A Role for Top-Down Attentional Orienting during Interference between Global and Local Aspects of Hierarchical Stimuli

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Various models of selective attention propose that greater attention is allocated toward target stimuli when conflicting distracters make selection more difficult, but compelling evidence to support this view is scarce. In the present experiment, 15 participants performed a cued global/local selective attention task while brain activity was recorded with event-related functional magnetic resonance imaging. The presence of conflicting versus nonconflicting distracters during target processing activated regions of frontal, parietal, and visual cortices that were also activated when participants oriented attention in response to global- and local-task cues. These findings support models in which conflict between target and distracter stimuli is resolved by more selectively focusing attention upon target stimuli. © 2002 Elsevier Science (USA)

INTRODUCTION

During the past decade, functional neuroimaging studies have revealed that widespread regions of a frontoparietal network enable selective attention (Corbetta *et al.,* 2000; Hopfinger *et al.,* 2000). For example, such studies have provided evidence that dorsal and lateral prefrontal regions maintain task goals (de Fockert *et al.,* 2001), that parietal regions focus attention on task-relevant features (Hopfinger *et al.,* 2000; Wojciulik and Kanwisher, 1999), and that midline frontal regions activate appropriate stimulus–response mappings (Petit *et al.,* 1998). Increased activation of sensory cortices that process attended stimulus features is also associated with selective attention (Desimone, 1998; Kastner *et al.,* 1999). Such activations may be driven by top-down signals from the frontoparietal network, which bias sensory cortical activity in favor of target versus distracter stimuli (Desimone, 1998; Kastner *et al.,*1998, 1999).

Recently, it has been suggested that top-down executive control mechanisms further increase attention toward target stimuli when selection is made more demanding by distracter incongruency (i.e., the presence of distracters that engender relatively greater conflict with targets at the perceptual, semantic, and/or response level) (Banich *et al.,* 2000b; Botvinick *et al.,* 2001; Posner and DiGirolamo, 1998). For example, it has been proposed that distracter incongruency in one trial of the Eriksen flanker task might lead to a narrower focusing of spatial attention around the central target letter during the next trial (Botvinick *et al.,* 2001). It has also been proposed that distracter incongruency should activate some of the same brain regions that are activated by attentional orienting in preparation for a target, such as lateral prefrontal regions that adopt or maintain an attentional set (Banich *et al.,* 2000b). Nonetheless, to our knowledge it has not yet been demonstrated that cued attentional orienting and distracter incongruency activate overlapping brain regions within the same task and participants. Such a demonstration is crucial, however, because neural activity produced by distracter incongruency may reflect not only processes that focus attention on task-relevant information, but also processes that detect perceptual, semantic, or response conflict between target and distracter stimuli (Carter *et al.,* 1999, 2000; MacLeod, 1991). Observing overlap in the brain areas activated by cued attentional orienting and distracter incongruency would provide key support for the view that one neural mechanism for dealing with conflicting distracter stimuli involves increasing attention toward the target stimuli.

To investigate this issue, we used a novel event-related fMRI paradigm (Woldorff *et al.,* 2002, 2001a,b) to record neural activity while participants performed a cued global/local selective attention task. In this paradigm, participants were cued on a trial-by-trial basis to attend to and identify either the global or the local form of an upcoming hierarchical stimulus (e.g., Navon, 1977), which could be either congruent (e.g., a large, global H made up of small, local Hs) or incongruent (e.g., a large, global S made up of small, local Hs). Using this paradigm, we were able to isolate neural activity associated with cued attentional orienting and directly compare it to activity associated with dis-

tracter incongruency within the same task and participants (see Materials and Methods).

Prior data have indicated a role for frontal, parietal, and occipital cortices in orienting attention toward global and local aspects of hierarchical stimuli (Robertson *et al.,* 1988; Wilkinson *et al.,* 2001). If the presence of conflicting versus nonconflicting distracters results in greater attention toward targets, then neural activity associated with distracter incongruency should partially overlap that associated with cued attentional orienting in these regions. Such overlap would likely reflect the sources and sites of processes that focus attention on target information. These processes could include frontal mechanisms that keep track of task goals, parietal mechanisms that focus attention, and occipital regions whose activity may be modulated by frontal and/or parietal circuits to favor the processing of task-relevant stimuli.

However, some models predict that conflict between targets and distracters engages brain mechanisms that differ from those engaged by attention-directing cues. In one such model, expectation of a target stimulus recruits regions of the posterior parietal, anterior cingulate, and occipital cortices that are quite distinct from regions of the thalamus that enable selection of the target when it actually appears (LaBerge, 1990). In another model, expectation of a target stimulus recruits lateral prefrontal areas, while the detection of response conflict recruits the anterior cingulate cortex (Carter *et al.,* 1999). Lateral prefrontal areas that bias attention toward task-relevant processing should be activated during cued orienting of attention, but not during distracter incongruency. In contrast, midline frontal regions that monitor for response conflict should be activated during distracter incongruency, but not during cued attentional orienting. It should be noted that while some evidence supports this view (MacDonald *et al.,* 2000), other evidence is more consistent with the present hypothesis because it demonstrates activation of lateral prefrontal regions in response to distracter incongruency (Milham *et al.,* 2001). Nonetheless, in their strong forms, both of the models above predict relatively less overlap between the regions activated by cued attentional orienting and distracter incongruency.

MATERIALS AND METHODS

Subjects

Fifteen participants were recruited from the Duke University community in accordance with the rules of the local human subjects committee. Participants (9 male, 6 female; age range, 20–36) were all right-handed, had normal or corrected-to-normal vision, and had no history of serious neurological trauma or disorders. Informed consent was obtained from each partic-

ipant prior to the experiment. Before the MR session, each participant practiced one or two blocks of the experimental task. Participants were paid $10 per hour for being in the study, which lasted approximately 2 h.

Apparatus

A PC was used for stimulus presentation and the recording of response data. Stimuli were projected onto a screen at the back of the magnet's bore. Participants viewed the stimuli through a mirror. Responses were made using the index and middle fingers of the right hand and were recorded with an MR-compatible response box. Behavioral data from 3 of the 15 of the subjects were lost due to technical problems.

Event-Related Functional Magnetic Resonance Imaging (FMRI) Paradigm

We used a fast-rate event-related fMRI paradigm recently developed by Woldorff and colleagues (Woldorff *et al.,* 2002, 2001a,b) (c.f., Ollinger *et al.,* 2001a,b; Shulman *et al.,* 1999). In this paradigm (Fig. 1A), compound-event trials containing a cue and a target stimulus were randomly interspersed with trials containing only a cue stimulus. At the beginning of each 3-s trial, participants viewed a cue (G, L, P, or O; 1.6° × 1.0° of visual angle; duration, 200 ms), which instructed them to attend for and identify either the global (G) or local (L) aspect of an upcoming hierarchical stimulus or to passively view (P or O). On cue-only trials (100% of passive trials and 33% of global-task and local-task trials), no target stimulus followed cue presentation. Contrasting neural activity for attention-directing global and local cues with activity for passive cues allowed isolation of neural activity associated with cued attentional orienting, while controlling for basic sensory and semantic processing of the global and local cue stimuli.

On cue-plus-target trials (66% of global-task and local-task trials), either a congruent (e.g., large H made of small Hs; 50% of trials) or an incongruent (e.g., large H made of small Ss; 50% of trials) hierarchical stimulus (global form, 3.3° × 2.1°; local form, 0.6° × 0.4°; target duration, 200 ms) appeared 1300 ms after cue offset (Fig. 1B). Contrasting neural activity for incongruent versus congruent targets allowed isolation of neural activity associated with distracter incongruency. Note that the cue-to-target interval typically used by Woldorff and colleagues (e.g., 1.5 s in the present experiment) is much shorter than that used in other studies (Corbetta *et al.,* 2000; MacDonald *et al.,* 2000) (e.g., 4.5–12 s). This procedure encourages participants to focus their attention as soon as an attention-directing cue appears. Moreover, it makes findings from our cued attention studies easier to relate to the large body of behavioral and event-related potential
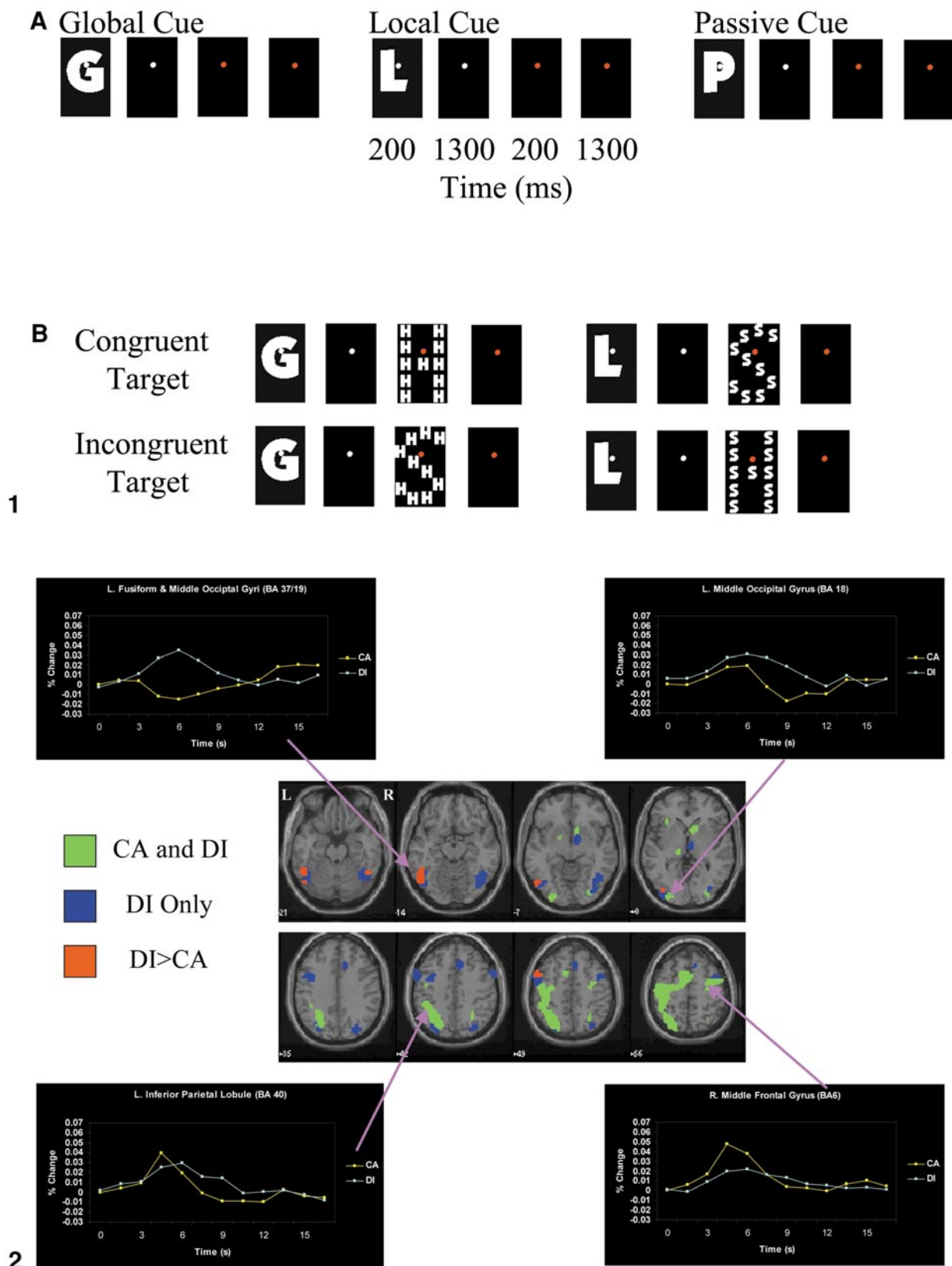
FIG. 1. Examples of stimuli and timing of stimulus presentation for the seven trial types used in this study (see text for more details). (A) Cue-only trials—cued orienting of selective attention. (B) Cue-plus-target trials—distractor incongruency.

(ERP) studies of cued voluntary attention, in which cues and targets are typically separated by approximately 1 second (see Mangun, 1995, for review).

All seven trial types were included within each run to equate the psychological conditions under which activation for each trial type was measured. They were presented equally often and in a pseudorandom order such that, on average, each trial type was preceded equally often by every trial type in the design. Such randomization allows subtraction of response overlap from adjacent trials when comparing the average time-locked responses to different trial types (Burock et al., 1998; Dale and Buckner, 1997; Woldorff, 1993). Most relevant for the present study, the presence of cue-only trials allowed calculation of independent parameter estimates for the response amplitudes to different types of cues (i.e., global, local, and passive) and targets (i.e., global congruent, global incongruent, local congruent, and local incongruent) within a multiple regression framework (Ollinger et al., 2001a,b).

Participants responded with the right hand using their index finger to press one button if an H appeared at the cued level (i.e., global or local) and their middle finger to press a different button if an S appeared. In all trials, the fixation dot changed color, from white to red, 1500 ms into the trial (i.e., coincident with target presentation in cue-plus-target trials). Participants were told that if no target appeared at this point following a global or a local cue, they should cease attending and simply wait for the next trial (which occurred 1500 ms later). This manipulation was performed to ensure that demands on pretarget attention-biasing processes would be equated for cue-plus-target and cue-only trials (Corbetta et al., 2000).

FMRI Data Acquisition and Analysis

An echo-planar imaging sequence was used to measure the blood oxygenation-dependent response (BOLD) signal (TR, 1.5 s; TE, 40 ms; flip angle, 90°). Each participant completed 10 runs, each of which lasted approximately 5 min (except one participant who completed nine). During each run, 206 brain volumes were collected, each of which contained 18 contiguous, 7-mm-thick slices (in-plane resolution, 3.75 × 3.75 mm). Structural images were collected using a T1-weighted spin echo sequence (TR, 500 ms; TE, 14 ms; flip angle, 90°). The first six functional images of each run contained no trials and were discarded prior to analysis of the functional data. The software analysis package SPM99 (Friston et al., 1995) was used to correct functional images for asynchronous slice acquisition and head motion, to normalize functional images to MNI (Montreal Neurological Institute) standard space, and to spatially smooth the functional data with a Gaussian filter (FWHM, 8 mm).

Event-Related Analyses

Responses to cue and target stimuli were modeled by convolving a vector containing the onset times of the different types of cues and targets with a canonical hemodynamic response function. This function was composed of the sum of two gamma functions. In total, there were seven regressors. These included regressors for passive cues, global cues, local cues, global congruent targets, global incongruent targets, local congruent targets, and local incongruent targets. Multiple linear regression, as implemented by SPM99, was performed to determine parameter estimates for each regressor within each participant.

We constructed two separate random-effects t-maps to perform the conjunction analysis. One t-map contrasted the average parameter estimate for global and local attention-directing cues with the parameter estimate for passive sensory/semantic control cues revealing regions involved in cued attentional orienting (Woldorff et al., 2002, 2001a,b). The second t-map contrasted the average parameter estimates for incongruent and congruent targets revealing brain regions activated by distracter incongruency. To maximize statistical power when contrasting incongruent with congruent targets, we averaged across global and local target stimuli.

Next, we performed a conjunction analysis to determine whether cued attentional orienting and dis-

FIG. 2. Areas activated by cued attentional orienting (CA) and distracter incongruency (DI). CA (i.e., attention-directing global and local cues versus passive cues) and DI (i.e., incongruent versus congruent targets) activated several common regions (*green*), including the middle frontal gyrus (MFG), inferior frontal gyrus (IFG), medial frontal gyrus, precentral gyrus, superior and inferior parietal lobules (IPL), middle occipital gyrus (MOG), thalamus (Th), basal ganglia, and cerebellum. We hypothesize that these areas increase selective attention toward perceptual and motor aspects of target processing during both CA and DI. Other regions (*blue*) were significantly activated by DI, but not by CA. These included portions of the MFG and IFG, anterior cingulate cortex, precuneus, fusiform gyrus (FG), MOG, and Th. Within these regions of the MFG, FG, and MOG, DI activated some voxels (*red*) significantly more than CA. These areas may implement processes that are specific to distracter incongruency, such as detecting and/or resolving conflict between target and distracter stimuli. Also shown are time courses for three regions that were significantly activated by both CA and DI (i.e., the right MFG, left IPL, and left MOG) and one region that was activated by DI, but not by CA (i.e., the left FG). Yellow time courses indicate difference waves created by subtracting the average response to passive cue-only trials from the average response to global and local cue-only trials. Blue time courses indicate difference waves created by subtracting the average response to congruent targets from that to incongruent targets. Time along the x axis is measured in seconds (s). All activations are overlaid on the canonical MNI normalized anatomical template provided by SPM'99. Anatomical slices range from $Z = -21$ mm to $Z = 0$ mm (top row) and from 35 to 56 mm (bottom row) in intervals of 7 mm; L, left; R, right.

tracter incongruency activated common brain areas. For this analysis, each individual t-map above was thresholded relatively liberally ($t = 2.01$, $P < 0.032$, uncorrected) to maximize our sensitivity for detecting voxels activated by both cued attentional orienting and distracter incongruency. The probability that any given voxel would be falsely activated in both t-maps was maximally $0.032 * 0.032 = 0.001$, uncorrected. However, it was likely much lower because we also required that a voxel in either t-map be part of a cluster of 25 or more activated voxels in order to be entered into the conjunction analysis. A large extent threshold better safeguards against false positives (Forman *et al.,* 1995; Xiong *et al.,* 1995).

We also analyzed each of the individual t-maps that was entered into the conjunction analysis above to determine whether either cued attentional orienting or distracter incongruency significantly activated voxels that were not identified by the conjunction analysis. For these analyses of individual t-maps, we used a higher t-threshold to guard against false positives ($t = 3.79$, $P < 0.001$, uncorrected) in combination with a five-voxel threshold that was more appropriate given the higher t-threshold (Forman *et al.,* 1995; Xiong *et al.,* 1995). These analyses revealed several significant activations for distracter incongruency, but none for cued attentional orienting. To determine whether these activations were specific to distracter incongruency, we tested whether any of the activated voxels was significantly more active for distracter incongruency than for cued attentional orienting. More specifically, we tested whether the difference between parameter estimates for incongruent and congruent targets was significantly larger than the difference between parameter estimates for attention-directing and passive cues. Since far fewer voxels were involved here, we used a relatively high t-threshold ($t = 3.79$, $P < 0.001$), but did not use an extent threshold.

In the analyses above, we averaged across global and local cues and global and local targets to increase statistical power. This raises the possibility that some of the overlapping and non-overlapping activations revealed by these analyses might have been driven by only a single type of cue (e.g., global) or by distracter incongruency during just one of the two tasks (e.g., local). If that were the case, then one might expect to find that either the two types of cues (i.e., global and local) or the two types of distracter incongruency (i.e., global-task and local-task) produced differential amounts of neural activity. To examine whether this might be the case, we performed two additional t-contrasts. One contrast tested whether global and local cues produced differential activity. The second tested whether neural activity due to distracter incongruency differed for the global and local tasks. Importantly, none of the voxels identified in the analyses above showed differential activation in either contrast ($P <$

0.001). Therefore, there was no evidence that any of the overlapping or non-overlapping activations were driven by just one type of cue (e.g., local) or by distracter incongruency during just one of the two tasks (e.g., global task).

Region of Interest Analyses

We also performed region of interest (ROI) analyses to determine whether distracter incongruency activated occipital regions that were differentially activated by global and local cues. For the left inferior occipital region, we compared the average parameter estimate for global incongruent targets (i.e., averaged across all voxels within the ROI) to that for global congruent targets. For the right middle occipital region, we compared the average parameter estimate for local incongruent targets to that for local congruent targets. Each analysis was performed using a one-sample random effects t test and P values less than 0.05 were considered significant.

Conversion from MNI to Talaraich Coordinates

Following statistical analyses in MNI space, we converted sites of activation to Talaraich coordinates so that we could present the neural loci of activations in tables that would facilitate comparison with activations from prior studies. Conversion from MNI to Talaraich coordinates was implemented with two nonlinear transformations used in other published studies (Calder *et al.,* 2001; Duncan *et al.,* 2000) (http://www.mrc-cbu.cam.ac.uk/Imaging/mnispace.html). Coordinates above the anterior commissure (AC) were transformed as follows: $X' = 0.99X$; $Y' = 0.9688Y + 0.0460Z$; $Z' = -0.0485Y + 0.9189Z$. Coordinates below the AC were transformed with the equations $X' = 0.99X$; $Y' = 0.9688Y + 0.0420Z$; $Z' = -0.0485Y + 0.8390Z$.

RESULTS

Behavior

Mean reaction times (RTs) for 12 participants were analyzed with repeated measures ANOVA using two factors: Level (Global, Local) and Distracter Type (Congruent, Incongruent). As expected (Navon, 1977), RTs were significantly faster for global (501 ms) than for local (566 ms) trials, $F(1,11) = 7.857$, $P < 0.02$. Also as expected (Kimchi, 1988, 1992; Lamb *et al.,* 1989), RTs were slower for incongruent (593 ms) than for congruent (538 ms) trials, $F(1,11) = 42.238$, $P < 0.001$. Contrary to early findings (Navon, 1977), these effects did not interact, $F(1,11) < 1$. Obtaining such an interaction was not crucial in the present study, however, and subsequent research has revealed that it may be more likely to occur with peripheral than with central presentation of task stimuli (Kimchi, 1992).

TABLE 1

Regions Activated by Both Cued Attention and Distracter Incongruency

Region	Cluster size	Lateralization	Brodmann Area	X	Y	Z	T-CA	T-DI
Middle frontal gyrus	58	R	6	45	3	51	2.37	5.61
Inferior frontal gyrus	12	L	45	−34	23	5	2.36	3.72
Medial frontal gyrus	416	L	32	−11	10	51	3.87	4.73
			6	−4	−1	58	3.16	3.99
Precentral gyrus	416	L	4	−41	−12	52	3.53	4.77
			6	−26	−12	52	3.26	3.20
	58	R	6	30	−12	52	3.18	2.74
Superior parietal lobe	416	L	40	−34	−52	48	4.29	4.99
			7	−26	−67	48	4.06	5.01
	17	R	7	30	−56	48	2.37	3.11
Inferior parietal lobe	416	L	40	−45	−35	47	3.57	5.86
Middle occipital gyrus	25	L	18	−30	−91	5	3.22	3.25
	13	R	18	30	−81	−2	2.76	3.57
Thalamus	7	L		−15	−22	1	2.72	2.56
Lateral globus pallidus	7	L		−15	0	−6	2.34	3.37
	29	R		11	7	−6	2.24	3.61
Caudate head	29	R		8	11	−1	2.74	2.85
Cerebellum								
Nodule	19	L		−4	−56	−33	3.74	3.17
Pyramis	19	L		0	−64	−32	2.29	4.57

Note. L, left; R, right; XYZ coordinates from Talaraich and Tournoux's (1988) atlas; T, T-score; CA, cued attentional orienting; DI, distracter incongruency.

An analogous ANOVA with the percentage correct as the dependent measure revealed that overall performance was quite high (91.9%). As in the RT analysis, there was a significant main effect of Distracter Type, $F(1,11) = 7.534$, $P < 0.02$, because responses were less accurate for incongruent (89.2%) than for congruent (94.5%) cue-plus-target trials. Both the main effect of Level and the interaction between Level and Distracter Type failed to achieve statistical significance ($P > 0.16$ in both cases).

Imaging

We performed a conjunction analysis to determine whether cued attentional orienting and distracter incongruency activated overlapping brain areas. As predicted, this analysis revealed partially overlapping activations in frontal, parietal, and visual cortices as well as the cerebellum, basal ganglia, and thalamus (Fig. 2; Table 1). Although contrasting incongruent with congruent targets might conceivably reveal regions that are deactivated by congruent targets as opposed to being activated by incongruent ones, this was generally not the case. To investigate this possibility, we used selective averaging (Dale and Buckner, 1997) to generate time courses for the different types of cue-plus-target and cue-only trials in our design. Exploratory contrasts between cue-plus-congruent trials and cue-only trials revealed that congruent targets rather uniformly produced positive activations rather than deactivations. Thus, the brain regions identified by the conjunction analysis reflect areas positively activated by both cued attentional orienting and distracter incongruency.

Cued attentional orienting considered alone did not activate regions beyond those identified by the conjunction analysis. This was somewhat surprising given evidence that directing attention to global and local object features relies on right and left regions of the temporoparietal cortex, respectively (Robertson and Lamb, 1991; Yamaguchi *et al.*, 2000). It is possible that this lack of hemispheric asymmetries was caused by averaging across global and local cues to gain statistical power in the conjunction analysis. To investigate this possibility, we directly contrasted neural activity produced by global versus local cues ($t = 3.79$, $P < 0.001$, 5 contiguous voxels). Unexpectedly, global cues activated a region of the left inferior occipital gyrus (31 voxels in BA 17; $x = −21$, $y = −97$, $z = −9$) more than local cues. Also unexpected, local cues activated a region of the right middle occipital gyrus (23 voxels in BA 19; $x = 40$, $y = −86$, $z = 19$) more than global cues. Neither of these regions was identified by the conjunction analysis, indicating that the activation of each one may have been specific to just one type of cue.

A fuller discussion of these unexpected hemispheric asymmetries in visual cortex is presented in the Discussion. However, given that these two occipital regions were involved in orienting attention in response to global and local cues, we wished to investigate whether they were also activated by distracter incongruency. Our hypothesis predicted that the left inferior occipital gyrus, which was activated more by global

TABLE 2

Regions Activated by Distracter Incongruency but Not by Cued Orienting of Attention

Region	Cluster size	Lateralization	Brodmann Area	X	Y	Z	T-DI
Middle frontal gyrus	48	L	8	−52	6	45	7.26[a]
	14	R	6	41	6	51	5.91
Inferior frontal gyrus	48	L	44	−41	5	32	5.30
	48	L	44	−45	16	25	3.84
	13	R	13	41	26	5	4.95
Anterior cingulate	23	R	32	11	24	37	4.98
	23	R	32	8	21	44	4.81
Precuneus	20	R	19	30	−71	36	5.12
Fusiform gyrus	59	L	37	−49	−52	−15	5.98[a]
	64	R	37	45	−55	−15	6.86[a]
	64	R	37	41	−59	−9	6.07
Middle occipital gyrus	59	L	19	−41	−69	−8	4.89
	59	L	19	−52	−63	−9	4.36[a]
	7	L	18	−38	−87	4	4.83[a]
Thalamus	16	R		4	−11	1	4.49

Note. L, left; R, right; *XYZ* coordinates from Talaraich and Tournoux's (1988) atlas; T, T-score; CA, cued attentional orienting; DI, distracter incongruency.

[a] Some voxels in the cluster were activated significantly more for DI than for CA ($P < 0.001$).

than by local cues, would be activated by distracter incongruency during the global task. Similarly, it predicted that the right middle occipital gyrus, which was activated more by local than by global cues, would be activated by distracter incongruency during the local task. Region of interest analyses confirmed both effects ($t = 2.02$, $P = 0.0315$ for the left inferior occipital gyrus; $t = 2.11$, $P = 0.0267$ for the right middle occipital gyrus).

The activation of some voxels appeared to be specific to distracter incongruency. First, distracter incongruency significantly activated voxels within frontal, parietal, and visual cortices that were not identified by the conjunction analyses ($t = 3.79$, $P < 0.001$, uncorrected, five contiguous voxels) (Fig. 2; Table 2). Since activation of these voxels failed to reach the same threshold during cued attentional orienting, we formally tested whether activation of these voxels was significantly greater for distracter incongruency than for cued attentional orienting. Voxelwise analyses (see Materials and Methods) revealed that voxels in certain regions (e.g., the left middle frontal gyrus and several extrastriate regions of the visual cortex) were indeed significantly more active during distracter incongruency than during cued attentional orienting (Table 2). Thus, the activation of some regions was highly specific to distracter incongruency.

DISCUSSION

A major aim of selective attention research is to identify the neural loci of attentional control processes and to reveal the situations in which these processes are used to enhance selection (Hopfinger *et al.,* 2000; Miller, 2000; Posner and Petersen, 1990). Recently, it

has been suggested that brain mechanisms involved in attentional orienting become additionally recruited when the presence of conflicting versus nonconflicting distracter stimuli (i.e., distracter incongruency) makes selection of task-relevant information more demanding (Banich *et al.,* 2000b). Consistent with this view, we found that cued attentional orienting and distracter incongruency activated overlapping regions of frontal, parietal, and visual cortices, as well as the basal ganglia and thalamus. In fact, cued attentional orienting did not activate any areas that were not also activated by distracter incongruency. This result suggests that distracter incongruency may recruit all of the processes involved in orienting attention toward task-relevant information. It should be noted, however, that passive cues probably engage some attentional processes since they must be attended and because they may lead participants to attend for the cue stimulus on the next trial. Thus, while passive cues served well as a sensory/semantic control for global and local cues in the present study, they may have been a somewhat conservative baseline for measuring attention-related activity associated with global and local cues. Future studies in which fixation is used as the baseline for attention-directing cues would be helpful for resolving whether cued orienting of attention recruits brain areas that are not also recruited by distracter incongruency.

An important issue to consider concerns the functional contribution of recruiting brain regions that orient attention during distracter incongruency. Increasing the amount of attention required to process targets is known to reduce behavioral interference from conflicting distracters (Lavie, 1995), as well as neural activity within brain regions that process irrelevant dis-

tracters (de Fockert *et al.,* 2001; Rees *et al.,* 1997). Activation of brain areas that support cued attentional orienting during distracter incongruency may therefore function to limit the processing of conflicting distracter stimuli.

The regions of the frontal and parietal cortices that were activated by both cued attentional orienting and distracter incongruency in the present study fit well with models of attentional control (Desimone, 1998; Mesulam, 1981; Miller, 2000; Posner and DiGirolamo, 1998). Dorsal regions of the middle frontal gyrus perform processes that keep track of current task goals (Cabeza, 2000), medial frontal cortices implement attentional processes (Posner and DiGirolamo, 1998; Murtha *et al.,* 1996), and inferior parietal regions play an important role in allocating spatial (Corbetta *et al.,* 2000; Hopfinger *et al.,* 2000) and nonspatial (Coull *et al.,* 2000; Le *et al.,* 1998; Posner *et al.,* 1984; Wojciulik and Kanwisher, 1999) attention. But middle frontal (Cabeza, 2000), medial frontal (Carter *et al.,* 1999, 2000; MacDonald *et al.,* 2000), and inferior parietal (Snyder, 1997) regions also likely play a role in motor preparation. For example, inferior parietal neurons appear to encode intended movements (Snyder, 1997), as well as the perceptual focus of selective attention (Hopfinger *et al.,* 2000). It is therefore difficult to draw a firm conclusion regarding which aspects of selective attention (e.g., selection of task-relevant perceptual information versus selection of task-relevant stimulus–response mappings) were performed by the frontal and parietal regions that were activated by both cued attentional orienting and distracter incongruency in the present study. The inability to distinguish between these two possibilities is not problematic for the present interpretation of our results, however, because selection has previously been shown to be implemented at both perceptual (Heinze, 1994a,b; Hopfinger *et al.,* 2000; Kastner *et al.,* 1999; Woldorff *et al.,* 1993) and response (Braver *et al.,* 2001; Luck, 1998; MacLeod, 1991; Pashler, 1994; Petit *et al.,* 1998) levels of processing. Increasing selective attention toward target stimuli may activate brain circuits that contribute to target selection as well as response selection.

The overlapping activations in visual cortex are likely to reflect attentional processes that operate at the perceptual level. Occipital regions play a role in encoding visual stimuli (Martin, 2001). Furthermore, this role appears to be modifiable by top-down attentional control processes, which can tune the responses of neurons in visual cortex such that they are driven more by task-relevant compared with task-irrelevant stimuli (Desimone, 1998; Kastner *et al.,* 1998, 1999). The overlapping activations in visual cortex may indicate the sites at which top-down attentional control processes act to tune perceptual cortices to be maximally responsive to task-relevant stimuli during both cued attentional orienting (Chawla, 1999; Hopfinger *et*

al., 2000; Kastner *et al.,* 1999) and distracter incongruency. The sources of these processes could include some of the commonly activated frontal and parietal regions.

The current findings are not as consistent with models of attentional control in which distinct regions are engaged by attentional orienting and distracter incongruency. Models in which expectation of a target stimulus recruits regions of the posterior parietal, anterior cingulate, and occipital cortices that are distinct from regions that enable selection of target information (e.g., the thalamus) (LaBerge, 1990) do not account well for our finding that, with the exception of the anterior cingulate cortex, all of these regions were recruited by both cued attentional orienting and distracter incongruency. Similarly, the present results do not support models in which attention-biasing processes performed by the middle frontal gyrus are recruited during cued attentional orienting but not distracter incongruency (MacDonald *et al.,* 2000). The present results indicated that cued attentional orienting and distracter incongruency recruited identical regions of the middle frontal, posterior parietal, and occipital cortices.

Hemispheric asymmetries were observed during cued attentional orienting to the global and local levels of hierarchical stimuli; however, the neuroanatomical loci and direction of these asymmetries were inconsistent with some current neuropsychological models of global/local processing. These models, derived largely from studies of patients with brain damage, suggest that temporoparietal structures underlie hemispheric asymmetries for global and local processing (Robertson and Lamb, 1991; Yamaguchi *et al.,* 2000). We did not observe any asymmetries in temporoparietal regions. It is known, however, that such asymmetries are less pronounced in neurologically intact populations than in patients, both behaviorally (Van Kleeck, 1989) and in functional neuroimaging experiments (Fink *et al.,* 1999, 1997b; Martinez *et al.,* 1997). The lack of asymmetries in temporoparietal regions is therefore not completely unexpected.

We did unexpectedly observe hemispheric asymmetries for global and local cues in inferior and middle occipital regions of the visual cortex. Moreover, the direction of these asymmetries was opposite to that which is predicted by current models of global/local processing. Left (not right) occipital regions were activated more by global than local cues, while right (not left) occipital regions were activated more by local than global cues. Varying patterns of hemispheric asymmetries for global and local target processing have been observed in the visual cortex in several prior block-design studies (Fink *et al.,* 1997a,b, 1999). It has been suggested that they may indicate differing patterns of eye movements for processing and/or orienting to global versus local stimulus dimensions (Mangun *et al.,* 2000; Sasaki *et al.,* 2001), although we cannot

exclude other interpretations here. For present purposes, it is important that the regions of visual cortex that were activated differentially by global versus local cues behaved as predicted by our hypothesis. Left inferior occipital regions, which played a relatively specific role in orienting to the global dimension (because they were activated more by global than by local cues), were activated by distracter incongruency during the global task. Right middle occipital regions, which contributed relatively specifically to orienting to the local dimension (because they were activated more by local than by global cues), were activated by distracter incongruency during the local task. These findings therefore provide further support for our hypothesis that some brain regions involved in cued attentional orienting should also be recruited by distracter incongruency.

The regions activated by distracter incongruency, but not by cued attentional orienting, also fit well with models of attentional control (Botvinick *et al.,* 1999; Carter *et al.,* 2000). In the present experiment, distracter incongruency significantly activated the middle frontal gyrus, the anterior congulate cortex, parietal areas, and regions of the extrastriate cortex that were not significantly activated by cued attentional orienting. Moreover, distracter incongruency activated the left middle frontal gyrus and several visual areas significantly more than cued attentional orienting activated these regions. These activations are consistent with the view that distracter incongruency recruits not only mechanisms that increase attention toward target stimuli, but also regions that detect and/or resolve processing conflict between target and distracter stimuli (MacDonald *et al.,* 2000). For example, the activation of unique frontal and visual areas during distracter incongruency may reflect the detection and/or resolution of perceptual conflict via interactions between frontal and perceptual cortices (Banich *et al.,* 2000a).

The present findings indicate that top-down executive mechanisms that increase selective attention toward specific stimulus features during cued attentional orienting are further recruited when the presence of conflicting distracters makes selection of those stimulus features more demanding. These findings provide key support for models of attentional control in which the presence of conflicting distracter stimuli triggers mechanisms that more selectively focus attention upon target stimuli (Posner and DiGirolamo, 1998). The results are also consistent with prior suggestions of overlap in the regions activated by attentional orienting and distracter incongruency (Banich *et al.,* 2000b), but are the first to actually demonstrate such an effect within the same task and participants. Future studies that distinguish attentional processes that operate on perceptual versus motor representations in frontal and parietal regions would be useful for identifying which frontal and parietal regions modulate perceptual processing in sensory cortices. It would also be useful to investigate which form(s) of conflict (e.g., perceptual, semantic, or response) must be present during target processing to trigger the activation of brain regions that play a role in attentional orienting. At present, we conclude that brain mechanisms involved in orienting attention toward global and local aspects of visual objects also become engaged when distracter conflict at multiple levels of processing makes target selection more demanding.

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