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The Generality of Parietal Involvement in Visual Attention

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Summary

Functional magnetic resonance imaging (fMRI) was used to determine whether different kinds of visual attention rely on a common neural substrate. Within one session, subjects performed three different attention experiments (each comparing an attentionally demanding task with an easier task using identical stimuli): (1) peripheral shifting, (2) object matching, and (3) a nonspatial conjunction task. Two areas were activated in all three experiments: one at the junction of intraparietal and transverse occipital sulci (IPTO), and another in the anterior intraparietal sulcus (AIPS). These regions are not simply involved in any effortful task, because they were not activated in a fourth experiment comparing a difficult language task with an easier control task. Thus, activity in IPTO and AIPS generalizes across a wide variety of attention-requiring tasks, supporting the existence of a common neural substrate underlying multiple modes of visual selection.

Introduction

Visual attention, which is the ability to selectively process only a subset of the information present in the retinal image, has been extensively studied over the last two decades, using a wide variety of experimental tasks and stimuli (e.g., Posner and Petersen, 1990; Allport, 1993; Desimone and Duncan, 1995). Despite the many differences in these experimental paradigms, researchers generally refer to the selective process in each of these situations as visual attention, implying a common mechanism. However, very little work has been directed to the crucial question of whether visual attention in fact consists of a single general-purpose mechanism involved in all forms of selective visual processing or whether it instead consists of a heterogeneous set of different mechanisms, each involved in a different kind of selection. In the present study, we used functional magnetic resonance imaging (fMRI) to address this question, asking whether there is any region of the human brain that is activated by each of three very different attention-requiring tasks yet not activated by a language task that is difficult but does not place heavy demands on visual attention.

Recent imaging results suggest that parietal areas, especially the superior parietal lobule (SPL) and the intraparietal sulcus (IPS), participate in many different attention tasks and may subserve a general visual attention function. Parietal activity has been associated with endogenous and exogenous shifts of spatial attention (Corbetta et al., 1993; Nobre et al., 1997), maintenance of attention on peripheral stimuli and divided attention (Vandenberghe et al., 1997), feature integration (Corbetta et al., 1995), attentive tracking of moving dots (Culham et al., 1998), nonspatial attention (Coull et al., 1996; Coull and Nobre, 1998), object-based attention (Fink et al., 1997), response selection to visually presented stimuli (Iacoboni et al., 1996), object-oriented action (Faillenot et al., 1997), and overt and covert attention shifts (with and without eye movements, respectively; Corbetta et al., 1998). A few studies have directly compared the effects of one type of attention with another and found overlapping parietal activations (SPL and/or IPS) for exogenous and endogenous attention (Corbetta et al., 1993; Nobre et al., 1997), object-based and space-based attention (Fink et al., 1997), spatial and temporal orienting (Coull and Nobre, 1998), overt and covert attention shifts (Corbetta et al., 1998), and attentive tracking and attention shifts (Culham et al., 1998). The great diversity of tasks used in previous studies, combined with the similarity of parietal activations across them, suggests that some regions of parietal cortex may play a very general role in visual attention, rather than supporting any one particular task-specific function. However, because the different attentional tasks in prior studies were rarely run on the same subjects, past results are consistent with the importantly different hypothesis that nearby but nonoverlapping cortical regions are activated by different attentional tasks, suggesting functional specificity.

To distinguish between these two alternatives, it is necessary to examine brain activation at a fine grain within individual subjects and to show that the same voxels are activated in each of the different attentional comparisons in a particular subject. In the present study, each of seven subjects participated in three different visual attention experiments within a single scanning session. The tasks and stimuli were very different across the three experiments (to provide a strong test of generality) yet identical in stimuli and motor requirements within each experiment (to provide a relatively pure measure of attentional effects). Data were then analyzed using a voxel-by-voxel analysis testing for Activation Overlap across Multiple Tasks (AOMT) for each subject's data individually (see also Price and Friston, 1997; Grill-Spector et al., 1998). Only voxels that showed significant activation in each of the three different attentional tasks are candidate loci for a common neural substrate involved in multiple types of visual selection.

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Experiment 1a (E1a) identified those areas that are involved in covert peripheral shifting/maintenance of attention. The display consisted of a clock-like pattern, with peripheral dots arranged in a circle and another dot presented in the center (Figure 1A). In the peripheral shifting/maintenance condition, subjects maintained central fixation and covertly attended to the peripheral dots, shifting (and maintaining) their attention between (on) the dots. In the easier central maintenance condition, subjects maintained their attention on the central dot. Their task was to press a button whenever the attended dot (peripheral or central) became smaller. Both stimuli and motor requirements were identical across the two conditions.

Experiment 1b (E1b) identified areas involved in sustained peripheral attention associated with an object-matching task. The displays consisted of two peripheral faces, two peripheral houses, and a colored fixation cross, all presented simultaneously (Figure 1B). In different blocks, subjects attended either to the faces or to the houses, or, in the less attentionally demanding condition, to the colored cross and performed a matching task on the attended stimuli while maintaining central fixation. As before, the stimuli and motor requirements were identical across conditions.

While E1a and E1b investigated different aspects of spatial attention, Experiment 1c (E1c) was designed to test nonspatial attention. Subjects performed a temporal visual detection task on textured letter stimuli presented in rapid serial visual presentation (RSVP) at fixation (Figure 1C). In alternate blocks, subjects had to detect a conjunction or a feature target (Treisman and Gelade, 1980). The two tasks were identical not only in retinal stimulation and response requirements (as in E1a and E1b) but also in the attended location (center of gaze). Regions showing stronger activity during the conjunction task than during the feature task should reflect mechanisms involved in nonspatial attention.

Although E1a and E1b differ in the mode of spatial attentional processing, tasks, and stimuli, they share some similarities. In both, subjects attend to the relevant peripheral stimuli and have to ignore irrelevant distractors present at other locations. In addition, maintenance of central fixation during the peripheral tasks

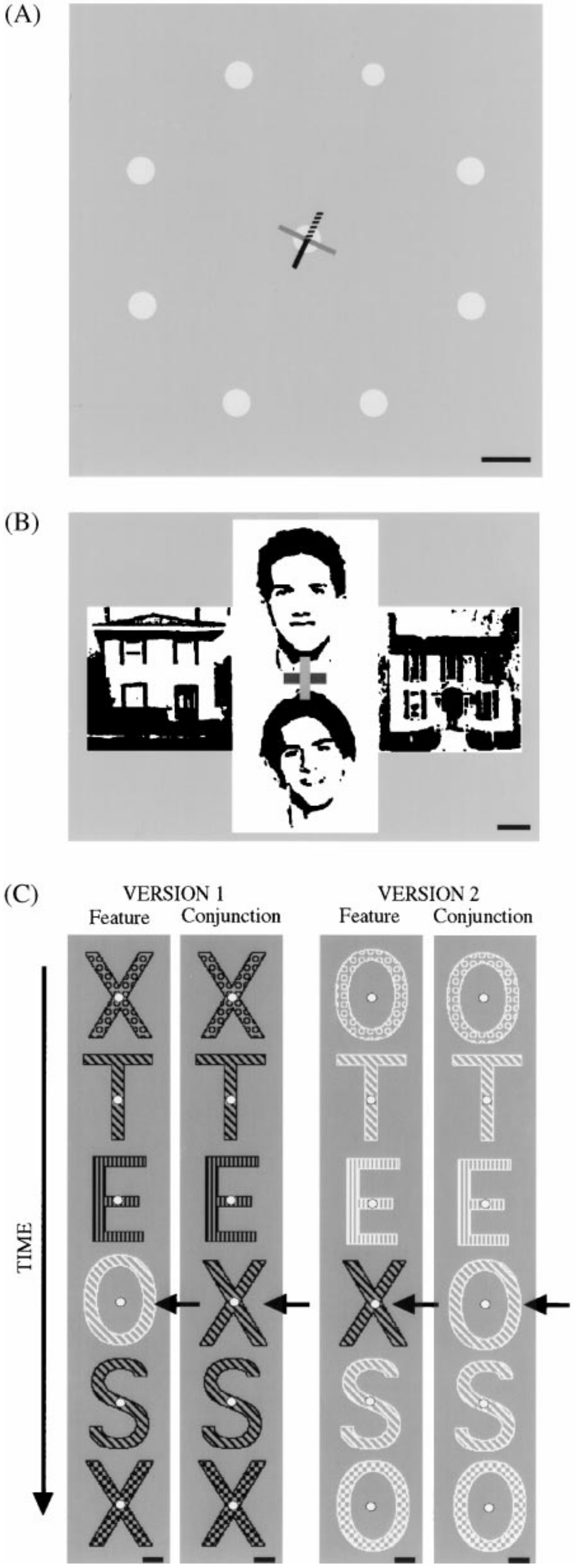

Figure 1. Sample Displays Used in E1

(A) The "clock" display in E1a (peripheral shifting/maintenance of attention versus central maintenance). In the shifting condition, subjects attended to the peripheral dot indicated by the red (or blue) arm of the cross (here, striped and black arms). The cross rotated every 4 s, indicating the adjacent peripheral dot for attentional shifting. In the central maintenance condition, subjects maintained their attention on the central dot. Their task was to press a button whenever the attended dot (peripheral or central) became smaller.

(B) A sample trial (200 ms display duration) used in E1b (peripheral object matching versus central color matching). In the peripheral task, subjects performed a matching task on the peripheral faces or, in separate epochs, on the houses. In the central maintenance condition, the matching task involved the color of the two arms of the cross (red or green). Subjects pressed a button when the attended stimuli were identical.

(C) The design and four sample trials used in E1c (nonspatial conjunction versus feature tasks). Subjects monitored RSVP sequences of letters (six letters per second) and pressed a button when they detected a target letter (arrows). Targets popped out on the basis of letter brightness in the feature condition but required accurate integration of features in the conjunction condition. Across two counterbalancing versions, both target and distractor letters were identical in the two tasks. Subjects were required to maintain central fixation in all experiments. Calibration bar, 2° of visual angle.

Table 1. Sensitivity (d′) and Response Times (in ms) in E1a (Detection of Size Changes), E1b (Object or Color Matching), E1c (Detection of Letter Targets), and E2

	Difficult Tasks	Easy Tasks	t
E1a	Peripheral Shifting	Central Maintenance	
d′	3.1	3.9	3.4*
RT	497	429	6.6**
E1b	Peripheral Object Matching	Central Color Matching	
d′	2.6	4.4	9.4***
RT	610	507	21.0***
E1c	Conjunction Task	Feature Task	
d′	3.1	3.7	4.1*
RT	593	496	8.9***
E2 (four subjects)	Language Task	Visual Task	
d′	3.1	3.6	1.3
RT	1282	607	8.0**

Seven subjects participated in E1a–E1c, four subjects in E2. Asterisk, $p < 0.05$; double asterisk, $p < 0.005$; and triple asterisk, $p < 0.0005$.

could require active suppression of eye movements. Thus, common regions of activation in E1a and E1b could reflect any of these similarities: space-based selection, active suppression of spatially irrelevant distractors, or suppression of eye movements. However, if E1c (nonspatial conjunction > feature task) produces stronger activity in some of the same voxels, then the alternative accounts can be discounted: in E1c, all stimuli are presented centrally, so that the same location is attended in both conditions; there is no need to make or suppress eye movements; and there are no spatially irrelevant distractors (although temporal distractors are present). Thus, voxels that show activations in all three comparisons (or AOMT) should reflect a common neural substrate subserving multiple modes of visual selective processing.

However, the AOMT regions could also be related to the differences in difficulty that are present in all three comparisons. To test whether the AOMT areas are related specifically to visual attention rather than general effort, we ran a control test (Experiment 2 [E2]) on four of the seven subjects who participated in E1a–E1c. In E2, subjects saw a single word presented in lower case letters at fixation. In the "difficult language" condition, they pressed one button if the word was both a verb and a noun, and another button if it was either a verb or a noun but not both. In the "easy visual" control task, they pressed one button if the word's first and last letters were the same height, and another button if not. As in E1a–E1c, both stimuli and motor requirements were identical across conditions. If the AOMT regions found in E1a–E1c are specifically involved in visual attention rather than general effort, they should not show stronger activity in the difficult language task than in the easier visual task, despite a large difference in the difficulty of the two tasks. That is, we should observe an interaction in these regions between type of difficulty (visual versus nonvisual) and level of difficulty (easy versus difficult tasks).

Results

Experiment 1: Behavioral Results

Table 1 shows subjects' sensitivity (d′) and response times (RTs) in E1a–E1c as well as the results of statistical comparisons. In all three tests, subjects were both significantly less sensitive and slower in the difficult than in the easy conditions (all ps at least < 0.05). These results indicate that the difficult tasks were more visually demanding than the easy tasks, as intended.

Experiment 1: Functional Imaging Results

AOMT

Table 2 and Figure 2A present the AOMT regions, which showed significant activation in each of the three attention comparisons in individual subjects at the AOMT threshold of $p < 10^{-9}$ (i.e., single comparison threshold, $p < 0.001$). Although each comparison separately produced extensive bilateral parietal activations, concentrated in the IPS and SPL, and in some experiments reached the postcentral sulcus (PCS), the areas of exact voxel-by-voxel activation overlap in individual subjects were small and were observed consistently in only two bilateral regions in the IPS. (Note that no distinction is drawn here between the IPS proper and its posterior segment, which is sometimes referred to as the intraoccipital sulcus; see Duvernoy, 1991.)

The most consistent AOMT in individual subjects was situated in the posterior fundus of the IPS, at or close to the junction with the transverse occipital sulcus (IPTO, Brodmann's area 19): seven of seven subjects showed it in the left hemisphere ($xyz = -29,-78,23$), and six of seven in the right ($xyz = 29,-77,28$). The size of this overlap was small, averaging about 250 mm^3 for left and 360 mm^3 for right IPTO (these volumes are likely to underestimate AOMT size; see below).

The second most consistent AOMT in individual subjects was found bilaterally in anterior IPS (AIPS) in five of seven subjects. The left AIPS ($xyz = -31,-52,46$) was approximately equal in size to IPTO, averaging about 270 mm^3, while the right AIPS ($xyz = 28,-51,50$) was considerably larger, averaging over 1 cm^3. In all five subjects, AIPS AOMT was located on the medial bank of the IPS (i.e., in the SPL, Brodmann's area 7).

Other small and less consistent areas of overlap (three subjects each, except for one area with four subjects; Table 2) were noted in right and left posterior IPS and SPL and in left middle occipital gyrus (MOG).

Because the primary question addressed here was

Table 2. Areas of Activation Overlap in Individual Subjects' Analyses (AOMT Threshold, $p < 10^{-9}$)

AOMT Areas	L−/R+	P−/A+	I−/S+	Volume (mm^3)	Number of Subjects
Left IPTO (BA 19)	−29 ± 4	−78 ± 6	23 ± 7	247	7/7
Right IPTO (BA 19)	29 ± 3	−77 ± 5	28 ± 7	360	6/7
Left AIPS (SPL bank, BA 7)	−31 ± 6	−52 ± 3	46 ± 2	271	5/7
Right AIPS (SPL bank, BA 7)	28 ± 3	−51 ± 3	50 ± 4	1055	5/7
Left post SPL (BA 7)	−15 ± 6	−64 ± 2	48 ± 4	730	3/7
Right post SPL (BA 7)	14 ± 6	−68 ± 3	48 ± 7	259	4/7
Left post IPS (SPL bank, BA 7)	−26 ± 5	−63 ± 6	34 ± 3	125	3/7
Right post IPS (SPL bank, BA 7)	20 ± 7	−65 ± 5	39 ± 2	297	3/7
Left MOG (BA 19)	−41 ± 3	−77 ± 2	7 ± 10	259	3/7

Coordinates represent the mean center of gravity for each region, ±1 sample standard deviation. Origin is at anterior commissure. Abbreviations: IPTO, intraparietal/transverse occipital sulci; AIPS, anterior intraparietal sulcus; SPL, superior parietal lobule; IPS, intraparietal sulcus; MOG, middle (lateral) occipital gyrus; post, posterior; and BA, Brodmann's area.

whether there is any AOMT (as opposed to none) for the different visual attention tasks, we intentionally designed a conservative test to determine the presence of activation overlap: the threshold of $p < 0.001$ (uncorrected), which, when applied independently to each of the three comparisons, resulted in an AOMT threshold (joint probability) of $p < 10^{-9}$. Thus, while we can be confident that IPTO and AIPS do show activation overlap, this procedure also means that (1) we may be underestimating the size of these AOMT areas, and (2) some regions that do not show AOMT (or show little consistency across subjects) may actually be AOMT. Indeed, when the AOMT threshold was relaxed to $p < 1.3 \times 10^{-7}$ (single-comparison threshold, $p < 0.005$), all AOMT areas listed in Table 2 became larger and/or more consistent across subjects; in particular, left AIPS and IPTO in both hemispheres approximately doubled in size, while right AIPS increased by 50%. In addition, the AOMTs in posterior IPS in both hemispheres and in right SPL were observed now in six of seven subjects, while left SPL was now found in five of seven subjects. Therefore, IPTO and AIPS are likely larger than calculated at the conservative AOMT threshold and may be part of a more extensive network of overlapping activations that span much of the IPS and SPL.

This hypothesis was further confirmed in the group analysis. As shown in Figure 2B, AOMT was observed bilaterally in the entire extent of the IPS, from its posterior segment at IPTO, through its middle section, to its anterior segment (AIPS), and in the right hemisphere extended medially into the SPL. The AOMT volume in the right IPS and adjoining SPL was about 15.4 cm^3, and 6.3 cm^3 in the left IPS, that is, substantially larger in the group analysis than in individual subjects. This difference in size of AOMT areas between the two types of analyses is not surprising. First, the accumulation of Type II error (accepting the null hypothesis of no AOMT when it is false) across the three comparisons is more pronounced in the statistically noisier individual subjects' data than in the averaged group analysis; second, averaging across subjects produces spatial blurring, possibly overestimating overlap in the group data. However, Figure 2B shows that the overlap remained extensive even when the group AOMT threshold was increased to $p < 10^{-15}$ (single comparison threshold, $p < 10^{-5}$), with 7 cm^3 and 2.3 cm^3 in the right and left hemispheres, respectively. Furthermore, at this threshold, the IPS overlap started to differentiate into separate foci, with IPTO starting to segregate from the more anterior areas of overlap. Thus, the group analysis completely confirmed the individual subjects' analyses.

Independent Reliability Test of AOMT at IPTO and AIPS

Using a separate data set (from three subjects) that was independent of the AOMT-defining data set (see Experimental Procedures), we tested with ANOVA the reliability of the differences in activation (percent signal change) between the difficult and easy tasks of each experiment in the AOMT areas at IPTO and AIPS. Highly significant main effects of task difficulty were observed in all four regions (all ps at least < 0.0005; right side of each graph in Figure 3), with the simple effects of task difficulty significant for each experiment in each AOMT (all ps at least < 0.05; main part of each graph in Figure 3). These results show that for the three subjects included in these analyses, all four AOMTs responded more strongly during the difficult tasks than during the easy tasks of each experiment. The ANOVA thus confirmed the results of the Kolmogorov-Smirnov (KS) tests, at least for these three subjects, even though the data set used in the ANOVA was separate from the data set used for defining the AOMTs.

None of the interactions between task difficulty and experiment were significant in any of the four regions (center of each graph in Figure 3), suggesting that the effect of task difficulty did not differ among the experiments in any of the four areas for these three subjects. This result reflects what Price and Friston (1997) refer to as "cognitive conjunction," the presence of a main effect of the manipulation of interest (here, visual attention/task difficulty) in the absence of an interaction with other contextual variables (here, different displays, stimuli, and tasks across the three experiments) and with the simple effects reliable for each experiment. This cognitive conjunction analysis suggests that visual attention can strongly modulate IPTO and AIPS activity independent of the changing context in which it operates.

Single Comparisons: Activations in Each Experiment, Considered Separately

Figures 4A–4C present, separately for E1a, E1b, and E1c, the anatomical regions that showed stronger activation in the difficult tasks than in the easy tasks (group

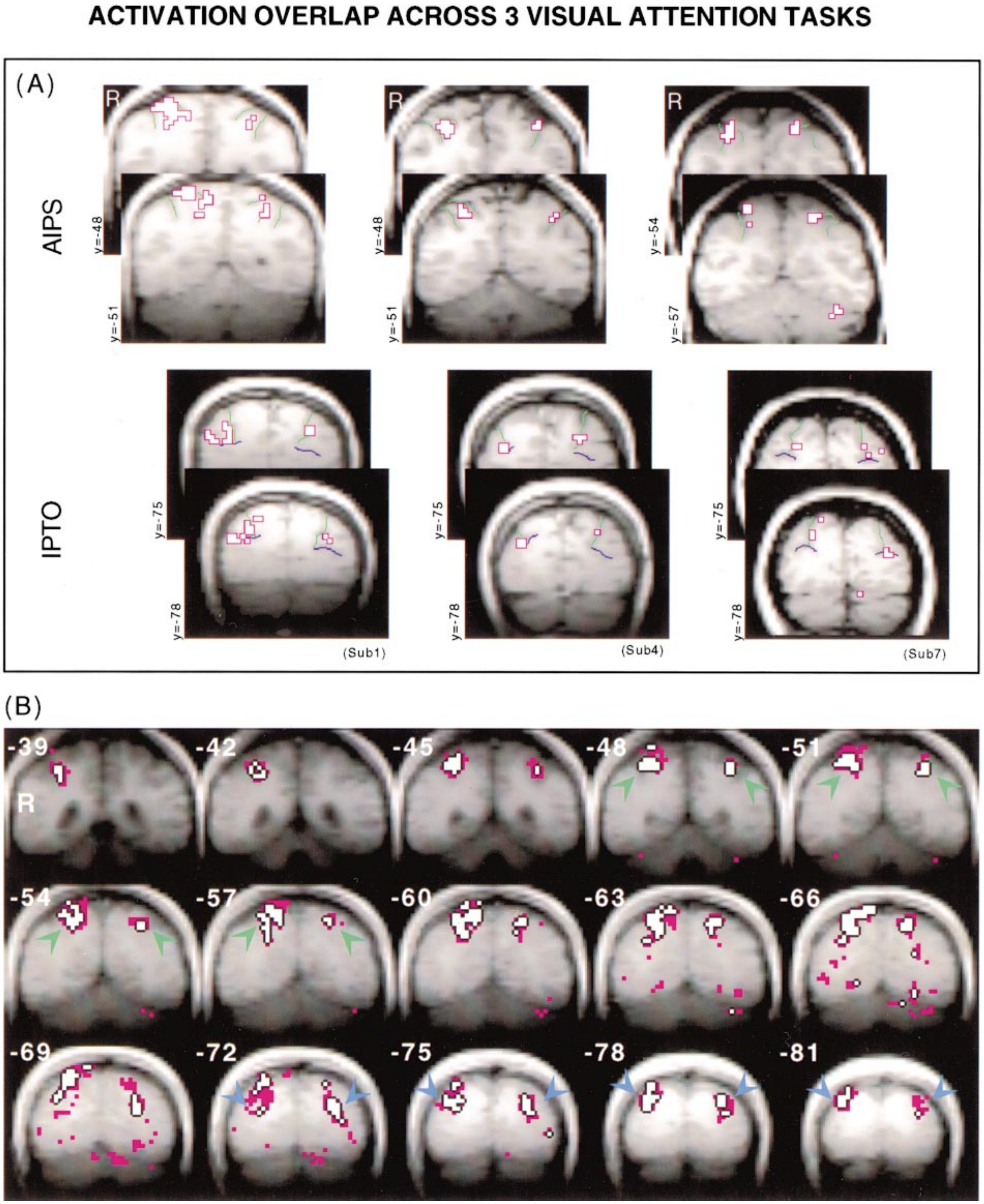

Figure 2. Activation Overlap across Multiple Visual Attention Tasks

(A) AOMT (outlined in pink) of three subjects showing IPTO and AIPS. AOMT is superimposed on each subject's normalized anatomical images (two slices per subject per region). These areas showed significant activations in peripheral shifting/maintenance (versus central maintenance), peripheral object matching (versus central color matching), and the nonspatial conjunction task (versus the feature task). AOMT threshold, $p < 10^{-9}$ (i.e., single comparison threshold, $p < 0.001$). Green, intraparietal sulcus; blue, transverse occipital sulcus.

(B) AOMT for the group analysis of seven subjects, superimposed on the averaged normalized anatomical images of all subjects. Group AOMT extends from the posterior end (bottom right) to its anterior end (top left). Pink indicates AOMT threshold of $p < 10^{-9}$; white, outlined in black, indicates AOMT threshold of $p < 10^{-15}$. Green and blue arrows mark AIPS and IPTO, respectively. The y coordinates of the slices are indicated in the top left of each image. Abbreviation: R, right hemisphere.

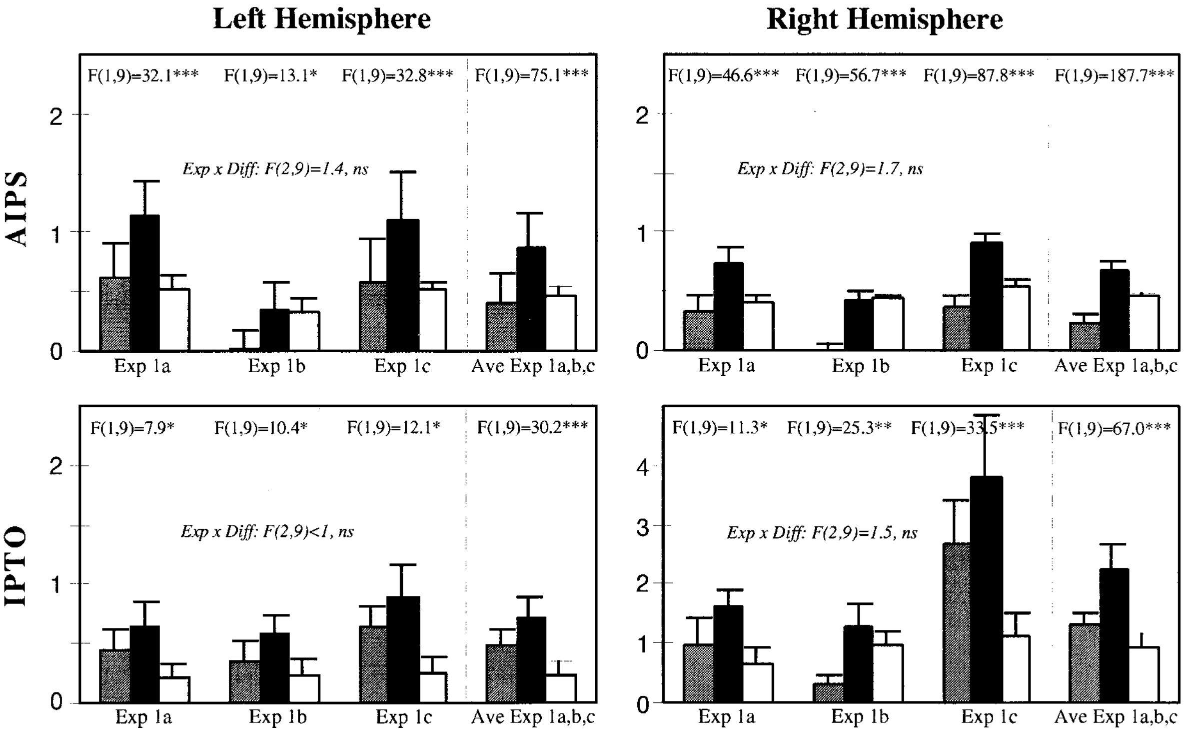

Figure 3. Independent Reliability Test of AOMT Activations

The ANOVA was conducted on the mean PSC for the difficult (black bars) and easy (gray bars) tasks of E1a–E1c, using a data set (three subjects) that was separate from the AOMT-defining data set. Difference in PSC of difficult and easy tasks is shown in white. The statistics above each set of bars show F values of the simple effects comparing the difficult and easy tasks of each experiment in each AOMT; interaction statistics (experiment by task difficulty) are shown in italics in the center of each graph. The main effect of task difficulty for each AOMT is shown on the right of each graph. The y axis plots PSC (scale is different for right IPTO); error bars indicate standard error. Note that the baselines used for PSC calculation were not identical across experiments (with PSC of E1b underestimated; see Experimental Procedures). Asterisk, $p < 0.05$; double asterisk, $p < 0.005$; and triple asterisk, $p < 0.0005$.

analyses). Figure 4D shows both overlapping and nonoverlapping regions of activations across the three experiments. Table 3 lists the areas of activation in each experiment both for group and for individual subjects' analyses.

Dorsal Pathway. All three comparisons (difficult versus easy tasks, considered separately for each test) produced significant and extensive activations in very similar regions, concentrated in the IPS and SPL of both hemispheres (with at least five of seven subjects showing these loci in each experiment, and with the effects reliable in the group analyses; Table 3 and Figures 4A–4C). Activations in the IPS extended from the junction with the transverse occipital sulcus (TrOS) in the occipital lobes through the parietal lobes. On the right, IPS activity often reached PCS, especially in the right hemisphere. In general, right hemisphere activations were larger and more consistent than on the left.

While the three comparisons showed similar patterns of dorsal activation, E1a (peripheral shifting > central maintenance; Figure 4A) resulted in some activations that were unique to this comparison. In particular, although all experiments produced activity in the SPL, it tended to spread more medially in peripheral shifting (E1a) than in the other two experiments, as shown in Figure 4D (blue voxels, $y = -39$ to -54). This pattern was evident both in group and in individual subjects' data.

These results are consistent with earlier reports of parietal activity in peripheral shifting tasks (e.g., Corbetta et al., 1993) and suggest that activity in the middle and anterior SPL can be dissociated from visual difficulty or effort (since E1b and E1c also compared difficult to easy conditions) and may thus be specifically involved in attentional shifting. The results of E1b (object > color matching) further indicate that dorsal activity is not restricted to location-matching tasks (e.g., Haxby et al., 1994) and that it can also be observed in object-matching tasks.

E1c provides the first unambiguous demonstration of extensive parietal involvement in nonspatial attention (Figure 4C). While previous reports on nonspatial attention produced conflicting results (see Discussion), here we found large and highly consistent activations (with at least six of seven subjects in each region; except for left SPL, with five of seven subjects) in posterior IPS and SPL and in anterior IPS, where it reached the right PCS. Although some of these activations overlapped with one or both of the other two experiments, a region in the middle/anterior segment of IPS spreading into inferior parietal lobule (IPL) appeared to be activated uniquely in this experiment (Figure 4D, yellow voxels, $y = -39$ to -66). This pattern was also apparent in individual subjects' data (seven of seven subjects in the right hemisphere and five of seven subjects in the left hemisphere). The more lateral IPS/IPL areas may thus support specifically nonspatial attention (see also Coull and Nobre, 1998), although such an interpretation of these nonoverlaps needs to be treated with caution given the many

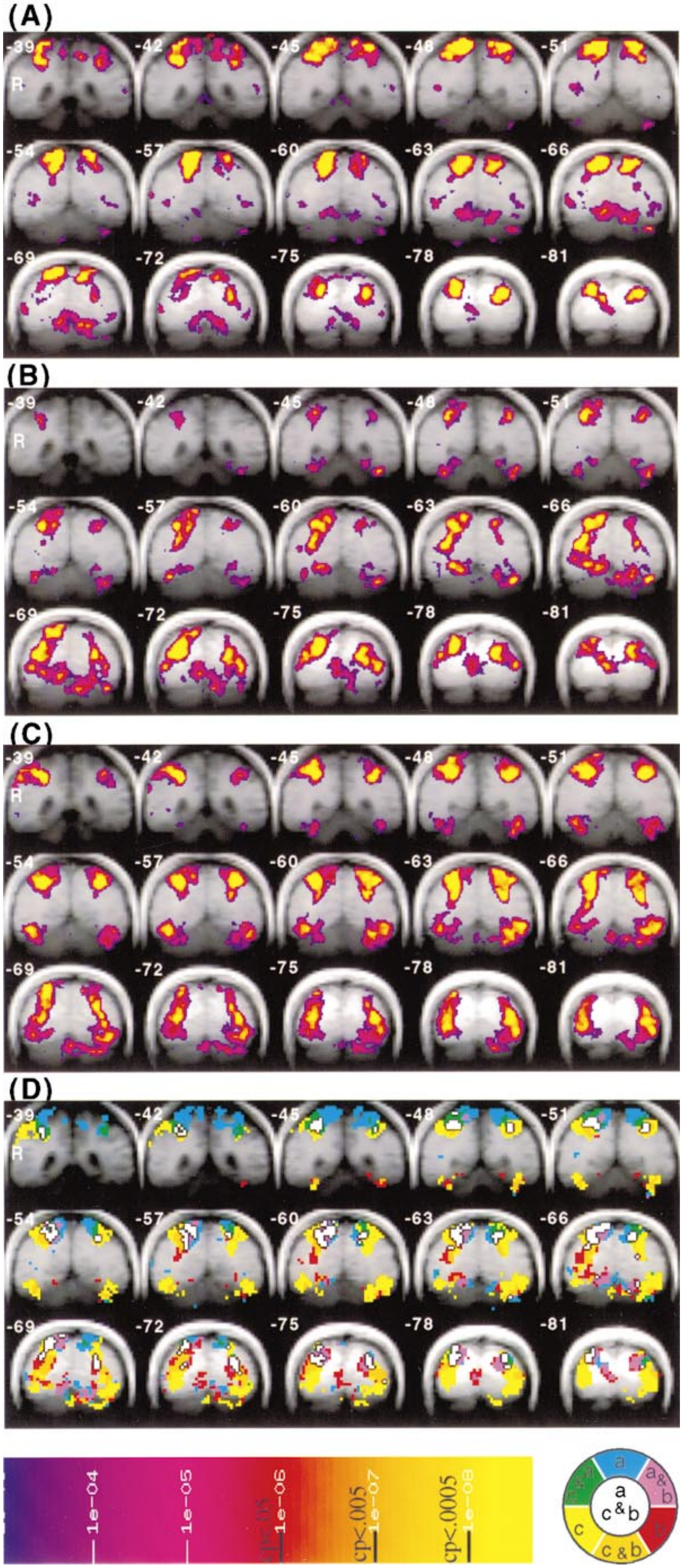

Figure 4. Group Analyses of Activations in Each Experiment

(A) Peripheral shifting/maintenance > central maintenance (E1a).

(B) Peripheral object matching > central color matching (E1b).

(C) Nonspatial conjunction > feature tasks (E1c).

Activations are superimposed on averaged normalized anatomical images of all subjects. Color bar indicates level of significance (cp, color corresponding to given significance levels after Bonferroni corrections for total number of examined voxels).

(D) Group analysis of the three comparisons superimposed on each other, showing overlapping and nonoverlapping activations as indicated in the color wheel (letters in the circle correspond to E1a, E1b, and E1c). Single comparison threshold, $p < 10^{-5}$ (AOMT, in white, $p < 10^{-15}$). Note the large regions of SPL apparently activating uniquely in attentional shifts of E1a (top row, blue voxels), and the more lateral IPS/IPL regions activating uniquely in the nonspatial conjunction task of E1c (top and middle rows, yellow voxels). The y coordinates of the slices are indicated in the top left of each image. Abbreviation: R, right hemisphere.

Table 3. Regions of Activation in E1a (Peripheral Shifting $>$ Central Maintenance), E1b (Peripheral Maintenance $>$ Central Maintenance), E1c (Nonspatial Conjunction $>$ Feature Task), and E2 (Difficult Language $>$ Visual Control)

	Left Hemisphere				Right Hemisphere			
	1a	1b	1c	2	1a	1b	1c	2
Parietal And Parietooccipital								
IPTO	7***	7***	7***	1/4	7***	7***	6***	
IPSpost	5***	6***	7***	3/4	7***	6***	6***	
AIPS	5***	5***	7***	2/4	5***	6***	7***	1/4
SPL	6***	5**	5***	2/4	6***	6***	6***	1/4
Precuneus	4		1	1/4	6	2	3	
PCS/PCG	5*		2*		5***	2*	6***	2/4
IPL (contig STG)				3/4***				2/4
Temporal And Temporooccipital								
CalcS	3	4	2	3/4	4*	5***	2	2/4
LG	4*	6*	4	1/4	6***	4**	1	
MOG	7*	6***	6***		5	6***	5***	
IOG				3/4***				4/4***
IOS/ITS	1	4***	7***	1/4	1	6***	5***	
FG/ColS occ	2	6**	5	2/4	3	5**	5	2/4
FG/ColS temp		5***	4***	1/4	1	6***	3	2/4
STS	3		2		4	2	5	
STG/MTG				4/4***				3/4***
Cerebellum	4**	4*	5***	3/4	4	2	4**	4/4***

Cells indicate the number of subjects (out of seven for E1a–E1c, out of four for E2) showing significantly stronger activations ($p < 0.001$, uncorrected) in the difficult conditions than in the easy conditions of each experiment, given separately. Asterisks indicate the peak significance of activations in the group analyses of each experiment separately, Bonferroni corrected for the number of voxels examined (asterisk, $p < 0.05$; double asterisk, $p < 0.005$; triple asterisk, $p < 0.0005$). The table lists only those regions that showed activations in at least four subjects in at least one experiment, except E2, for which all activations are listed. Abbreviations: CalcS, calcarine sulcus; FG/ColS, fusiform gyrus/collateral sulcus; IOG, inferior occipital gyrus; IOS/ITS, inferior occipital/temporal sulcus; IPS, intraparietal sulcus; IPL, inferior parietal lobule; LG, lingual gyrus; MOG, middle (lateral) occipital gyrus; PCS/PCG, postcentral sulcus/gyrus; SPL, superior parietal lobule; STS, superior temporal sulcus; contig, contiguous with; post, posterior; occ, occipital; and temp, temporal.

differences between the experiments (in particular, attention to peripheral versus foveal locations). Regardless of the specificity interpretation, these data show that nonspatial attention tasks do activate large regions of parietal cortex.

Dorsal Pathway: Attention Shifting in the Right versus Left Visual Fields (Experiment 1a). No consistent parietal differences were observed in individual subjects' data for attention to the right visual field (RVF) versus the left visual field (LVF); there were no dorsal areas that showed laterality differences in more than three subjects. More posterior or ventral regions showed no consistency either, except that attention shifts in the LVF produced stronger activity in the right occipital pole (six of seven subjects) and weaker activity in the right lingual gyrus (five of seven subjects) as compared with shifts in the RVF. The increased activation in the right occipital pole likely reflects attentional modulation of early retinotopic areas (e.g., Kastner et al., 1998), while the decreased activity in lingual gyrus may reflect inhibition of the early representations of unattended locations (Tootell et al., 1998).

The lack of consistent parietal differences for attending to the RVF versus the LVF is surprising given that unilateral parietal damage leads to contralateral attention deficits (e.g., Mesulam, 1981). On the other hand, other imaging studies also failed to find laterality differences (e.g., Vandenberghe et al., 1997; but see Corbetta et al., 1993; Nobre et al., 1997).

Ventral Pathway. In general, activations in ventral regions differed between the experiments more than they did in the dorsal pathway, as would be expected on the basis of ventral preferences for particular types of stimuli. The MOG was the only region where significant (but mostly nonoverlapping) activations were noted in the three comparisons (although they were small and more anterior in E1a than in E1b or E1c; see Figures 4A–4C, $y = -72$ to -81). This region shows close correspondence (in anatomical location and coordinates) to area LO (lateral occipital complex), which is involved in object processing (Malach et al., 1995; Grill-Spector et al., 1998).

In both E1b and E1c, which used complex shapes as stimuli, consistent activations were also found more anteriorly in the ventral pathway, in the fusiform gyrus (FG/ColS) and inferior occipital/temporal sulcus (IOS/ITS). The active regions in E1c (conjunction $>$ feature task with textured letters) tended to be larger in the left than in the right hemisphere and more lateral than in E1b (face/house $>$ color matching; Figures 4B–4D, $y = -48$ to -63). These data are consistent with reports of preferential responses of these areas to letter strings (IOS/ITS; e.g., Puce et al., 1996) and faces (FG/ColS; e.g., Kanwisher et al., 1997) but further suggest a dissociation of attentional modulation for different stimulus types (see also Wojciulik et al., 1998). However, the interpretation of these nonoverlaps between experiments is not straightforward, as not only the stimuli and tasks differed but also the spatial layout of stimuli.

Finally, the tests that compared peripheral to central attention (E1a and E1b) also resulted in some activations in the lingual gyrus (Figures 4A and 4B, $y = -63$ to -72). These occipital activations may reflect attentional

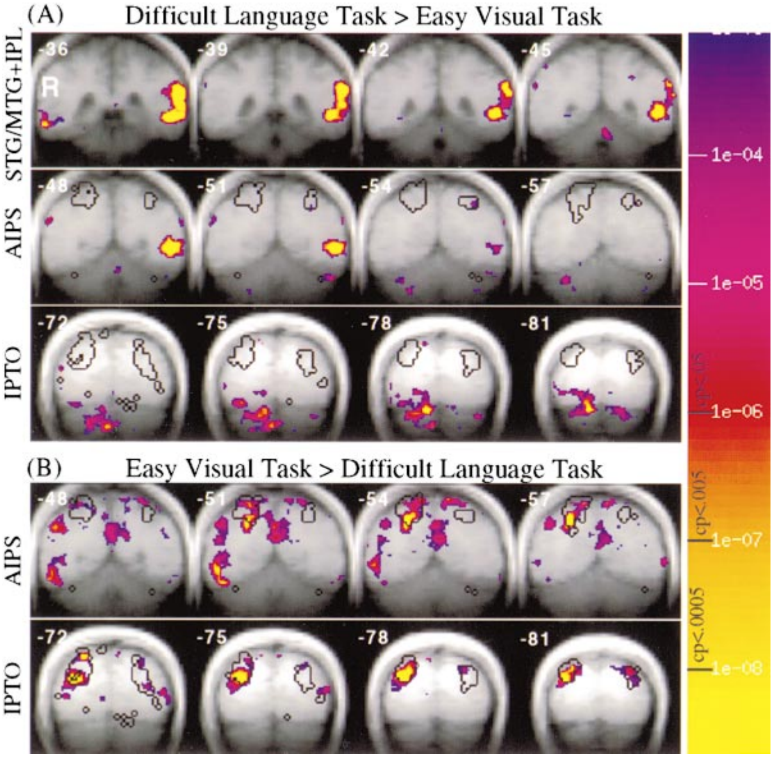

Figure 5. Results of E2 (Group Data), Comparing the Difficult Language Task to the Easier Visual Task

(A) Regions showing significantly stronger activity in the language task than in the visual control task. Significant activations were observed in left superior temporal cortex (top and middle rows) but not in the AOMT regions at IPTO and AIPS (indicated in black outline). (B) Regions showing significantly stronger activity in the easier visual task than in the difficult language task. Right IPTO and AIPS, as well as parts of left IPTO, show such activations. Color bar indicates level of significance (cp, color corresponding to given significance levels after Bonferroni corrections for total number of examined voxels). The y coordinates of the slices are indicated in the top left of each image. Abbreviation: R, right hemisphere.

modulation in early retinotopic areas found in this anatomical region (e.g., Kastner et al., 1998).

Cerebellum. All three comparisons produced some activity in the cerebellum. Group data showed activations in left posterior cerebellum in all three comparisons and right cerebellar activity in E1c, but these activations were not consistent in individual subjects' data (Table 3).

Experiment 2: Behavioral Results

Subjects were much slower in the language task than in the visual control task (1282 versus 607 ms, $p < 0.005$; Table 1) and showed a nonsignificant trend of lower sensitivity in the language task ($d' = 3.1$) than in the visual task ($d' = 3.6$, $p > 0.3$; note that the cutoff point for counting a response as correct was 2.5 s in this experiment versus 1 s in E1a–E1c, such that we should observe a significant difference in absolute RTs but not necessarily in sensitivity; see Experimental Procedures). The difference in RTs between the difficult and easy tasks in this experiment (over 650 ms) was much larger than in E1a–E1c (on average, 90 ms). These data indicate that the language task was significantly more difficult than the visual task and therefore serves as a good control to test for dorsal activation sites due to nonvisual effort.

Experiment 2: Functional Imaging Results

There were very few parietal sites that were more active in the difficult language task than in the easier visual task (see Table 3 and Figure 5A). In the individual subjects' analyses, the most consistent parietal activation was observed in left IPL (three of four subjects) and in left posterior IPS (three of four subjects). Regarding IPTO and AIPS, one of four subjects showed activity near left IPTO, one of four near right AIPS, and two of four near left AIPS. However, these activations, which occurred in the vicinity of the AOMT regions, showed strictly no overlap in the individual subjects' data with the activations in E1c run within the same session as E2, and therefore zero overlap with AOMT regions. Similarly, the group analysis showed a significant activation focus in left IPL (contiguous with the superior temporal activations; see below) but no activations in the AOMT regions, except for five voxels in left AIPS (Figure 5A).

Conversely, all four of four subjects showed large activations in the language task (versus the visual control task) in the left superior (STG) and middle (MTG) temporal gyri (Brodmann's areas 22 and 21, respectively; Figure 5A), consistent with neuropsychological reports of severe language disorders following lesions to this region (Ardaman et al., 1996). This area also appears to correspond to regions active during word reading (e.g., Price et al., 1994). Additional activations were noted bilaterally in inferior occipital gyrus and cerebellum.

These analyses did not find stronger activity for the difficult language task than for the easier visual task in the AOMT regions, consistent with our prediction. We further checked whether these regions may show the reverse pattern of stronger activity for the easier visual task than for the difficult language task, as one might expect if the letter size judgment task placed higher demands on visual attention than did the grammar judgment task. Although the individual subjects' data did not show this pattern consistently, group analysis revealed stronger activity for the easier visual task than for the more difficult language task in right IPTO and AIPS and, though smaller, in left IPTO, showing a large amount of

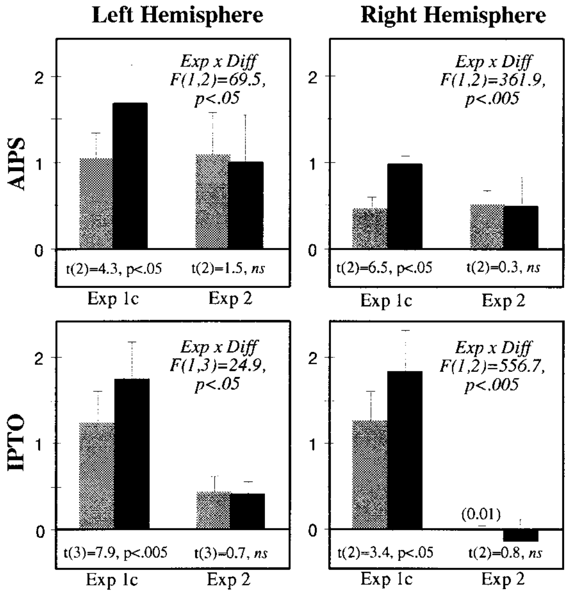

Figure 6. Interaction of Task Difficulty (Easy/Difficult) by Experiment (E1c/E2) in the AOMT Regions

Results of the comparisons between the easy (gray bars) and difficult (black bars) tasks of each experiment are shown below the corresponding bars in each graph (p values are one tailed for E1c). The y axis plots PSC; error bars indicate standard error. PSC was extracted for each subject and each AOMT separately.

overlap with the group AOMT voxels (Figure 5B). The group analysis suggests that there may not have been sufficient power in the individual subjects' data to detect this difference (note that the number of trials in E2 was about half of that in each of E1a–E1c, since the difficult language task required a longer interstimulus interval to allow for the much longer response times; this procedure reduced the power in the individual subjects' analyses).

Visual versus Nonvisual Effort: Interaction of Experiment by Difficulty

The apparent interaction in the AOMT regions between task difficulty and experiment (i.e., significant activations for the difficult versus easy tasks in E1 but not in E2) was further tested by ANOVA. The ANOVA compared the percent signal change (PSC, extracted for each subject and each AOMT separately) of easy and difficult conditions of E1c and E2 (i.e., the two experiments that all four subjects completed within the same session as the language control experiment; see Experimental Procedures). As shown in Figure 6, a significant interaction between task difficulty (easy and difficult) and experiment (E1c and E2) was found for all four AOMT regions (all ps at least < 0.05). The significant interactions indicate that the AOMT areas responded most strongly during the visually demanding task and only weakly during all other tasks (difficult language or two easy visual tasks). Planned comparisons, comparing difficult with easy conditions for each experiment separately, revealed significantly stronger activity for the conjunction task than for the feature task in all four AOMT regions (all one-tailed ps at least < 0.05) but no significant differences between the difficult language task and the visual control task in any region (all two-tailed ps > 0.25; note, however, that this analysis was based on the AOMT regions of each subject individually, therefore reducing the power to find greater activity for the easier visual task than for the difficult language task, as observed in the group analysis; see above).

In summary, there is no evidence that IPTO and AIPS activity is related to general (not specifically visual) effort. Although the language task produced consistently higher activity in left temporal cortex than did the easier visual task (four of four subjects), this was not true in the AOMT regions, as tested either with the KS test or with ANOVA. Furthermore, all AOMT regions showed significant difficulty by experiment interactions, with strongest responses for the difficult visual task and only weak responses for the difficult language or easy visual tasks. It appears that these areas are specifically involved in visually demanding tasks.

Discussion

fMRI was used to determine whether multiple visual attention tasks may activate common regions of parietal cortex, therefore showing a generality of function rather than functional specificity. Within a single session, subjects performed three different visually demanding tasks (each with its own control condition) that differed widely from each other in the kind of attentional selection involved as well as in stimuli and their spatial layout. The common element across the three experiments was that each contrasted one condition that placed high demands on visual attention with another condition (using identical stimuli and matched motor components) in which attentional requirements were minimal. The AOMT analysis allowed us to look for exact voxel-by-voxel overlap in activation within subjects across the three attention-requiring tasks: peripheral shifting/maintenance of attention, peripheral object matching, and a nonspatial conjunction task.

Two bilateral regions showed activation overlap across all three visual attention experiments. One was found in the posterior fundus of the IPS, at or close to the junction with the transverse occipital sulcus (IPTO; Brodmann's area 19). Although the size of the IPTO overlap in individual subjects was small (averaging about 300 mm^3 at the most stringent AOMT threshold), it was very consistent across subjects (present in six of seven subjects in the right hemisphere and seven of seven in the left). The second area of activation overlap was found in AIPS in five of seven subjects; for all five subjects, this area lay on the medial bank of the IPS (i.e., SPL, Brodmann's area 7). The left AIPS was about the same size as the more posterior AOMT at IPTO, while the right AIPS was substantially larger (about 1 cm^3).

The group analysis confirmed these results, showing massive bilateral activation overlap through the entire extent of the IPS, from its posterior end at IPTO, where it extended into posterior SPL in the right hemisphere, to the anterior segment close to the PCS (Figure 2B). The large size of the activation overlap in the group data (15.4 and 6.3 cm^3 in right and left hemisphere, respectively) suggests that the individual subjects' analyses underestimated the extent of the overlap. On the other hand, averaging across subjects produces spatial blurring due to imperfect coregistration and differences in anatomical and functional organization across subjects, which can possibly result in an overestimate of the overlap in the group data. Nonetheless, even when the group AOMT threshold was increased to $p < 10^{-15}$ (i.e., single comparison threshold of $p < 10^{-5}$), the IPS overlap remained extensive (7.0 and 2.3 cm^3 in right and left hemisphere, respectively) but began to differentiate into a posterior focus at IPTO and a more anterior IPS focus, as observed for individual subjects. Thus, the group and the individual subject analyses yielded a highly consistent and robust pattern of activation overlap in at least two bilateral areas in the IPS. (Note, however, that it is possible that future research with higher spatial resolution may uncover functional specialization at a finer grain than we can resolve with present techniques.)

The overlapping activations at IPTO and AIPS suggest that these regions perform a more general attention function than could be inferred based on any one experiment in this study or on previous studies with single comparisons. Alternative accounts of the overlapping activations in terms of either more general processes (e.g., any effortful task) or more specific ones (e.g., attentional shifting alone) can be discounted. First, while a difficult language task (as compared with an easier visual task) performed on visually presented words produced strong activations in left superior temporal cortex, it failed to do so in IPTO and AIPS. Indeed, the group analysis revealed stronger activity for the easier visual task than for the difficult language task in left and right IPTO and right AIPS, as would be expected if the visual task placed higher demands on visual attention than did the language task. Furthermore, a significant interaction of experiment (E1c versus E2) by task difficulty was found in all four regions, with strongest responses for the attentionally demanding task of E1c (conjunction task) and only weak responses for the easy visual tasks of both experiments or the difficult language task of E2. Thus, the IPTO and AIPS areas are not simply activated by any effortful task.

Second, while some of the activations in both E1a (peripheral attention shifting > central maintenance) and E1b (peripheral object matching > central color matching) may reflect peripheral space–based selection, and possibly active suppression of spatial distractors or of eye movement, these mechanisms should not be active in E1c (nonspatial conjunction > feature task). In that comparison, all stimuli were presented at fixation and without spatial distractors, such that subjects attended to the same location in both conditions, and there was no need to plan, make, or suppress eye movements. These results show that eye movement preparation, execution, or suppression is not necessary to activate these areas, while focused attention is sufficient for their activation. Finally, while the stimuli and their spatial layout differed between experiments, emphasizing the general response properties of these areas, the displays and motor requirements were kept identical within each experiment, thus excluding any potential confounds due to differences in retinal stimulation or motor components.

Our results fit well with the heterogeneity of attentional deficits observed in visuospatial neglect, a disorder characterized by a marked impairment in the ability to detect or respond to objects in the contralesional space. Parietal neglect patients show the classic deficits not only in spatial attention (exogenous and endogenous orienting as well as feature integration in the contralesional space; e.g., Posner et al., 1984; Eglin et al., 1989) but also in object-based attention (e.g., Driver and Halligan, 1991; Behrman and Tipper, 1994) and temporal (nonspatial) attention (Husain et al., 1997). Husain et al. (1997) showed that when neglect patients have to identify a target object in a rapid visual stream, their ability to detect a second object is profoundly impaired, even though both objects are presented in the same (foveal) location. Furthermore, the severity of the temporal impairment correlated strongly with the magnitude of the spatial bias, suggesting a close link between spatial and temporal attention, as observed in our data. These and our results indicate that parietal function cannot be reduced to one single mode of visual selection; instead, our data suggest that IPTO and AIPS reflect a common neural substrate underlying multiple modes of visual selective processing.

IPTO and AIPS: Location and Function

A comparison of the location of IPTO with respect to the retinotopic areas of the human brain (Sereno et al., 1995; Tootell et al., 1997) suggests that it is located in the vicinity of area V3A, which is transected by the TrOS but which does not appear to continue in the IPS. In humans, area V3A has a retinotopic representation of the whole contralateral visual field and shows high responsiveness to motion (Tootell et al., 1997). However, our stimuli were stationary. In addition, the overlapping activation at IPTO often extended beyond the junction into posterior IPS, a region that is likely to be beyond the borders of V3A. These considerations suggest that IPTO may constitute a functional and anatomical region that is separate from V3A. In a recent paper, Tootell et al. (1998) found that, among other areas, both V3A and “V7” (a newly discovered retinotopic visual area adjacent to V3A) were strongly modulated by spatial attention. Based on the anatomical location of V7 and its susceptibility to attentional manipulations, it is possible that IPTO corresponds to V7.

Several recent imaging papers reported activations in an area that showed close correspondence to IPTO coordinates. Culham et al. (1998) found a posterior intraparietal focus active during both discrete attentional shifting and continuous attentive tracking. In addition, Faillenot et al. (1997) reported a similar activation focus in the right hemisphere in a task involving the matching of (as opposed to pointing at or grasping) successive novel shapes, and both Jonides et al. (1993) and Courtney et al. (1996) found that visuospatial memory tasks also activate a similar right hemisphere region. More surprisingly, a focus very similar to IPTO was activated during the viewing of various objects (as compared with textures) defined by luminance, texture, or motion (Grill-Spector et al., 1998). Although this study did not manipulate attention explicitly, one might expect that attention is more engaged by passive viewing of objects than of random texture fields. These papers not only extend the range of visual attentional tasks IPTO is involved in but further show that overt responses are not necessary to activate this area (Culham et al., 1998; Grill-Spector et al., 1998), suggesting that its activity can be dissociated from motor/premotor components of attention (cf. Rizzolatti et al., 1987).

Finally, Corbetta et al. (1998) found that both covert and overt shifts of spatial attention produced overlapping patterns of activity, including areas similar to IPTO and AIPS, emphasizing the close link between the two attention systems. Our results, however, suggest that the function of these areas is not limited to attentional shifting and/or eye movement preparation or execution, since it was also highly active in a nonspatial attention task performed on foveal stimuli. These results demonstrate that activity in IPTO and AIPS reflects attention (Colby, 1996), not intention (i.e., motor preparation; Rizzolatti et al., 1987; Andersen, 1995).

While we have concentrated here on visual attention, it is possible that attention to other modalities may rely on some of the same regions. In particular, although the posterior locus of IPTO suggests that it may be involved in purely visual attention, the function of the more anterior AIPS region may be more general: activity in anterior/middle IPS (or adjacent superior/inferior parietal cortex) has been associated not only with many different visual attention tasks, visual memory (e.g., Jonides et al., 1993), and visual imagery (e.g., Roland and Decety, 1993) but also with auditory attention (e.g., Pugh et al., 1996), sustained attention in anticipation of tactile stimulation (Pardo et al., 1991), and tactile shape and length discrimination (Roland et al., 1998). Future research will determine whether IPTO and AIPS may indeed perform these different attention functions, with IPTO involved specifically in visual attention and AIPS generalizing across modalities. It will also be important to investigate the attentional role played by frontal areas that form part of the anterior attention network (Mesulam, 1981; Posner and Petersen, 1990) but that could not be imaged with the surface coil used here. In a recent review, Duncan and Owen (1999) found that very similar frontal regions are active in a wide range of cognitive tasks, underscoring the general rather than specific response properties of frontal lateral and anterior cingulate cortex. It is likely that these frontal areas may also show activation overlap across multiple attention tasks.

The present results allow us to reject the notion that IPTO and AIPS areas are involved in any one single type of visual selection (e.g., spatial shifts of attention alone), suggesting instead a more general role in visual attention. But what exact function is performed in these areas? Although a definitive answer must await further research, we next discuss the hypothesis that these parietal regions may be involved in the suppression of task-irrelevant distractors.

Although both excitatory and inhibitory mechanisms are commonly invoked in theories of visual attention, most physiological and behavioral experimental paradigms do not have a neutral baseline condition that allows one to distinguish between the enhancement of attended information and the suppression of unattended information. Nonetheless, some evidence for suppressive processes in attention comes from the behavioral phenomena of negative priming (Tipper, 1985) and inhibition of return (Posner et al., 1985) and from the fact that spatial cueing can produce costs as well as benefits (Posner et al., 1980).

The hypothesis that some parietal areas may be involved in distractor suppression is consistent with prior imaging studies. The majority of imaging studies that report parietal activity in visual attention tasks, including all three tasks described here, used displays that contained irrelevant stimuli, with inhibition of the unattended information likely to occur, particularly in the more demanding tasks. Interestingly, the two papers that did not find parietal activations for visual attention tasks used displays without irrelevant distractors. In the first one, Corbetta et al. (1991) compared selective attention to different visual attributes (shape, color, or speed) with divided attention to all three attributes (or passive viewing); although selective attention to these attributes strongly modulated activity in extrastriate areas, which appear specialized for their processing, no parietal activity was observed. While the displays in this study contained multiple stimuli, and in the selective attention conditions some attributes were irrelevant, there were no distractor stimuli that were irrelevant to the task.

In the second study, which found no parietal activity, Rees et al. (1997) investigated temporal feature integration; subjects performed either a conjunction or a feature categorization task on stimuli presented one at a time at fixation. The only activation, showing stronger response for the conjunction task than the feature task, was observed in right frontal cortex. The lack of parietal activation in this study is particularly interesting given its similarity to our nonspatial conjunction task (E1c), in which we observed extensive bilateral activations in the IPS. Unlike our study, in which targets were presented among multiple temporal distractors, there were no irrelevant stimuli in the Rees et al. experiment. Although one very recent study (Kastner et al., 1999) found parietal activity in the absence of visual stimulation, when distractor suppression cannot occur (i.e., a baseline shift during expectation of forthcoming stimuli), these activations do not appear to correspond to the AOMT areas described here (with the possible exception of left IPTO).

Thus, parietal cortex, and especially the AOMT areas described here, may perform an inhibitory function in selective attention, suppressing task-irrelevant distractors. While this hypothesis is consistent with our findings and with previous data, the evidence is not definitive, as no study has yet directly compared the effect of presence versus absence of irrelevant distractors on parietal activity. Note further that inhibition and enhancement are not mutually exclusive; while some areas/networks may act to inhibit irrelevant distractors, others may act to enhance relevant information. Indeed, recent formulations of visual attention view selection as a mechanism that biases competition between visual inputs toward relevant information, both by enhancing the neural representation(s) of the relevant object and by inhibiting the representation(s) of distractors (Desimone and Duncan, 1995; Duncan et al., 1997; Behrmann and Haimson, 1999; note, however, that whereas Duncan et al. propose that the biasing mechanism is not anatomically localized, with competition integrated across multiple brain areas, our results suggest that competitive integration may be supported by areas in the IPS). This hypothesis is readily testable and makes straightforward predictions: if some of the IPS areas support an inhibitory function, they should be more active in situations that require distractor suppression; on the other hand, if some of them contribute to enhancement, they should show stronger activity in attentionally demanding tasks than in control tasks, independent of the presence of distractors.

Whether or not this hypothesis is confirmed, the important point to note here is that none of the attentional functions that have been previously attributed to parietal regions (e.g., shifts of spatial attention and processes related to eye movement preparation or execution) can account for activity in IPTO and AIPS. Instead, the broad range of attentional tasks that activate the same IPS areas indicate that these regions play a more general role in visual attention.

Attention Shifts and Nonspatial Attention in Parietal Cortex

Although the three comparisons generally resulted in similar regions of activation, some parts of the SPL (lateral, but medial to the AOMT regions) appeared to be activated uniquely in peripheral shifts of attention, while activity in lateral IPS (IPL) appeared to be associated uniquely with nonspatial attention (Figure 4D). The apparent specificity of these activations for the two different types of attention tasks has to be treated with caution given the many differences between the experiments (in particular, differences in the attended, peripheral versus foveal, locations). Nonetheless, the procedure of running multiple attentional tasks in the same subjects allows us to dissociate the activity in these regions from visual effort (i.e., all three tasks compared difficult conditions with easy ones, but these two regions showed activity specific to only one of the comparisons). Our results thus extend previous findings that have associated spatial shifts of attention with posterior parietal cortex (e.g., Corbetta et al., 1993; Nobre et al., 1997), suggesting that parietal involvement in attentional shifting can be dissociated from visual effort.

Conversely, the results of the nonspatial conjunction task show that spatial shifting of attention is not necessary to activate parietal cortex; extensive regions in the IPS and SPL also subserve mechanisms involved in nonspatial attention, with lateral IPS/IPL apparently activating uniquely in the nonspatial task. Previous imaging research produced conflicting results; whereas Rees et al. (1997) found no parietal activity in a nonspatial attention task, Coull et al. (1996) and Coull and Nobre (1998) both reported activations in SPL or IPS. However, the task of Coull et al. (1996) did not dissociate nonspatial attention from working memory, and Coull and Nobre (1998) found only one parietal region more active in their temporal than in their spatial cueing tasks (left IPS) or in both spatial and temporal tasks as compared with the neutral baseline (left parietal cortex). The most likely reason why we found such extensive and highly consistent parietal activations and the previous studies found none (Rees et al., 1997) or few (Coull and Nobre, 1998) is that in our experiment, the displays contained multiple temporal distractors. Our results thus clearly demonstrate that parietal activity is not constrained to spatial shifts of attention but rather generalizes to nonspatial attention tasks as well (see also Husain et al., 1997).

Finally, our results extend the findings of Corbetta et al. (1995), who reported parietal involvement in a spatial conjunction task, to also include nonspatial conjunction. Parietal cortex appears to be involved in feature integration, independent of whether the task depends on spatial (Corbetta et al., 1995) or temporal (E1c) selection, although this conclusion is not yet definitive given the differences in difficulty between the conjunction and feature tasks of both studies.

Conclusion

In summary, we demonstrated that at least two regions in the dorsal pathway, IPTO and AIPS, were activated in each of three different visual attention tasks tested, despite wide variation in task, stimuli, and spatial layout. Their function cannot be reduced to one single type of visual attention (e.g., attentional shifting alone) nor can it be accounted for by effortful processing in general. These findings provide evidence for the existence and precise anatomical locus of a common neural substrate underlying multiple modes of visual selective processing.

Experimental Procedures

Subjects

Seven healthy subjects (two men; all under 40 years old) participated with informed consent in E1a–E1c within one session. Four of these subjects (all women; three were native speakers of English, and one was a nonnative but fluent speaker) also participated in E2. Two of them participated in E2 within the same session as in E1, and two in another session on a separate day; the latter two also performed E1c within the second session. Six subjects described themselves as right-handed, and one as left-handed. One subject's data from E1b were used to test attentional modulation of face processing (Wojciulik et al., 1998). The experimental procedures were approved by the Harvard University Committee on the Use of Human Subjects in Research and by the Massachusetts General Hospital Subcommittee on Human Studies.

Experiment 1a: Peripheral Shifting versus Central Maintenance

Stimuli and Experimental Design

The displays (Figure 1A) consisted of one central dot and eight peripheral dots arranged in a circle whose diameter was about 15°. The dots were light gray and appeared on a darker gray background. A colored cross, one arm gray, the other half red and half blue, was superimposed on the central dot. The cross rotated counterclockwise once every 4 s, such that with each rotation, the red (or blue) part of the cross pointed to the next peripheral dot. The whole display, except for the cross, blinked on and off every 400 ms. Each time the display blinked on, the central dot or one of the four dots indicated by the arms of the cross became smaller (i.e., there was always one smaller dot in the display). The cross remained in a particular orientation (e.g., red arm pointing to top right dot) for 4 s (five blinks of the display) and then rotated counterclockwise, pointing to the next dot, and so on for all eight dots. During the 4 s when the cross was in a particular orientation, on one of the five blinks (determined randomly) the attended dot, peripheral or central, became smaller and reverted back to the larger size on the next blink. The large dots were about 1.3° in size. When the dots became smaller, they were about 1° in the periphery and 0.8° in the center.

There were 18 epochs in total, 6 epochs of the central (C) maintenance condition, which alternated with six periods of peripheral shifting; the latter periods were split into 6 left (L) and 6 right (R) visual field epochs. Each epoch (C, L, or R) lasted 16 s. For four subjects, the order of the epochs was C-L-R, repeated six times, and for three subjects, C-R-L, repeated six times. Before the central maintenance and peripheral shifting conditions, there was a 2 s instruction display indicating the task for the subsequent epoch, "RING DOTS" for peripheral shifting and "CENTER DOT" for central maintenance. Each run lasted 5.5 min, which included a fixation-only period (18 s) at the end.

Procedure

Subjects were instructed to maintain central fixation for the duration of the scan. In the peripheral shifting condition, they covertly attended to the peripheral dot indicated by the rotating red (three subjects) or blue (four subjects) part of the cross, while in the central maintenance condition, they attended to the central dot. Subjects pressed a button whenever the attended dot (peripheral or central) became smaller.

fMRI Comparison

fMRI comparison tested which regions were more active during peripheral shifting than during central maintenance. As there were no consistent differences across subjects for attention shifts in LVF and RVF, the activation in the peripheral shifting task was combined across the two visual fields.

Experiment 1b: Peripheral Object Matching versus Central Color Matching

Stimuli and Experimental Design

A single trial (Figure 1B) consisted of two faces, two houses, and a colored fixation cross, all presented simultaneously on a gray background for 200 ms, followed by an 800 ms display with a white fixation cross. The faces and houses were two-tone thresholded versions of front view photos of faces and houses (see Kanwisher et al., 1997, for details of stimulus set); the colored fixation cross could be all red or all green or could have one arm red and one green. The displays subtended about 28° horizontally and 21° vertically.

There were 18 epochs, with 6 epochs in each of the face- (F), house- (H), and color- (C-) matching conditions. Each epoch lasted 16 s (i.e., 16 trials). Epoch order (H-F-C-F-C-H-C-H-F-C-F-H-F-H-C-H-C-F) counterbalanced across the three tasks the novelty of stimulus sets and the spatial layout of stimuli (see Wojciulik et al., 1998, for counterbalancing details). During epochs 1–3, 7–9, and 13–15, faces were arranged horizontally (left and right of fixation) and houses vertically (above and below fixation), and vice versa for the remaining epochs. The matches (or "sameness") of the two houses, two faces, and two colors were independent of each other and occurred with 50% probability in each epoch. Trials were presented in a pseudorandom order (with the constraint that no more than three consecutive trials required a response). A 6 s visual instruction display preceded each epoch, indicating the relevant stimuli for that epoch; it consisted of one word ("HOUSES," "FACES," or "COLOR"), presented foveally. Each run lasted 6 min, 42 s, including a 6 s fixation-only display at the end.

Procedure

In separate epochs, subjects performed a matching task on the houses, faces, or color of the cross and pressed a button when the relevant stimuli matched. They were required to fixate on the central cross, attending covertly to the relevant stimuli. Because stimulus presentations were brief (200 ms), subjects did not have time to make saccades to the peripheral stimuli. Indeed, if subjects did not fixate in the center, they could not do the task accurately.

fMRI Comparison

fMRI comparison tested which regions were more active during peripheral object matching (combined across face- and house-matching epochs) than during central color matching.

Experiment 1c: Nonspatial Conjunction versus Feature Tasks

Stimuli and Experimental Design

The displays consisted of a sequence of black and/or white textured letters (subtending about 7.5° × 8.5° of visual angle) presented at fixation on a gray background in rapid serial visual presentation (RSVP) at a rate of six letters per second (with no interstimulus interval; Figure 1C). The fixation was marked by a red dot (about 1°) superimposed on the letters. In the conjunction task, the target letter was defined by a conjunction of letter identity and texture; in the feature task, the target letter popped out on the basis of letter brightness.

Across two counterbalancing versions of the experiment (Figure 1C), all stimuli (both targets and distractors) were exactly matched in the feature and conjunction conditions as follows. The stimulus sets were composed of the letters X, O, E, H, L, S, and T, which could be tilted-striped, vertical-striped, ringed, or checked; one set of the textured letters was black, the other set was white. "White tilted-striped O" was a feature target when distractor letters were black (Version 1) and was a conjunction target when distractors were white (Version 2). "Black tilted-striped X" was a feature target when distractor letters were white (Version 2), and a conjunction target when distractors were black (Version 1). Thus, distractors were kept constant within each version for the two conditions, and targets were identical across the two versions. The targets occurred on half of the trials, with a trial defined as six consecutive letters presented in 1 s. All trials in an epoch were presented as a continuous sequence of letters, but targets were always separated by at least two intervening distractor letters. No two consecutive letters had the same identity. Targets occurred in a pseudorandom order within an epoch, with the constraint that not more than three consecutive trials contained a target.

Each version consisted of 32 s epochs of the feature task alternating with the conjunction task (3 epochs of each). Each epoch was preceded by a 16 s fixation-only display and a 4 s instruction display ("BLACK TILTED-STRIPED X" or "WHITE TILTED-STRIPED O") that indicated the target letter for the subsequent epoch. A run lasted 5.5 min, including a final 18 s period of fixation.

Procedure

Subjects monitored the sequences and pressed a button when they detected the target letter, while maintaining fixation on the central red dot. All subjects were run twice on both versions (ordered 1–2–2–1 for three subjects and 2–1–1–2 for four subjects).

fMRI Comparison

fMRI comparison tested which areas were more active during the conjunction task than during the feature task.

General Procedure for Experiment 1

Subjects were scanned on each experiment four times within the same session (except for one subject who performed E1a only twice because of time constraints). Three subjects completed an additional two scans for each experiment in that session (for a total of six scans per experiment) in order to allow an independent reliability test of activations in the AOMT regions (see below). For E1c, the additional two scans used both counterbalancing versions. All runs of each experiment were done with the same stimulus sequences. Subjects practiced at least 1 epoch of each condition before the first run of each experiment.

Experiment 2: Difficult Language Task versus Visual Control Task

Stimuli and Experimental Design

Single lower case words (four to eight letters long) were presented at fixation (marked by a red dot) in black on a white background. The words subtended between 7.5° and 15° horizontally and up to 4.5° vertically. Each word was presented for 200 ms, followed by a 2.3 s display of the fixation dot.

There were 2 epochs of each task, ordered language(L)-visual(V)-visual(V)-language(L) for two subjects and V-L-L-V for the other two. Epochs lasted 60 s each (24 trials) and were separated by 16 s periods of fixation. Each epoch was preceded by a 4 s instruction display ("VERB + NOUN" for language and "LETTER SIZE" for the visual task).

The 24 words occurring in 1 epoch consisted of equal numbers of words (6) requiring a positive (e.g., "drink") or a negative (e.g., "bring") response in both tasks—positive in the language but not in the visual task (e.g., "search"), or positive in the visual but not in the language task (e.g., "tent"). Half of the negative trials in the language task consisted of words that can be used as verbs only, and half that can be used as nouns only.

Within a single scan, two sets of 24 words were used. One set was used during the first 2 epochs, and the other in the last 2. This equated retinal stimulation and stimulus novelty across tasks within a scan (e.g., for subjects who did V-L-L-V, the first V epoch used novel words, but in the first L epoch they were no longer novel, whereas the second L epoch used novel words, and in the second V epoch they were not novel). Across scans, stimulus novelty was counterbalanced across subjects. Different sets of words were used for each scan, with a separate set used for practice.

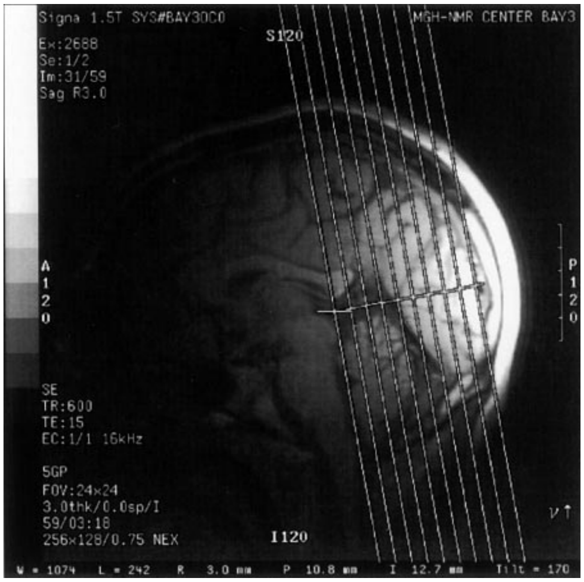

Figure 7. Typical Slice Orientation Shown on a Midsaggital Image

Procedure

Subjects were asked to maintain fixation throughout a scan. They pressed the right button for positive responses and the left button for negative responses. Each run lasted 5.5 min, including a 10 s fixation-only period at the end. Before the first run, subjects practiced at least 1 epoch of each condition. Each of the four subjects was run on this experiment four times; two subjects performed it in the same session as for E1a–E1c, and two subjects in a separate session in which they were also run on E1c for the second time.

fMRI Comparison

fMRI comparison tested which regions were more active during the difficult language task than during the easier visual task and vice versa.

Eye Movements

Eye movements were not monitored inside the scanner. However, six subjects were experienced psychophysical observers highly practiced at maintaining fixation, and for two subjects eye movements were monitored outside the scanner on several epochs of E1a (peripheral shifting). No eye movements larger than 2° were detected. Furthermore, in E1c, all stimuli were presented at fixation, such that no eye movements would be expected.

Stimulus Presentation

The entire stimulus sequence for each experiment was recorded on VHS tapes and backprojected on a ground glass screen. The subject, lying on his/her back, viewed the screen through a tilted mirror placed above his/her forehead.

Data Acquisition

Anatomical and functional scans were performed with a 1.5 T GE Signa MRI scanner (Milwaukee, WI) equipped with EPI (Instascan; ANMR Systems, Wilmington, MA), using a bilateral quadrature receive-only coil (made by Patrick Ledden) at Massachusetts General Hospital's Nuclear Magnetic Resonance Center (Charlestown, MA). Functional images were obtained with an asymmetric spin echo sequence ($TR = 2$, $TE = 70$ ms, flip angle $= 90°$, $180°$ offset $= 25$ ms). The ten 7 mm thick near-coronal slices covered the posterior half of the brain (Figure 7). Voxel size was $7 \times 3.1 \times 3.1$ mm. Head motion was minimized with a bite bar. Of the nine sessions (five subjects with one session, two subjects with two sessions), two sessions were corrected for head motion with Automatic Image Registration software (Jiang et al., 1995). Each session lasted 3 hr.

Data Analysis

Data were analyzed in two ways: for each subject separately and for the whole group of subjects. The group analyses were identical to the individual subjects' analyses described below, except that the functional data were averaged across subjects, separately for each experiment.

Each subject's data from the four runs of each experiment (the first four runs for subjects with six runs per experiment) were averaged and then analyzed by a KS test after smoothing with a Hanning kernel over a 3×3 voxel area to produce an approximate spatial resolution of 6 mm. The KS test was run on each voxel after incorporating a 6 s estimated hemodynamic delay, testing which voxels were more active during the difficult condition than during the easier condition of each experiment separately (peripheral shifting versus central maintenance in E1a, peripheral object versus central color matching in E1b, conjunction versus feature task in E1c, and language versus visual task in E2). Images obtained during instruction and fixation periods were excluded from analyses. Significance threshold was set at $p < 0.001$ (uncorrected) for each experiment separately (but see AOMT threshold and reliability test below); for group analyses, the threshold was Bonferroni corrected for the total number of examined voxels.

All individual subjects' analyses were performed on the original native space data (i.e., in the plane from which they were acquired), except that the coordinates and size of the AOMT regions were obtained in normalized space (Talairach and Tournoux, 1988). Group analyses were performed after normalization. Anatomical sulcal and gyral landmarks were identified on the basis of Duvernoy (1991) and Talairach and Tournoux (1988).

AOMT Analysis

For the analysis of activation overlap across E1a–E1c, all active voxels that crossed the significance threshold of $p < 0.001$ (uncorrected) independently for each of the three comparisons were superimposed on each other and on high-resolution anatomical images. Regions of overlap were determined by applying a logical-AND operation on all voxels that crossed the threshold independently for each comparison (i.e., all AOMT voxels were above threshold in each of the three comparisons). The activations of each comparison alone as well as the overlap with activations from the other two comparisons were coded in different colors, as shown in the color wheel of Figure 4 (e.g., to determine all regions showing greater activity in peripheral shifting than central maintenance [E1a], one has to consider all regions marked in blue, purple, green, and white). Because the significance threshold of $p < 0.001$ was applied separately for each experiment, the AOMT threshold was $p < 10^{-9}$, that is, the joint probability of the thresholds for the three experiments.

To obtain normalized coordinates of the AOMT regions, each subject's scans were transformed into a standard space (Talairach and Tournoux, 1988). The statistical analyses and the logical-AND operation were carried out as described above. Voxels showing AOMT were then classified into separate AOMT regions on the basis of contiguity, with contiguity defined as any two or more voxels adjoining each other by at least one vertex, within a slice or across contiguous slices. Coordinates of each AOMT region for each subject were then obtained by computing the center of gravity of all voxels belonging to that region, with mean coordinates of each AOMT calculated by averaging across the corresponding coordinates of all subjects. The size of AOMT regions was calculated based on the number of contiguous voxels in each region and averaging across subjects.

Reliability Test of AOMT Activations

The KS test has been criticized on the grounds that it can find a significant difference when only the variance and not the means differ across conditions and that it can produce a high rate of false positives at liberal thresholds (Aguirre et al., 1998). While it is unlikely that the AOMTs are due to false positives (given the conservative AOMT threshold of $p < 10^{-9}$), we conducted a reliability test of AOMT activations using a new data set and different statistics (ANOVA). The ANOVA allowed us to verify that the differences we find with the KS test in the AOMT regions do reflect significant differences in means between the difficult and easy tasks of each experiment. Note that because the data set used for this ANOVA was separate from the AOMT-defining data set (see below), this analysis requires no correction for multiple spatial hypotheses.

The new data set came from the three subjects who completed six runs for each of E1a–E1c within one session. The first four runs of each experiment were used to define the AOMT regions as described above; the last two runs of each experiment provided the separate (previously unused) data set for the reliability analysis. Raw (unsmoothed) time course data were extracted from all AOMT voxels within each AOMT region (predefined with the first four runs) separately for each of the last two runs of each experiment. PSC was then computed for the easy and difficult tasks of each run with the standard formula: (MR signal − Baseline)/Baseline * 100%, in which baseline is usually estimated from the average MR signal during fixation/rest periods. Because only E1c had a good fixation baseline (i.e., several fixation periods), the baselines for E1a and E1b used poorer estimates (a short period of fixation at the end of E1a and instruction epochs for E1b). This procedure is not optimal, as it introduces noise (increasing variance) in PSC estimations for E1a and decreases PSC estimations for E1b (since the instruction epochs contained a visual stimulus). However, this is not problematic with respect to the critical statistical comparison, which involves the difference in PSC between the difficult and easy conditions in each experiment, and therefore this procedure produces an unbiased estimate of the difference.

The PSC for each type of task was then averaged across all time points and all epochs of the same kind within a run (after incorporating the hemodynamic delay) to produce two PSC data points per run (one for each task). This procedure resulted in two observations for each task in each of the three experiments per subject per AOMT.

The ANOVA, carried out separately for each AOMT, was run only on the four AOMT regions that were found most consistently across all seven subjects (i.e., IPTO and AIPS in both hemispheres). Because we had only three subjects with the additional data set, and each subject had only two runs per experiment (as opposed to four runs in the KS tests), we did not have enough power to carry out the tests with subjects as the random variable; instead, we treated run as the random variable. Thus, for each AOMT, the factors were experiment (E1a, E1b, E1c), task difficulty (easy, difficult), and subject (each with two runs); task difficulty was treated as a repeated-measures variable (as data for both levels of this factor were collected within the same run). Note that by including subject as a factor and treating run as the random variable, we can generalize the results only to the subjects included in the ANOVA (but recall that this analysis is conducted on a new data set that is separate from the AOMT-defining data set). The comparisons of interest are the simple effects of task difficulty at each level of experiment for the four AOMT areas. Because of the different baselines across experiments, the main effect of experiment is not interpretable and is not discussed further.

Interaction Analysis of Visual versus Nonvisual Effort by Task Difficulty

To further verify that AOMT regions show preferential activity during visually demanding tasks, we tested for the interaction of task difficulty by experiment type (E1c and E2 only; see below) using ANOVA. Time course data were extracted from all AOMT voxels in each AOMT region separately for each of the four runs of E1c and E2. PSC was then computed for each task within each run by treating the average response during fixation periods of that run as baseline (both experiments had interleaved fixation periods). The PSC for each task was then averaged across all time points and all epochs of the same kind across the four runs of each experiment to produce two PSC data points per experiment (one for each task) per subject. In the ANOVA, which was carried out separately for each AOMT, the factors were task difficulty (easy, difficult) and experiment (E1c, E2), with both factors treated as repeated measures. Note that unlike in the reliability test, subject is the random factor in this analysis; because here each data point was based on four runs of each experiment (as opposed to only two runs in the reliability test), it produced a better estimate of the mean PSC for each task and each subject, compensating for the small number of subjects. Planned comparisons further tested whether the difficult task produced a significantly greater response than the easy task in each experiment and area. Note that N was not equal for each ANOVA, as of the four subjects who were run on E2, left IPTO was observed in four subjects, and right IPTO, left AIPS, and right AIPS were observed in three subjects.

Two subjects completed all four experiments within one fMRI session, while the other two were run on E1a–E1c in one session and on E1c and E2 in a second session on a separate day. For the former two subjects, raw (unsmoothed) time course data were extracted from AOMT regions defined within the same session. For the latter two subjects, the locations of AOMT regions defined in the first session were estimated for the second session based on the gyral/sulcal patterns of the high-resolution T1-weighted scans of both sessions. Raw time course data were then extracted from these estimated AOMT regions. The data from these latter “two-session subjects” therefore strengthen this analysis, since the AOMT-defining data set (first session) and the interaction data set (second session run on a separate day) are completely independent.

The interaction analysis included only E1c for two reasons. First, E1c included multiple periods of fixation as baseline, and this made it most comparable to E2, which had a similar baseline. Second, the two-session subjects completed only E1c and E2 in the second session.

Behavioral Data Analysis

Subjects’ responses were recorded through a response box connected to a Macintosh IIvx computer. The computer recorded the time of each button press from the beginning of the recording. Because of some variability in the synchronization of stimulus tapes and the response recording program, absolute RTs are estimates, but the differences in RTs (between the difficult and easy tasks) within an experiment are exact. A response was treated as correct if it occurred within a second after target onset. Because the language task of E2 was much more difficult than any of the tasks in E1, correct responses were defined as those that occurred within 2.5 s of stimulus onset (duration of one trial), as opposed to 1 s in E1. If we had used the shorter period to accept responses as correct in E2, most responses in the language task would have been rejected. Thus, what we expect here is a large difference in RTs between the visual and language tasks, and not necessarily in accuracy. A measure of sensitivity (d′) was computed by subtracting the Z score for false alarms from the Z score for hits (Green and Swets, 1966). RTs were calculated by using only correct responses.

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