to the expected distractor. Middle, activations elicited by preparation for T-with-D > T-only (i.e., for expectation of distractor presence), separately calculated for (A) trials with a distractor on the left (target on the right) or (B) a distractor on the right (target on the left), as standard glass-brain renderings of the whole-brain SPM(T), thresholded at $p < .001$ and $k > 4$ voxels. Note that the peaks for preparation for a left or right distractor were located in the *distractor-contralateral* occipital cortex, as circled in the glass-brain renderings with coordinates given above, and that no modulations were found in the hemisphere corresponding to the expected target location as a function of whether a distractor was expected or not on the other side. Left, plots of the mean-adjusted signal for all four preparation conditions, extracted from the peaks indicated in the glass-brain rendering. These plots show for both peaks that expectation of distractor presence led to an increased BOLD signal (i.e., now the *difference* between dark gray and light gray bars) only when the stimulus contralateral to the peak was a distractor, but not when it was a target (i.e., no difference between other pair of bars). The time course plots (right) confirm that the increase in BOLD signal at these peaks for trials with a contralateral distractor present versus absent did indeed involve preparatory processes. This increase clearly started at the typical hemodynamic delay of 4 sec after the cue onset, and thus before the onset of the peripheral stimuli for trials with longer cue–target intervals. The time course plots show the activation increase in the best-fitted adjusted data for trials with contralateral distractors, relative to the corresponding periods for trials without contralateral distractors, plotted over time (X axis) separately for trials with different preparation durations (in different colors). The first and third plots show this difference temporally aligned to the *cue* onset (with stimulus onset marked by the colored arrows), whereas the second and fourth plots show the same difference aligned to the *stimulus* onset (with cue onset marked by the colored arrows). Note that an effect of contralateral distractor presence also did arise during the processing of the subsequent peripheral stimuli (positive values later than 4 sec poststimulus), as would be expected for this visual region of the brain, but that the cue-locked preparation effects in the same region started too early to reflect only stimulus effects.

known to be absent) on the right was located in the left fusiform gyrus ($x, y, z = -12, -79, -6$), whereas that for a distractor expected on the left was located in the right middle occipital gyrus ($x, y, z = 45, -67, 1$). These clusters found for distractor preparation (Figure 4) did show some spatial overlap with those for the other separate effect of expecting a target on one side versus the other (regardless of distractor expectancy, Figure 3) in the left lingual gyrus (for a distractor or target expected in the right hemifield) and in the right lingual gryus and cuneus (for a distractor or target expected in the left hemifield).

Further analysis of the signal extracted from the occipital activation peaks in each hemisphere (see histograms in Figure 4) confirmed that these activations were indeed only driven by expectation of a contralateral distractor. That is, we observed significant activation differences between trials with expected distractor presence versus absence only when the expected contralateral stimulus was a distractor, not when it was a target; Friedman analyses of variance: left hemisphere: $\chi^2(1,15) = 12.25, p < .001$; right hemisphere: $\chi^2(1,15) = 9, p < .05$ (see plots at left of Figure 4). Together with the lack of any effect of distractor anticipation on target-related preparatory activations (see above and plots in Figure 3), we thus did not find any indication that preparation for distractor presence changed anticipatory activity in occipital areas corresponding to expected target location. Finally, time course analyses of the activation differences between trials with a contralateral distractor expected to be present versus absent (Figure 4, right) confirmed that the effects contralateral to the expected distractor really did reflect anticipatory activations, and not just modulations of the subsequently presented stimuli, as they were time-locked to *cue* onset and could begin *prior* to stimulus onset (see Figure 4 legend).

Parietal and Frontal Structures Involved in Attentional Preparation

We next attempted to identify structures that were active during preparation for all trials, independent of expected target side and anticipated distractor presence or absence. The results of a conjunction analysis (Price & Friston, 1997) testing for such activation (with the contrast [D-absent minus baseline 1] and [D-present minus baseline 2] for the cue regressors, see Methods) are shown in Figure 5A (top) and listed in Table 3. Strong and extensive activations were observed bilaterally in the superior parietal lobule (SPL) and middle frontal gyri/precentral gyri, in close proximity to the putative location of the human frontal eye fields (FEFs, e.g., Grosbras, Laird, & Paus, 2005).

In contrast to these structures apparently involved in spatial attention and task preparation in general, we also identified some neural structures that may be spe-
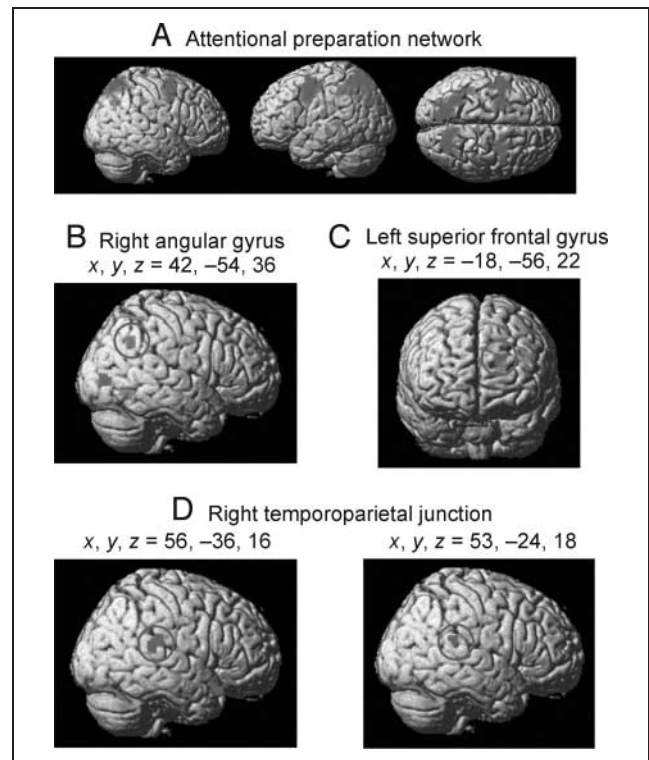

Figure 5. Control regions involved in different aspects of attentional preparation. (A) Bilateral superior parietal lobule and precentral sulci (frontal eye fields) activated by attentional preparation for both a single target *and* a target with a distractor, relative to the sensorimotor control condition, and regardless of expected target side (conjunction analysis of the contrasts [prepare single target > control] and [prepare target-with-distractor > control]). (B and C) Right angular gyrus and left superior prefrontal gyrus are more active during preparation for a target-with-distractor than for a single target, again regardless of target side (contrast [prepare target with distractor > prepare single target]). (D) Two independent psychophysiological interaction analyses reveal similar clusters in the right temporoparietal junction (TPJ), which show stronger functional coupling with the left (left side of figure) and right (right side of figure) lingual gyrus peak during preparation for a single target versus a target with distractor. (A–D) All SPM(T)s were thresholded at $p < .005$ for height and $k > 10$ voxels for display purposes, and rendered onto the MNI brain template employed in SPM2.

cifically involved in preparation for distractor trials, by comparing the preparatory periods of D-present versus D-absent trials, pooled over expected stimulus side (Figure 5B and C, Table 3). Apart from the expected activation of occipital structures (lingual and middle occipital gyri, as also in Figure 4), now arising bilaterally due to pooling over expected distractor side, this analysis also revealed areas in the right angular gyrus and left anterior and dorsomedial superior prefrontal gyrus that showed higher activation during preparation for distractor trials (see Table 3 and Figure 5B–C). Conversely, no neuronal structures were activated more strongly overall during preparation for D-absent than for D-present trials.

Table 3. Cortical Regions Involved in Nonlateralized Aspects of Attentional Preparation

Location	Z Score	Size (No. of Voxels)	Talairach Coordinates x	y	z
Preparation: Active trials > sensorimotor control (conjunction analysis)					
Parietal					
L inferior/superior parietal lobule (BA 7)	5.22	350	−15	−59	50
R precuneus/superior parietal lobule (BA 7)	6.08	129	15	−64	61
Frontal					
L precentral/middle frontal gyrus	5.04	262	−24	−1	44
R precentral/middle frontal gyrus	4.98	141	33	0	53
Preparation: Distractors present > absent					
Occipital					
L middle occipital gyrus (BA 19)	3.67	10	−45	−81	4
R middle occipital gyrus (BA 19)	4.07	6	39	−78	7
L lingual gyrus (BA 19)	3.45	6	−24	−64	−4
R fusiform/lingual gryus (BA 19)	3.67	8	27	−61	−4
Frontal					
L superior frontal gyrus (BA 10)	3.91	4	−18	56	22
L superior frontal gyrus (BA 6)	4.19	5	−6	29	51
Parietal					
R angular gyrus	3.41	4	42	−57	36
Coupling: Cortical regions for distractors expected absent > present					
Coupling with left lingual gryus					
R TPJ inferior parietal lobule/superior temporal gyrus	4.12	11	56	−34	16
R superior temporal gyrus	3.67	7	42	17	−18
Coupling with right lingual gyrus					
R TPJ inferior parietal lobule/superior temporal gyrus	4.00	9	53	−34	18
Coupling: Cortical regions for distractors expected present > absent					
Coupling with right lingual gyrus					
R middle occipital gyrus	3.94	11	39	−70	3
R lingual gyrus	3.55	5	18	−79	−1
R superior frontal gyrus	4.23	4	21	56	14

Note that preparation for all types of active trials versus for baseline trials activated regions in a bilateral network of frontal and parietal cortices, whereas anticipation of distractor presence (on right or left side) activated areas in the left prefrontal and right angular gyrus (relative to preparation for trials with single targets). The table also shows that both right and left lingual gyrus peaks involved in preparation for contralateral targets showed (in independent analyses) increased coupling during anticipation of single targets with a region in the right temporoparietal junction (TPJ), whereas only one of these lingual gyrus peaks (the one on the right) showed any increased coupling during preparation for targets with distractors, specifically with ipsilateral occipital and prefrontal areas. All SPM(T)s thresholded for height at $p = .001$, and for spatial extent at $k > 4$ voxels. Location, Z score, and Talairach coordinates refer to the peak voxel of the cluster. Correspondence to Brodmann's areas (BA) is only listed when applicable. L = left; R = right.

Our final analysis addressed whether any regions might show stronger *functional coupling* with the occipital cortex in that context. We ran two "psychophysiological interaction" (PPI) analyses (Friston, Buechel, et al., 1997) to identify any regions that showed higher coupling during D-absent preparation than during D-present preparation with the signal time series extracted from the right lingual gyrus or from the left lingual gyrus. Remarkably, both these independent analyses led to strikingly similar results (see Figure 5D and Table 3), each providing a conceptual replication of the other. Specifically, clusters in the right temporoparietal junction (TPJ), their peaks less than 1 cm apart, showed stronger coupling with the left or right lingual gyrus during preparation for single targets than during preparation for targets with distractors. Note that these two similar TPJ clusters were identified in independent analyses of time courses from the visual cortex in one or the other hemisphere, which displayed separate (but complementary) contralateral occipital preparation effects. In contrast, we did not find any regions that consistently showed stronger functional coupling with both lingual gyri during anticipation of trials with distractors (although some occipital and prefrontal regions showed a tendency for such effects for the lingual gyrus peak in the right hemisphere only; see bottom of Table 3).

DISCUSSION

Our behavioral study showed that trial-by-trial knowledge that a distractor will be presented in the hemifield opposite to an upcoming target can reduce the behavioral impact of that distractor. Our related fMRI study, which used an analogous design to the cued-distractor blocks from the behavioral experiment, showed that expecting a distractor on a particular side can lead to preparatory activations of the visual cortex contralateral to the expected *distractor*, without any additional activity changes in the visual cortex contralateral to the expected target (to be presented in the opposite hemifield to the distractor). Our fMRI data also identified candidate control structures that may be associated with preparation specifically when a distractor is expected to be present, plus some increase in functional coupling between target-contralateral visual cortex and the right TPJ when an isolated target was expected to be present on either side without a distractor.

Behavioral Benefit of Expecting a Distractor on a Particular Side

In the psychophysical Experiment 1, we found that advance information about the presence and side of a single remote distractor (in the hemifield opposite to the target) led to a reduction in the behavioral cost it went on to produce, as compared with blocks where distractor presence/absence was unpredictable. On the other hand, advance knowledge that a distractor would be *absent* did not affect behavior. This indicates that the effect of distractor foreknowledge was not merely due to arousal or other unspecific effects, but specifically allowed participants to counteract the impact of an upcoming distractor when forewarned of its presence and side.

With just a few exceptions, most previous psychophysical cuing studies of spatial attentional preparation studied preparation for a target at one or another location (e.g., Pashler, 1998) rather than preparation for a distractor at a different particular location. Nevertheless, some prior psychophysical work has been taken as indirect evidence for attentional mechanisms that may specifically exclude distractor information (rather than just enhancing target information). Awh et al. (2003) reported that the disruptive effects of presenting many visual distractors close to a target can be reduced to some extent with advance knowledge about the likelihood (in terms of long-term probabilities, rather than just trial-by-trial information as here) of multiple distractors being presented near a particular target location or not. The present behavioral results provide further evidence that preparation for distractors can aid performance. But importantly they go beyond prior work in showing that the disruptive influence of a *single* distractor presented at location *remote* from a target (i.e., in the opposite hemifield) can be reduced by covert spatial preparation regarding that distractor. Indeed, it was this spatial separation between target and distractor here that allowed us to examine in our fMRI experiment any spatial preparatory modulations specific to one or the other type of anticipated stimulus (i.e., for the expected target or for an expected distractor instead; see below).

Occipital Activations Related to an Expected Target or Distractor on a Particular Side

Several previous fMRI studies (e.g., Macaluso et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999) have shown modulation of the visual cortex contralateral to an expected upcoming visual target, as also found here (see Figure 3). The most novel and striking result of our study was that expectation of a distractor on a particular side, in the opposite hemifield to the target, led to anticipatory modulation of distractor-contralateral visual cortex (see Figure 4). To our knowledge, this is the first demonstration of anticipatory modulation of spatiotopic visual cortex representing the location of an expected distractor (rather than the location of an expected visual target).

One recent fMRI study (Serences et al., 2004) sought to examine how preparatory activations may be related to distractor anticipation. It reported that anticipatory activations in the visual cortex were stronger for target quadrants in which the target was expected to be surrounded by multiple distractors than for target quadrants in which targets would be presented alone. However, because the anticipated distractor arrays were located close to the upcoming target within a particular quadrant, that study could not examine whether spatiotopic occipital representations of the locations corresponding to the expected distractors were activated differentially as a function of distractor anticipation. Thus, the reported anticipatory effect in those ROIs (Serences et al., 2004) could have several possible explanations, potentially including participants concentrating harder, or with a different strategy, on the target locations when nearby distractors were expected additionally. Here, by contrast, we were able to distinguish visual cortex corresponding spatially to a target from that corresponding to a distractor (in opposite hemispheres). The anticipatory effects in distractor-contralateral occipital cortex that we found (Figure 4) clearly implicate preparatory processes related to the expected distractor location.

Indeed, we did not find any differential preparatory modulations of the occipital cortex (neither increases nor decreases) contralateral to the upcoming target when a distractor was expected on the other side versus when distractor absence was expected (see Figure 4). Thus, attentional modulation of the occipital visual cortex when expecting a competing distractor only affected occipital distractor representations here, not those occipital regions that would subsequently process the target (at least in the context of targets/distractors in opposite hemifields as here; a different outcome may have applied in Serences et al., 2004). The present finding may thus have some implications for the long-standing debate about whether visual selective attention mainly involves enhancement of target-related signals (e.g., Carrasco, Ling, & Read, 2004; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Hawkins et al., 1990), exclusion of signals from distractors (e.g., see Awh et al., 2003; Lu et al., 2002), or a combination of both mechanisms (e.g., Dosher & Lu, 2000; Cheal & Gregory, 1997). Our data indicate that expecting a distractor on the opposite side to the target can lead to modulations of representations for that distractor location, consistent with a role of these neurobiological processes in anticipatory distractor exclusion, in addition to the separate modulations reflecting the expected target side.

However, it is noteworthy that the preparatory modulations in the hemisphere contralateral to the expected distractor here took the form of an *increase* in BOLD signal (see Figure 4). Several previous studies observing such preparatory BOLD increases when anticipating targets had assumed that these reflect top-down enhancement of target properties in particular (e.g., Macaluso et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999). This interpretation might now need to be reexamined in the light of our present finding. One possible way to explain our observations is that anticipatory positive BOLD increases related to both targets and distractors may index occipital ''predictive coding'' (cf. Rao & Ballard, 1999) of the pattern of expected stimulation. Although targets and distractors differed in their response relevance here, both could be ''predicted'' under the appropriately cued conditions, which might therefore have led to analogous predictive effects on spatiotopic visual cortex. A related possible explanation is that preparatory selective attention for any type of visual display may take the form of imagining the precise pattern of expected visual input (i.e., the target *and* the distractor). It is known that imagery can increase activity in spatiotopic occipital regions, via top-down feedback connections from higher-level areas (e.g., Mechelli, Price, Friston, & Ishai, 2004; Kosslyn, Ganis, & Thompson, 2001). Moreover, a possible relation between the neural mechanisms of attention and of imagery has been proposed elsewhere (see Driver & Frith, 2000). Finally, the distractor-related baseline shifts found here could, in principle, indicate anticipatory neuronal *inhibition*, as no fMRI study can determine on its own whether an increase in BOLD signal is due to excitatory or inhibitory neural processes (see Caesar, Gold, & Lauritzen, 2003; Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001). The above possibilities are not mutually exclusive and could be addressed by further variations on the paradigm introduced here, with a combination of methods (e.g., fMRI plus recording of local field potentials, etc.). But note that the novel and most critical point from our findings will still stand independent of these further issues: Advance knowledge of the location of an expected distractor side can lead to modulation of visual cortex *spatiotopically corresponding* to the anticipated distractor (rather than target), which has not been shown (or tested for) by any previous study.

Control Structures and Distractor Preparation

During attentional preparation for all types of active trials (as compared with the sensorimotor baseline), regardless of target or distractor side and of anticipated distractor presence, we found activity in a bilateral network (see Figure 5A) comprising the superior parietal lobule plus prefrontal regions in close proximity to the putative location of the FEFs (e.g., Grosbras et al., 2005). This pattern resembles the activations of such higher-level control structures found in many other studies of attentional preparation (e.g., Macaluso et al., 2003; Hopfinger et al., 2000; Kastner et al., 1999) and is

consistent with the commonly suggested role for this "superior attentional network" (Corbetta & Shulman, 2002) in endogenous aspects of attention, such as covertly directing attention to a part of the visual field (e.g., see Shulman et al., 2003; Yantis & Serences, 2003). A more novel finding on control structures here was that preparation for target-with-distractor trials, as compared to preparation for target-only trials, additionally activated the right angular gyrus and regions in the left prefrontal cortex, independent of which side the distractor was expected to appear at. Thus, these regions may play specific control functions when preparing to overcome distraction by visual stimuli that are irrelevant for the present task. The finding of anticipatory right angular gyrus activation in this context may be of clinical interest, given that right-sided lesions centered here are associated with spatial neglect and extinction, in patients who miss stimuli mainly when distracted by competing bilateral stimulation (see Karnath, Milner, & Vallar, 2002; Driver & Mattingley, 1998). The present data indicate that mere *anticipation* of such interhemifield stimulus competition can be sufficient to trigger top-down processes related to the resolution of such competition in the right angular gyrus. The additional left superior prefrontal cortex activation during distractor preparation appears consistent with a putative role for the prefrontal cortex in attentional control (Barcelo, Suwazono, & Knight, 2000; Miller, 2000), although the reason for the left laterality here remains unknown.

In contrast to these activations of higher-level structures in the context of distractor preparation, attentional preparation for trials with single targets (minus that for target-with-distractor trials) did not elicit higher overall activity in any region. But coupling analyses indicated that the left and right occipital cortex (lingual gyri) both showed, in separate independent analyses, stronger "effective connectivity" (Friston, Buechel, et al., 1997) with the right TPJ during preparation for single targets than for distractor trials. In previous work, the right TPJ has been associated with the onset of an attention-attracting stimulus (Shulman et al., 2003; Downar, Crawley, Mikulis, & Davis, 2002; Kiehl, Laurens, Duty, Forster, & Liddle, 2001; McCarthy, Luby, Gore, & Goldman-Rakic, 1997) and has recently been proposed to play a role in stimulus-driven rather than endogenous attentional selection (Corbetta & Shulman, 2002). This may fit well with the present finding because the occipital cortex on either side was more strongly coupled in advance with the right TPJ when isolated targets were expected. This context would allow stimulus-driven direction of attention to the single target on either side to be successful, unlike anticipation of a target accompanied by a distractor on the other side, where stimulus-driven attention alone would be insufficient to determine which of the two stimuli should be selected. At a general level, this coupling result underlines that attentional control processes may not only involve activity changes in regions in the frontal and parietal cortex, but may also operate by modulating the coupling between such putative control areas and sensory regions (see also Friston & Buchel, 2000).

Conclusions

We have shown with both behavioral and fMRI data that preparatory selective visual attention can be employed to prepare for an anticipated distractor that is spatially remote from an expected target. Trial-by-trial knowledge about the presence of an upcoming distractor in the opposite hemifield to the expected target led to a reduction in the behavioral cost produced by that distractor. Critically, such foreknowledge about distractor presence also elicited preparatory activity changes in occipital regions exclusively in the hemisphere contralateral to the expected distractor, without any additional influences on visual cortex contralateral to the expected target. Our findings go beyond other work by showing unequivocally that contralateral spatiotopic representations of the distractor location (rather than just of the target location) can be modulated in advance when a distractor is anticipated. Our data also provide initial evidence that distinct higher-level control structures, and distinct coupling with some of these, may be involved when anticipating either a single target or a target with a spatially remote distractor. Taken together, these results underline that distinct neurobiological components of preparatory visual selective attention may be devoted exclusively to distractor processing.

METHODS

Behavioral Experiment 1

Participants

Seventeen volunteers (9 women, 22–39 years old) had normal or corrected vision and no history of neurological or psychiatric illness. All gave written consent in compliance with local ethics and were paid £10.

Materials and Procedure

All testing was conducted in a dark soundproof booth. Stimuli were displayed on a PC (30° × 23° screen, gray background, 0.5° × 0.5° white central fixation diamond always present) using the custom software Cogent (www.fil.ion.ac.uk/Cogent2000) implemented in MATLAB (The Mathworks, Natick, MA). Eye position was recorded at 60 Hz, with an ASL 504 Remote Optics Eyetracker (Applied Science Laboratories, Bedford, MA).

Each trial began with a small central instructional cue (0.5° visual angle), created by redrawing the left or right side of the fixation diamond in one of three cue colors (red, green, or blue). Across all conditions, the colored side of the diamond was 100% predictive of the hemifield the target would subsequently appear in on that particular trial. In D-unknown blocks, the cue side was always drawn in blue, not giving any information about whether or not a distractor would appear on the side opposite to the target. In D-cued blocks, the target side was drawn in red for distractor-present trials (meaning a distractor would subsequently appear on the opposite side) and in green for trials with no distractor. This allowed participants to prepare, on each single trial, for the subsequent appearance or absence of a distractor at a particular location (opposite to the upcoming target, whose side was always cued). The target and any distractor, displayed 3000 msec after cue onset for 200 msec, were curved black and white checkerboards (4 × 4 matrix, 3.5° × 6° visual angle, 4.5° gap to central fixation symbol), which contained one black or one white "deviant" check each (black or white deviance randomly determined, as also employed in the neuro-imaging experiment; see Figure 2 for example stimuli). Participants judged whether the deviant check in the target checkerboard was black or white, as rapidly as possible via a two-choice button press with the right hand, and were instructed to "use all the information given by the cues, that is, target side *and* distractor presence/absence, to prepare optimally for this judgment," while still maintaining central fixation throughout the trial.

Participants completed two training blocks (not analyzed), then four D-unknown and four D-cued blocks in alternating order. Each block comprised a randomly determined sequence of 96 trials, representing an equal number of the four types of stimuli (left target only, right target only, target left with right distractor, target right with left distractor). The only difference between the two types of blocks was whether stimuli were preceded by cues informative only with respect to target side on a trial-by-trial basis (D-unknown) or informative about both target side and distractor presence/absence on the other side (D-cued). The experimental session lasted 45 min and resulted in 96 trials for each of the eight conditions.

Data Analysis

Error and response-time data were analyzed with conventional nonparametric statistical tests, at a significance level of alpha = 0.05 (one tailed) for tests with a directional hypothesis. However, note that analysis with the corresponding parametric tests did not change the pattern of significant results. Data were pooled across the factor of target side, after initial analyses confirmed no behavioral differences between trials with targets in the left or right hemifield (for both D-absent and D-present blocks) and no interactions of target side with any other experimental factor. The critical effect of distractor foreknowledge (see Results) in reducing the behavioral cost on latency due to distractor presence was not due to any speed–accuracy trade-off between trials with and without distractor foreknowledge [no significant differences in error rates between the D-present trials in the D-unknown and D-cued condition, $\chi^2(1,16) = 0.07$, $p = .80$], nor to any influence from outlier trials with unusually high response times [no difference in standard deviations of response time data, relative to mean response time, between D-present trials that were cued (0.22) vs. not cued, 0.23; $\chi^2(1,16) = 0.53$, $p = .47$]. Finally, distractor foreknowledge reduced the behavioral cost equally for distractors whose deviant check was congruent (-17.52 msec reduction) or incongruent (-15.96 msec) with the black or white nature of the deviant check in the target, $\chi^2(1,16) = 0.06$, $p = .81$, indicating that attentional preparation for distractors did not interact with target-distractor congruency (which itself had no effect, probably because the deviant check in the distractor was hard to perceive when attending to the target).

Eyetracking data were available for each trial from onset of the cue until response to the target (~3500 msec). These traces were filtered for blinks, and a trial trace was classified as loss of fixation if any deviation exceeded 2° from initial fixation. There was no difference in the mean number of identified fixation losses between trials with and without a distractor, both in the D-unknown condition, 1.82% vs. 1.68%, $\chi^2(1,16) = 0.77$, $p = .78$, and in the D-cued condition, 2.17 vs. 1.87%, $\chi^2(1,16) = 1.67$, $p = .20$. Moreover, there was no difference in mean eye position between trials with the target in the left or right hemifield, both for D-unknown trials, 0.27° vs. 0.50°, $\chi^2(1,16) = 0$, $p = 1$, and D-cued trials, 0.30° vs. 0.44°, $\chi^2(1,16) = 1$, $p = .32$.

Experiment 2: fMRI Study

Participants

Sixteen new right-handed volunteers (7 women, 20–40 years old) had good health, normal or corrected vision, and no history of neurological or psychiatric illness. All were screened for MRI compatibility and gave written informed consent in accord with local ethics. Participants were paid £15 and given a CD of brain images.

Materials and Procedure

Participants completed a training session (four runs with similar stimuli and timing as in the subsequent fMRI experiment) on the day before testing. In the scanner, the same software as in the behavioral experiment was

used to present the stimuli by means of a video projector and a rear projection screen mounted at the back of the magnet bore. Participants viewed the screen (uniform gray background, $29° × 15°$) via a mirror system attached to the head coil. This mirror system was also used to monitor eye position at 60 Hz, again with an ASL 504 Remote Optics Eyetracker. Volunteers held a custom MRI-compatible response device with four buttons (three of which were used here) in their right hand for responses.

The fMRI experiment comprised five different cued attentional-preparation conditions. In the four "active" task conditions, participants were cued (with 100% validity) for both target side (left/right) and for distractor presence/absence on the *other side* to the target, by redrawing the left or right side of the fixation diamond in red or green, respectively (see Figure 2 for examples and stimulus timing). Note that these intermingled conditions thus fully correspond to those in the D-cued blocks from behavioral Experiment 1. The instruction was again "to use the cue information about both target side and distractor presence/absence to prepare optimally for judging the subsequent target cross" (black or white) in the checkerboard on the target side for that trial as fast as possible, while maintaining central fixation. This was also emphasized on the preceding training day. Because the main interest of the experiment was in any BOLD effects during the *preparation* period, the SOA between the onset of the cue and the appearance of the stimuli was varied between 3 and 10 sec, in steps of 1 sec. This allowed for a decorrelation of the regressors used to estimate the hemodynamic responses elicited by preparation separately from those for the subsequent stimuli (see Sakai & Passingham, 2003; Visscher et al., 2003, for a similar methodology). The multiple linear regression procedure used by statistical parametric mapping (SPM) only identified the *unique* effects of each regressor (e.g., the preparation period) after the effects of all other regressors (e.g., the stimuli) were partialled out (Friston, Holmes, et al., 1995). Note that we also conducted time course analyses of the occipital activations (right panels of Figure 3 and Figure 4) to confirm that the reported effects really did reflect anticipatory activations, and not just modulations of the subsequently presented stimuli (see Figures 3 and 4, legends). The target and distractor stimuli shown after the cue interval were identical in appearance, visual angle, and spatial arrangement to those used in the behavioral study (see Figure 2 for examples and stimulus timing).

In contrast to these four active task conditions, there was an additional more "passive" sensorimotor control condition, in which participants were instructed simply to press a third button unrelated to the target judgments as fast as possible whenever any peripheral stimulus appeared. The stimuli and display timing for this condition were identical to the active task conditions, but the small central cues now consisted of drawing the upper half of the fixation diamond (instead of the left or right half) in blue (instead of in red or green), which was thus not predictive of the type of stimulus to appear subsequently.

Each experimental run contained eight trials for each of the four active task conditions (prepare for target left or right, with distractor expected to be present or absent on the other side), each with a different cue-stimulus SOA between 3 and 10 sec; plus 18 trials of the sensorimotor control condition. Half of these control cues were followed by bilateral stimulation (distractor present), the other half by unilateral (distractor absent) stimulation. The cue-stimulus SOAs for these control events were two instances of 4–10 sec and four instances of 3 sec in order to shorten the experiment overall. Each participant completed four runs, resulting in 32 trials for each of the four active task conditions and 64 trials for the sensorimotor control condition.

Imaging was performed with a SIEMENS 3T ALLEGRA MRI head scanner (Siemens, Erlangen, Germany). BOLD-sensitive images were collected with a T2*-weighted echo-planar imaging sequence effectively covering the whole cortex (32 slices, $3 × 3$ mm in-plane resolution, 3.75 mm slice thickness, TR 2080 msec, TE 30 msec, FOV $192 × 192$ mm, $64 × 64$ matrix, 3551 Hz/pixel bandwidth). A total of 300 images were acquired in each run of 624 sec, and each participant completed four of these runs (see above). At the end of the session, a high-resolution, T1-weighted MPRAGE anatomical image of each participant's head was acquired.

Data Processing and Analysis

The behavioral data obtained inside the scanner were analyzed with the same procedures as the data from Experiment 1 (see above). Note that the pattern of significances did not change when the corresponding parametric tests were used.

All image processing and analysis steps were performed with SPM2 (www.fil.ion.ucl.ac.uk). Functional images were reconstructed offline, and the first six images of each run were discarded. Images were realigned to the first image of the series by rigid-body corrections, underwent slice-time correction to the middle slice of each volume, were normalized to the Montreal Neurological Institute (MNI) anatomical standard space, and were spatially smoothed with a 6-mm full width at half maximum Gaussian kernel. All reported peak voxel coordinates in this article correspond to the original anatomical Talairach space.

Data were analyzed with a two-step random-effects procedure. The voxelwise effects of the experimental conditions were estimated separately for each participant by a multiple regression of the voxel time series onto a composite model containing 12 covariates per

session. These covariates corresponded to the preparation periods and stimuli during the four active conditions and during the sensorimotor control condition, with the latter randomly split into two separate regressors to allow for conjunction analyses (see below). Preparation periods were modeled as a sustained "mini-block" of the respective duration (continuous series of delta functions from onset of cue to onset of stimuli; 3–10 sec), whereas stimuli were modeled as discrete events. Both types of covariates were then convolved with the canonical hemodynamic response function employed in SPM2. In addition to the experimental conditions (effects of interest), the model also contained regressors representing a 0.007-Hz high-pass filter and an AR(1) process to exclude low-frequency drifts and short-term temporal autocorrelation of scans, respectively (Friston, Penny, et al., 2002). After model estimation, linear compounds (contrasts) were used to assess and compare the regression parameters for the different conditions. In the second step of the random-effects analysis, the contrast images representing the subject-specific parameter estimates for the condition comparisons were submitted to t tests. Please note that any variance *shared* between two nonorthogonal regressors in a multiple linear regression as here is *not* considered by t contrasts of SPMs, such as those employed here. This means that any results we report only reflect variance unique to one or the other regressor (preparation or stimulation), but not any shared variance (Friston, Holmes, et al., 1995).

Any common effects of attentional preparation for all types of displays on activity in putative attentional control regions were tested by means of a "conjunction analysis" (Price & Friston, 1997). For this purpose, the differential contrast of preparation for targets-with-distractors versus baseline trials (one half of these trials, randomly selected) was masked inclusively with the differential contrast of preparation for single targets versus baseline trials (the other half of trials). This analysis thus only displayed those regions that showed activations during both preparation for single targets and preparation for targets with distractors, relative to the sensorimotor baseline.

Two PPI analyses of functional coupling (Friston, Buechel, et al., 1997) were calculated to separately identify candidate control structures coupling with the left or right lingual gyrus. Mean-adjusted data were extracted from all voxels within a spherical ROI (radius 6 mm), centered in the left or right lingual gyrus peak identified for preparation for targets in the right or left visual hemifield, respectively. The PPI procedure embedded in SPM2 was used to create regressors representing the neuronal time course of activation in these source regions and their interaction with preparation for single targets or targets and distractors (Gitelman, Penny, Ashburner, & Friston, 2003). These regressors were then added to the existing subject-specific models, and two

new random-effects models were calculated to identify any regions (across the whole brain) that across subjects reliably displayed differential coupling with the side-specific target regions during preparation for a single target versus for a target with a distractor, or for the opposite comparison.

Given the a priori hypotheses of the experiment (concerning occipital cortices contralateral to targets or distractors; as well as attentional control structures), the statistical threshold for all analyses was set to $p < .001$, with a cluster extent threshold of $u = 4$ voxels to minimize noise and false positives. For ROI analyses outside of SPM2, the mean parameter estimates extracted from the relevant ROIs (one per participant and condition) were directly contrasted with conventional nonparametric tests, at a significance level of $p < .05$ (one tailed) for comparisons with a directional hypothesis. Note that the patterns of significance did not change when the corresponding parametric tests were used instead.

Eye-Position Data in the Scanner

Eye-position data were available during scanning for each trial from the onset of the central cue until the response to the subsequent peripheral target, and were analyzed as for the eye data from the behavioral experiment (see above). There was no difference in mean eye position during preparation for trials with targets on the left or right, both for target-only trials, $-0.10°$ vs. $0.11°$, Friedman analysis of variance, $\chi^2(1,15) = 2.57$, $p = .11$, and for target-with-distractor trials, $0.01°$ vs. $0.05°$, $\chi^2(1,15) = 0.29$, $p = .59$. In accord with these results, the mean number of classified losses of fixation was not different for target-only trials or target-with-distractor trials either, both for trials with the target on the left side (3.8 vs. 5.4; $\chi^2(1,15) = 3$, $p = .08$), and for trials with the target on the right side (5.0 vs. 4.66; $\chi^2(1,15) = .69$, $p = .41$).

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