

Although most previous work focused on covert spatial orienting (e.g., Posner & Cohen, 1984) or on the selection of target stimuli among competing distracters (e.g., Treisman & Gelade, 1980), much less is known about possible interactions between spatial and nonspatial attention in conditions requiring simultaneous monitoring of several sensory streams (i.e., divided attention). As far as the spatial aspects of divided attention are concerned, two main hypotheses have been put forward (Kraft et al., 2005; McMains & Somers, 2004; Müller, Malinowski, Gruber, & Hillyard, 2003; Castiello & Umiltà, 1992). According to the “unitary view,” spatial attention acts as a single, not divisible, spotlight with all stimuli within the spotlight undergoing enhanced processing (Eriksen & St. James, 1986; Eriksen & Yeh, 1985; Posner & Cohen, 1984; Posner, 1980). The attentional spotlight may be adjusted in size to encompass noncontiguous locations, albeit with a tradeoff between size and processing efficacy (Müller, Malinowski, et al., 2003; Eriksen & St. James, 1986; but see also LaBerge & Brown, 1989; Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Downing & Pinker, 1985; Hughes & Zimba, 1985), confuting the very existence of any attentional spotlight. Conversely, the “multiple spotlights view” asserts that attentional spotlights can be divided to simultaneously select distinct spatial locations, ignoring intervening regions (McMains & Somers, 2004, 2005; Awh & Pashler, 2000).

Irrespective of the specific mechanism, monitoring of multiple streams at different locations consistently results in a decrement of processing efficacy, as documented both behaviorally and neurophysiologically (McMains & Somers, 2004; Müller, Malinowski, et al., 2003; Müller, Bartelt, Donner, Villringer, & Brandt, 2003; Castiello & Umiltà, 1990; Eriksen & St. James, 1986; Shaw & Shaw, 1977). The nature of such costs is still not fully understood. As pointed out by McMains and Somers (2004), attentional effects in the visual cortex during divided attention may be linked to top-down control signals from higher-level areas (e.g., frontal eye fields, or the parietal cortex; see also Tong, 2004). Capacity limitations at this higher/later processing level may contribute to the behavioral costs observed in situations of divided attention (see also Nebel et al., 2005; Driver, 2001).

Recently, Nebel et al. (2005) investigated the role of high-level processing costs during divided spatial attention by manipulating task difficulty. The authors compared brain activity during divided attention and focused attention (easy task and difficult task). The results showed that the divided-attention task activated prefrontal and parietal areas, but only when compared with the “easy” focused-attention task. Accordingly, the authors concluded that fronto-parietal activation associated with divided spatial attention may mainly reflect greater demands on executive control (rather than any spatially specific process). However, it should be noted that in order to increase the difficulty of the focused-attention task, the authors introduced a greater working

memory load component (i.e., $2 - n$ back vs. $1 - n$ back, for focused and divided task, respectively). Because fronto-parietal regions are also involved in working memory (e.g., D’Esposito, 2001; Courtney, Ungerleider, Keil, & Haxby, 1997) and the working memory component was not assessed in the divided condition (i.e., spatial and nonspatial components were not manipulated in a full factorial manner), this study could not test for the specific contribution of each factor or for the interaction between these two cognitive processes.

One previous study that experimentally manipulated location-based (spatial) and feature-based (nonspatial) selection is the PET study by Vanderberghe et al. (1997). This study used attention to one or two features (position/orientation of oriented gratings) belonging either to the same object/grating or to two different objects in the opposite hemifields. When subjects attended different features in opposite hemifields, the left lateral frontal cortex and the right ventral occipital cortex activated at an intermediate level compared with focused-left and focused-right attention. The authors interpreted the frontal pattern as representing the amount of attention to the ipsilateral hemifield, and the occipital effect as the contralateral attentional modulation of incoming sensory input. But again, also this study did not manipulate “number of locations” and “number of features” in a fully factorial design, because the experiment did not include an “attend the same feature in opposite hemifields” condition. Hence, the analysis was unable to assess precisely the relative contribution of dividing spatial attention versus monitoring multiple features, and—most critically—could not test for possible interactions between these two selective attention processes.

Here, we used fMRI to address the issue of capacity limitation and processing costs during attention to multiple streams of visual information. We asked to what extent observed costs reflect processes specifically associated with divided spatial attention, or more general interference effects due to simultaneous monitoring of multiple streams (dual-task performance). With this aim in mind, we manipulated orthogonally the number of task-relevant positions (one or two: left/right hemifield, or both) and the number of task-relevant stimulus categories (one or two: red shapes/green shapes, or both). Our paradigm differs from previous studies in at least two aspects: First, the most recent fMRI studies on divided spatial attention restricted their investigation to the occipital cortex, leaving open the issue of the role of higher-level regions in the control of divided spatial attention (McMains & Somers, 2004, 2005; Müller, Malinowski, et al., 2003; see also Tong, 2004). The second and more important point relates to a methodological confound inherent in most paradigms previously employed to study divided spatial attention (i.e., McMains & Somers, 2005; Castiello & Umiltà, 1990; Eriksen & St. James, 1986). These typically contrasted conditions when subjects attended to a single stream of stimuli in one hemifield

with conditions when subjects attended two streams located at different positions in the visual field. This type of comparison cannot determine whether any effect (behavioral cost or change of brain activity) associated with “divided-attention condition” truly reflects the process of dividing (or zooming out) spatial attention, or whether additional processes are required to monitor several information streams simultaneously (dual-task interference). Using whole-brain fMRI and a factorial manipulation of location-based and category-based divided attention, we investigated the neural substrate for multiple stream selection, dissociating spatial and non-spatial attentional processes.

METHODS

Participants

Fourteen right-handed healthy volunteers (7 men, mean age = 25 years, range = 21–30 years) took part in the

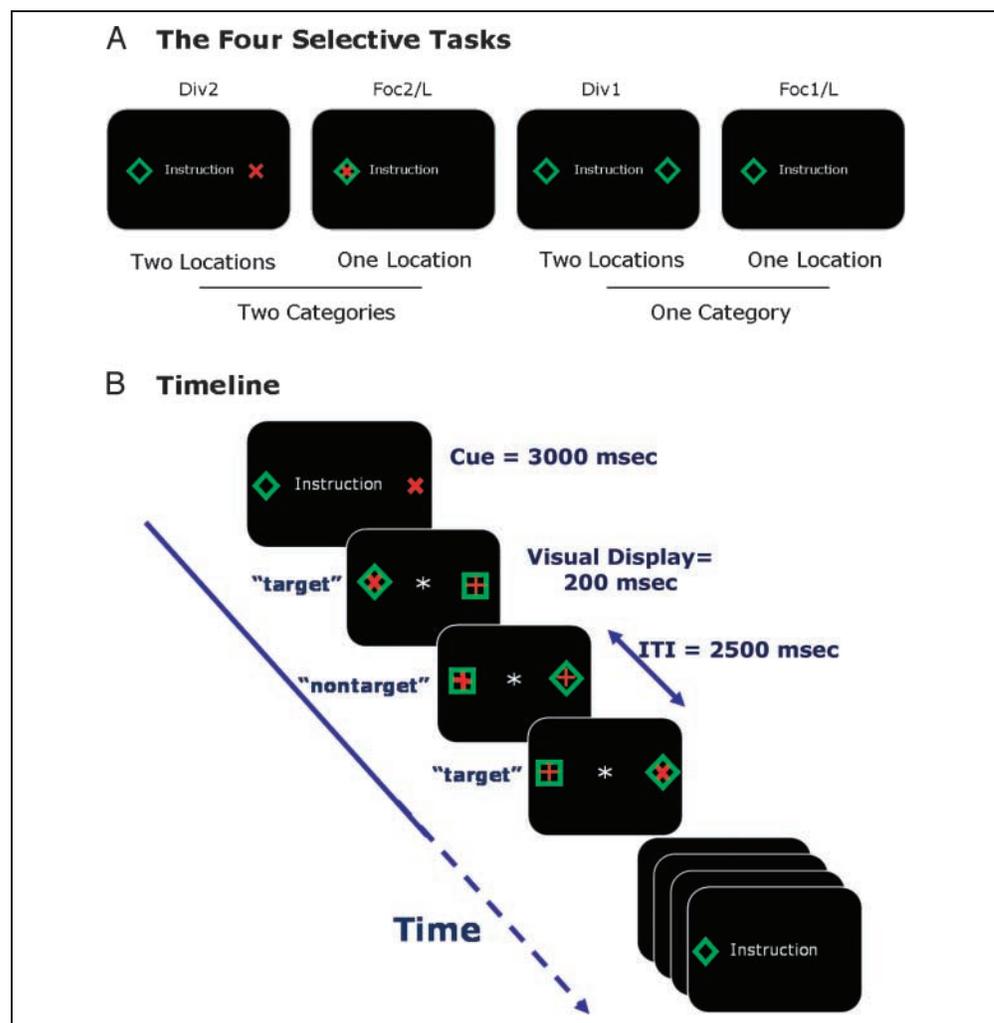
experiment. After receiving an explanation of the procedures, participants gave written informed consent. The study was approved by the independent ethics committee of the Santa Lucia Foundation (Scientific Institute for Research Hospitalization and Health Care).

Paradigm

In all conditions, participants were presented with two overlapping visual stimuli in each hemifield (red shapes and green shapes on each side; see Figure 1B). According to instructions, subjects performed one of four attention tasks in blocks of 30 sec. The four tasks were (see also Figure 1A):

- (A) Attend to one stimulus category in one hemifield (*Foc1/L* or *Foc1/R*, for focused attention to the left or the right hemifield); e.g., “attend only green shapes on the left side.”

Figure 1. Schematic depiction of the behavioral paradigm. (A) The four selective attention tasks. Subjects performed one of four attention tasks, which varied according to the number of locations and number of categories that required monitoring. The four tasks were: *Div2*: Attend to one stimulus category in one hemifield, and the other category in the opposite hemifield (in the example: “attend green shapes on the left side and red shapes on the right side”); *Foc2/L* or *Foc2/R*: Attend to both stimulus categories in the same hemifield (in the example, *Foc2/L*: “attend green shapes and red shapes on the left side”); *Div1*: Attend to one single stimulus category, but monitor both hemifields at the same time (e.g., “attend green shapes both on the left and on the right side”); *Foc1/L* or *Foc1/R*: Attend to one single stimulus category in one hemifield (e.g., *Foc1/L*: “attend only green shapes on the left side”). (B) Timeline of a block of trials. Each 10-trial block began with a cue signaling the task to come. This displayed the relevant target stimuli, given by a combination of position, color/shape, and orientation (see A and the first display in B). On each trial, the visual stimulation was always bilateral with two independent visual streams on each side (see displays 2 to 4 in B). Depending on the selective attention condition, subjects monitored one or two visual streams, ignoring all task-irrelevant stimuli.



- (B) Attend to both stimulus categories in the same hemifield (*Foc2/L* or *Foc2/R*); e.g., “attend green shapes and red shapes on the left side.”
- (C) Attend to one single stimulus category, but monitor both hemifields at the same time (*Div1*); e.g., “attend green shapes both on the left and on the right side.”
- (D) Attend to one stimulus category in one hemifield, and the other category in the opposite hemifield (*Div2*); e.g., “attend green shapes on the left and red shapes on the right side.”

Therefore, the basic design was 2×2 factorial, with the number of attended positions (one or two) and number of attended categories (one or two types of shape/category) as independent factors. The two main effects highlight brain region associated with dividing spatial attention (irrespective of category selection) and monitoring multiple stimulus categories (irrespective of spatial location). Critically, the interaction term reveals whether the two processes operate independently, or engage a common neural substrate for both types of selective attention processes.

In addition, our analyses permit testing of hemifield-specific effects by considering only the four focused-attention conditions (*Foc1/L*, *Foc1/R*, *Foc2/L*, or *Foc2/R*). These also constitute a 2×2 design, with the number of categories (one or two) and the attended hemifield (left or right) as independent factors. Thus, we asked whether the number of categories needing monitoring during focused attention influences spatially specific attentional modulation in the contralateral visual cortex (e.g., see Martinez et al., 1999; Heinze et al., 1994).

Stimuli and Task

Participants lay in the scanner in a dimly lit environment. All visual stimuli were projected onto a translucent screen at the back of the MR tunnel and were made visible through a mirror mounted on the interior of the head coil. On each trial, four shapes were presented simultaneously on the screen (shape width = approx 2° , centered at 7° visual angle from central fixation): two on the left and two on the right of the central fixation point. There was a red and a green shape on each side, one above the other (see Figure 1B). Each shape could be presented in one of two orientations: for example, a red “+” or a red “x,” a green square or green rhombus. On each trial, the orientation of the four shapes changed independently and unpredictably. This resulted in four independent streams of visual stimuli, changing orientation on consecutive trials. According to instructions, subjects monitored one or two of these streams (see “Paradigm” above) and responded with a right-hand keypress when a target shape was presented in a task-relevant stream (see also Supplementary Material for a short video showing an example of the stimuli and the four attentional tasks).

At the beginning of each 30-sec block, an instruction display informed subjects about relevant location/s and

stimulus category/s. The instruction display (duration = 3000 msec) consisted of a text string “Instruction,” plus one or two shapes indicating the relevant position and stimulus category (see Figure 1A). In practice, the display showed target stimuli (defined by position, shape, and orientation) that subjects should detect and respond to. To minimize task-switching requirements, a single pair of shapes served as targets throughout an experiment in each subject (red “+” and green rhombus; or red “+” and green square; or red “x” and green rhombus; or red “x” and green square, counterbalanced across subjects). All stimuli in task-irrelevant streams had to be ignored, including shapes of a currently relevant category and orientation presented in an unattended position (e.g., a green rhombus presented in the right hemifield, when subjects were monitoring green shapes on the left and red shapes on the right; see second trial in Figure 1B).

Each block comprised 10 trials. In each trial, the visual display was presented for 200 msec, followed by a fixed interstimulus interval of 2500 msec. We used a brief stimulus presentation time in order to discourage any overt eye movement to fixate the target stimuli. Two constraints were implemented when preparing stimulus sequences. First, when subjects were asked to attend to multiple streams (conditions *Foc2*, *Div1*, and *Div2*), the display never included two target stimuli in the same trial (e.g., when a subject monitored green shapes on the left and red shapes on the right, the display never included a green rhombus on the left and a red “x” on the right). Second, the frequency of target shapes in attended streams was adjusted so that, irrespective of condition (single vs. multiple streams), there were always five targets in each 10-trial block. Subjects were asked to maintain gaze on the central fixation point while covertly monitoring the sensory stream/s.

All participants underwent four fMRI scanning runs (lasting approx. 6 min each). Every fMRI run comprised 12 blocks, thus repeating each attention task twice (*Foc1/L*, *Foc1/R*, *Foc2/L*, *Foc2/R*, *Div1*, *Div2*). Over an entire experiment, each subject was presented with 480 trials (80 repetitions for each condition).

Image Acquisition

Functional images were acquired with an Allegra scanner operating at 3 T (Siemens, Erlangen, Germany). BOLD contrast was obtained using echo-planar T2*-weighted imaging (EPI). The acquisition of 32 transverse slices (2.5 mm thick, 50% distance factor), with an effective repetition time of 2.08 sec, provided coverage of the whole cerebral cortex. The in-plane resolution was 3×3 mm.

Data Analysis

The fMRI data were processed with SPM2 (www.fil.ion.ucl.ac.uk). The first four image volumes of each run were

discarded to allow for stabilization of longitudinal magnetization. For each participant, the remaining 720 volumes were realigned with the first volume and the acquisition timing was corrected using the middle slice as reference (Henson, Büchel, Josephs, & Friston, 1999). To allow intersubject analyses, all images were normalized to the Montreal Neurological Institute standard space (Collins, Neelin, Peters, & Evans, 1994), using the mean of all 720 functional images. All images were smoothed using an isotropic Gaussian kernel (full width at half maximum = 10 mm).

Statistical inference was based on a random effects approach (Penny & Holmes, 2003). This comprised two steps. First, for each subject, data were best-fitted (least-square fit) at every voxel using a linear combination of the effects of interest. These were the timing of the stimulus-display presentation for each of the six attention conditions (Foc1/L, Foc1/R, Foc2/L, Foc2/R, Div1, Div2). In addition, the instruction display and all error trials were modeled as separate event types that were not considered further in group analyses. All event types were convolved with the SPM2 standard hemodynamic response function. Linear compounds (contrasts) were used to determine the effects of the six critical attention conditions, averaged across all four fMRI runs. This led to the creation of six contrast images per subject. The contrast images then underwent a second step (group) analysis that comprised a within-subject ANOVA, modeling the six attention conditions, plus mean effects per subject. Finally, linear compounds were used to compare these effects using between-subject variance (rather than between-scan variance). Correction for nonsphericity (Friston et al., 2002) was used to account for possible differences in error variance across conditions and any nonindependent error terms from repeated measures.

Our main analysis aimed to highlight the effect of dividing attention between separate spatial positions and of monitoring two stimulus categories during attention to multiple visual streams. To reveal regions involved in divided spatial attention, we compared all divided-attention conditions versus all focused-attention conditions ($[Div1 + Div2] > [Foc1 + Foc2]$, averaging for focused attention to the left or right hemifield). To reveal activity associated with monitoring multiple stimulus categories at the same time, we compared $[Div2 + Foc2] > [Div1 + Foc1]$, again averaging leftward and rightward attention in the “focused-attention” conditions. For these comparisons, the SPM threshold was set to p -corrected = .05 (minimum cluster size = 5), considering the whole brain as a volume of interest.

As these analyses showed largely overlapping activations for these two attentional functions (see Figure 2A), we carried out additional statistical tests to confirm that the same areas were involved in location-based and category-based divided attention, and that an increase in task difficulty could not explain the results. Overlapping activation clusters may result from interdigitated

populations of neurons with different functions, and/or the limited spatial resolution of fMRI. Critically, however, if two populations operate in an independent manner whenever a task engages two functions, the level of activity should simply add up to the sum of activities associated with each process separately (Laurienti, Perrault, Stanford, Wallace, & Stein, 2005; or possibly to a lesser value accounted for by nonlinearities of the BOLD signal; Friston, Mechelli, Turner, & Price, 2000). On the other hand, if the *same* population is engaged by both functions, activity may add or increase supra-additively (e.g., see Beauchamp, 2005; Calvert, 2001 for an example concerning brain regions responding to stimulation by two sensory modalities). It should be noted that this statistical criterion (i.e., supra-additive responses, yielding to positive interactions within a factorial design) is just an indirect evidence of a common underlying neuronal response, but it is considered one of the most conservative approaches (Beauchamp, 2005) to tackle this inevitable limitation of noninvasive hemodynamic neuroimaging techniques.

Thus, we tested for an interaction between location-based and category-based attention, expecting maximal activity when subjects divided attention between left and right hemifields while monitoring both stimulus categories ($[Div2 - Foc2] > [Div1 - Foc1]$). For this comparison, p values were corrected, taking into account those voxels showing both an effect of divided spatial attention and of multiple category monitoring as a limited volume of interest (Worsley et al., 1996). Further, to address the possibility that the observed pattern of activation related to a mere increase in task difficulty, we performed an additional within-subject ANOVA, now including the mean reaction times (RTs) for each subject and condition as a covariate of no interest (cf. Table 2B).

Finally, we asked whether category-based attention affected any spatially specific attentional modulation in the contralateral visual cortex. We compared focused attention to the left versus right hemifield (and vice versa), while subjects monitored one or two visual streams at the attended location. We tested for the main effect of attended side ($[Foc1/R + Foc2/R] > [Foc1/L + Foc2/L]$ for rightward attention; or $[Foc1/L + Foc2/L] > [Foc1/R + Foc2/R]$ for leftward attention) and Side by Number of streams interactions at a threshold of p -corrected = .05 (minimum cluster size = 5), considering the whole brain as volume of interest.

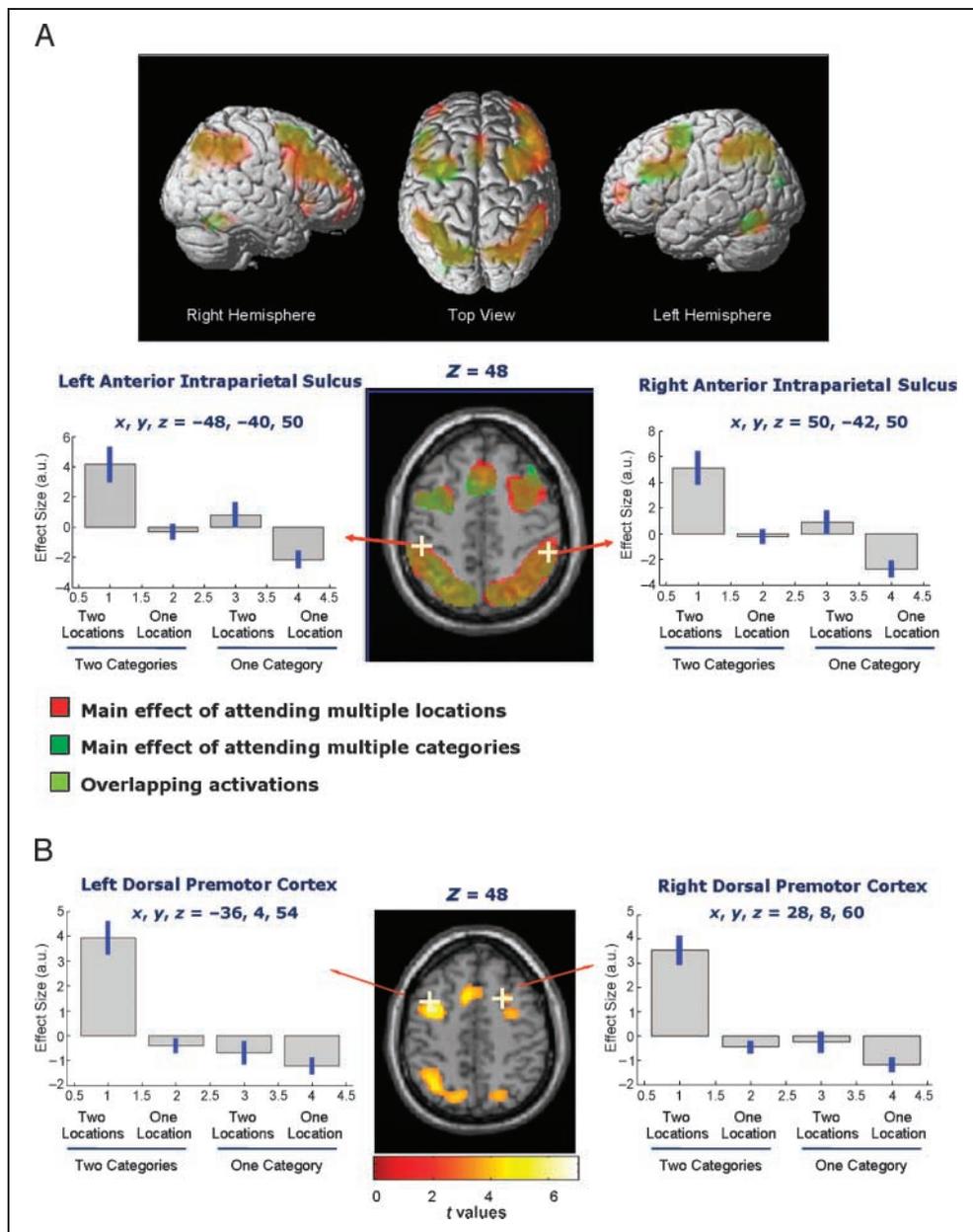
RESULTS

Behavioral Data

Mean RTs (*SEM*) for the six experimental conditions were: Foc1L: 580 (21); Foc1R: 584 (20); Foc2L: 666 (19); Foc2R: 667 (18); Div1: 635 (15); and Div2: 727 (16). A two-way ANOVA, taking into account the number of attended locations (one vs. two; averaging across leftward

Figure 2. (A) Main effect of divided spatial and nonspatial attention. The top shows surface-rendered projections of the activations associated to divided spatial attention (main effect of attention to two vs. one hemifield, in red) and monitoring of multiple categories (main effect of attention to two vs. one categories, in green) overlaid on the MNI brain template. The bottom shows a horizontal section and signal plots for the fronto-parietal regions that showed increased activation during divided spatial attention and monitoring of multiple categories. These two orthogonal main effects showed largely overlapping activation (in brown). The signal plots show the pattern of activation for the anterior intraparietal sulcus (cf. the white cross on the anatomical section), with activity increasing both for divided spatial attention (Bars 1 and 3 vs. Bars 2 and 4) and for monitoring multiple categories (Bars 1 and 2 vs. Bars 3 & 4).

(B) Interaction effect. Activity in the fronto-parietal cortex showed a significant interaction between spatial and nonspatially divided attention, suggesting an underlying common neural substrate for these two functions. The signal plots in the frontal regions (possibly corresponding to the frontal eye fields) demonstrate that activity in the Div2 condition (attending different categories in opposite hemifields; see Bar 1 in each plot) did not merely reflect the sum of dividing attention to two locations and two stimulus categories. The level of activation for the four conditions is mean-adjusted (i.e., the four values sum to zero) and is expressed in arbitrary units (a.u., $\pm 90\%$ confidence interval). SPM display threshold: p -uncorr = .001.



and rightward attention in the “focused-attention” conditions) and the number of attended categories (one vs. two), revealed a main effect of “locations” [$F(1, 13) = 46.7, p < .001$] and a main effect of “categories” [$F(1, 13) = 77.18, p < .001$]. Participants were slower when attending to two stimulus categories compared to one category (697 vs. 608 msec, respectively), as well as slower when selecting two locations compared with one location (681 vs. 624 msec, respectively). However, the interaction term was not significant ($F < 1$), indicating that the behavioral cost of monitoring two categories at different locations (Div2 condition) could be fully explained as the

sum of dividing attention in space (Div1 – Foc1), plus the cost of having to judge two different categories (Foc2 – Foc1) simultaneously.

A second analysis controlled for possible biases associated with directing spatial attention toward the left or the right visual field. A new two-way ANOVA used “attended side” (left vs. right) and “number of attended categories” (one or two) as within-subject factors. As expected, this showed again a main effect of “number of attended categories” [$F(1, 13) = 71.41, p < .001$], but critically no effect of side or interaction between categories and side ($F < 1$, for main effect of attended side

and the interaction term). As participants made very few errors (less than 5%), no data analysis was performed on error rates.

Dividing Attention in Space and Category Dimensions

Our analyses first compared attention to opposite hemifields versus attention to one hemifield (i.e., divided location-based attention); and monitoring of two categories versus a single category (i.e., divided category-based attention). Notably, these two main effects revealed largely overlapping activations in the fronto-parietal cortex bilaterally (see Figure 2A and Table 1).

In the frontal lobe, one activation cluster extended from the lateral surface of the hemisphere to the depth of the precentral sulcus, likely to also include the frontal eye fields. The activation extended also ventrally to the ventral premotor areas and rostrally to the prefrontal cortex (see 3-D rendering in Figure 2A). Another cluster was located on the medial surface of the brain, encompassing the anterior supplementary motor area (pre-SMA; see coronal section in Figure 2A). In the parietal lobe, the entirety of the intraparietal sulcus showed overlap of the two main effects of divided attention (location-based and category-based). The insula and the inferior occipital

gyrus showed an analogous effect, with activation both for divided spatial and nonspatial attention bilaterally (see also Table 1).

The pattern of activity for the anterior intraparietal sulcus (aIPS) is also plotted in Figure 2A. The signal plots show greater activity when subjects attended two positions compared to one irrespective of the number of attended categories (compare Bar 1 vs. Bar 2, and Bar 3 vs. Bar 4 in each plot of Figure 2A). In addition, the very same region showed a main effect of “number of attended categories” with greater activation during monitoring of two categories irrespective of focused or divided spatial attention (compare Bar 1 vs. 3, and Bar 2 vs. 4). As a consequence of the combination of these two main effects, maximal activity was observed when subjects monitored two different categories in opposite hemifields (Div2 condition; see Bar 1 in the signal plots of Figure 2A). Also note that the estimated activity for the experimental conditions (Bars 1–4 in each signal plot) is mean adjusted to zero, thus only relative differences (but not the absolute values) are meaningful. In fact, it is quite likely that also the focused-attention conditions (all requiring selective processing, covert attention to one hemifield, target discrimination, etc.) would activate these fronto-parietal regions, if these were compared to a rest baseline. However, such low-level

Table 1. Anatomical Location and Statistical Scores for the Regions that Activated during Selection of Multiple Locations or Multiple Categories

Anatomical Region	A. Main Effect of Monitoring Two Locations vs. One Location				B. Main Effect of Monitoring Two Categories vs. One Category			
	Hem	Coordinates	p-corr	Z Value	Hem	Coordinates	p-corr	Z Value
Dorsal premotor cortex	R	28 12 56	<.001	7.0	R	28 8 60	<.001	6.5
Dorsal premotor cortex	L	-32 6 56	<.001	6.8	L	-34 4 56	<.001	7.1
Ventral premotor cortex	R	52 14 32	<.001	6.8	R	48 8 28	.031	4.7
Ventral premotor cortex	L	-46 2 34	<.001	6.4	L	-44 2 30	<.001	6.6
Prefrontal cortex	R	48 32 22	<.001	6.8	R	44 30 22	<.001	5.9
Prefrontal cortex	L	-48 26 30	<.001	6.1	L	-50 32 28	<.001	5.8
Anterior supplementary area	R	4 22 44	<.001	6.3	L	-6 14 48	<.001	6.2
Insula	R	34 24 -4	<.001	6.5	R	34 24 -2	.008	5.0
Insula	L	-30 24 -4	.02	4.8	L	-30 22 -2	.149	4.2
Posterior intraparietal sulcus	R	30 -68 44	<.001	7.2	R	30 -68 44	<.001	6.0
Posterior intraparietal sulcus	L	-28 -64 48	<.001	6.8	L	-30 -62 48	<.001	6.7
Anterior intraparietal sulcus	R	44 -44 44	<.001	6.8	R	40 -46 40	<.001	5.6
Anterior intraparietal sulcus	L	-42 -44 40	<.001	6.7	L	-40 -46 40	<.001	6.5
Inferior occipital gyrus	R	58 -46 -22	<.001	5.0	R	42 -66 -18	.133	4.3
Inferior occipital gyrus	L	-46 -68 -18	<.001	5.5	L	-46 -64 -16	<.001	5.7

For each region, we report (A) the main effect of two positions versus one; and (B) the main effect of two categories versus one category. The *p* values are corrected for multiple comparisons considering the whole brain as the volume of interest. Hem = hemisphere; L/R = left/right.

baseline was not included in the current study because it was of no interest for our central aim (i.e., testing for the interplay between location-based and category-based attentional selection).

Interactions between Space-based and Category-based Attention

Next, we asked whether the two effects of dividing attention (location-based and category-based) simply overlapped in the same cortical regions, or whether they added up nonlinearly, indicating interactions at the neuronal level (see Methods section and Beauchamp, 2005; Calvert, 2001). Thus, we tested formally for the interaction term between these two experimental factors within the fronto-parietal network that activated with both main effects (cf. Figure 2A). Indeed, this demonstrated that in both the frontal and parietal cortex, the signal increase for monitoring two stimulus categories at two nonadjacent locations (Div2 condition) was not simply due to a summation of divided spatial attention plus monitoring of two categories. The sole exception to this finding was the right anterior parietal cortex, where the interaction term was not significant. Figure 2B shows the anatomical location of those regions where the interaction term reached statistical significance and the signal plots for two areas in the frontal cortex. The plots show selective activation in the Div2 condition (see Bar 1), demonstrating an interaction between location-based

and category-based attention in these areas. Anatomical locations and p values for the interaction effect are reported in Table 2A.

In order to rule out the alternative explanation that task difficulty accounted for enhanced activity in the Div2 condition, we performed an additional analysis now including behavioral performance as a covariate of no interest. This new analysis replicated our interaction result (statistical scores and peak coordinates were virtually identical to the initial analysis; cf. Table 2A and B), thus suggesting that a simple increase in task difficulty was an unlikely explanation of the interaction found in the fronto-parietal network.

Main Effect of Focused Attention to the Left or Right Hemifield

Finally, our experimental design allowed us to ask whether the number of categories that subjects had to monitor during (spatially) focused attention to one or the other hemifield affected attentional modulation associated with spatially selective attention. Accordingly, we directly compared leftward and rightward attention (main effect of attended side), expecting increased activity in the occipital cortex contralateral to the attended hemifield (e.g., Martinez et al., 1999; Heinze et al., 1994). Notably, for the first time, we were able to test any further influence of category-based attention on this

Table 2. Anatomical Location and Statistical Scores for the Regions that Activated during Selection of Multiple Locations and Multiple Categories (Location by Category Interaction)

Anatomical Region	A. Interaction between Spatial and Nonspatial Selection				B. Interaction Corrected for RTs		
	Hem	Coordinates	p -corr	Z Value	Coordinates	p -corr	Z Value
Dorsal premotor cortex	R	28 8 60	<.001	5.6	28 8 60	<.001	5.5
Dorsal premotor cortex	L	-36 4 54	<.001	6.0	-36 4 54	<.001	5.5
Ventral premotor cortex	R	48 10 26	.021	3.9	48 10 26	.020	3.9
Ventral premotor cortex	L	-44 2 32	<.001	4.9	-44 2 32	.001	4.8
Prefrontal cortex	R	44 28 20	.008	4.2	44 28 20	.010	4.1
Prefrontal cortex	L	-46 22 26	.001	4.7	-46 22 26	.001	4.6
Anterior supplementary area	R	-6 14 48	.002	4.6	-6 14 48	.002	4.5
Insula	R	34 24 -4	.022	3.9	34 24 -4	.022	3.9
Insula	L	-30 24 -4	n.v.i.	4.4	-30 24 -4	n.v.i.	4.3
Posterior intraparietal sulcus	R	22 -70 48	.044	3.7	30 -70 42	.047	3.7
Posterior intraparietal sulcus	L	-28 -74 34	<.001	4.8	-30 -76 26	.001	4.7
Anterior intraparietal sulcus	L	-36 -48 40	<.001	4.7	-36 -48 40	.001	4.7

p Values are corrected for multiple comparisons, considering the areas that activated both for selection of two positions (cf. Table 1A) and selection of two categories (cf. Table 1B). On the right side of the table, we report coordinates and statistical scores of an additional analysis that considered reaction times (RTs) as a covariate of no interest. n.v.i. = not in the search volume of interest.

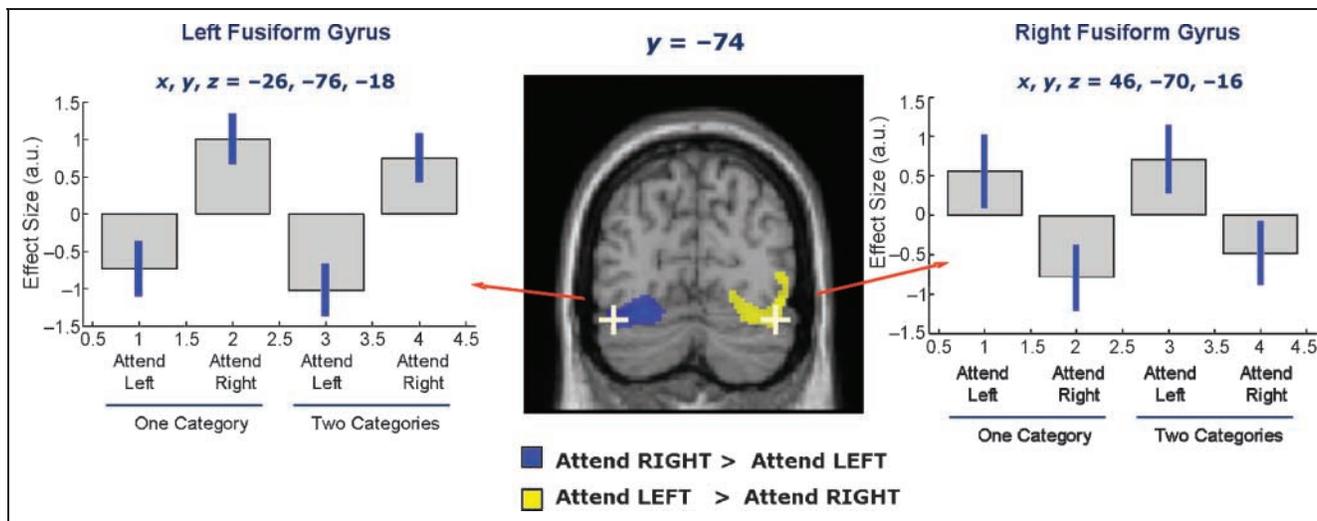


Figure 3. Contralateral attentional modulation in the visual cortex during focused spatial attention. In the visual occipital cortex, activity increased for contralateral minus ipsilateral focused spatial attention. The signal plot of the left hemisphere (see graph on the left side of the figure, activation rendered in blue) shows greater activity for attention to the right hemifield compared with attention to the left hemifield. This side-specific effect was found irrespective of the number of attended categories (attend one category: Bar 2 > Bar 1; and attend two categories: Bar 4 > Bar 3). Conversely, in the right hemisphere (rendered in yellow on the coronal section), activity was larger for leftward than rightward attention, again irrespective of the number of attended categories (attend one category: Bar 1 > Bar 2; and attend two categories: Bar 3 > Bar 4). The level of activation for the four conditions is mean-adjusted (i.e., the four values sum to zero) and it is expressed in arbitrary units (a.u., $\pm 90\%$ confidence interval). SPM display threshold: p -uncorr = .001.

spatially selective modulation of visuospatial attention (Side \times Category interaction).

The main effect of attended side manifested as increased activity in the ventral occipital cortex, contralateral to the attended hemifield (see Figure 3). Critically, this spatially specific attentional modulation was observed irrespective of the number of categories that subjects monitored on the attended side. Signal plots in Figure 3 show spatially specific attentional modulation in the left fusiform gyrus (panel on the left; $x, y, z = -26 -76 -18$; Z value = 6.4; p -corr < .001) and in the right fusiform gyrus (panel on the right; $x, y, z = 46 -70 -16$; Z value = 4.9; p -corr = .010). In the left hemisphere, activity was higher for Foc1/R than for Foc1/L (Bar 2 vs. 1, in the signal plot on the left side of Figure 3; activation rendered in blue on the coronal section), with a comparable attentional modulation when subjects monitored two categories (Foc2/R minus Foc2/L, cf. Bar 4 vs. 3). A corresponding pattern of activation was found in the right hemisphere, now with greater activity with attention to the left hemifield (Foc1/L minus Foc1/R, Bar 1 vs. 2, for the single-category conditions; and Foc2/L minus Foc2/R, Bar 3 vs. 4, when monitoring two categories; activation rendered in yellow on the coronal section). Thus, spatially specific attentional modulation in the occipital cortex was observed irrespective of the number of monitored categories, suggesting uncoupling of early spatial selection in the visual cortex from category-based attention. Note that although we did not record gaze position during the experiment, this lateralized pattern of activation in the occipital cortex suggests that, indeed,

subjects complied with the instruction to maintain central fixation while performing the covert attention tasks.

DISCUSSION

The aim of this study was to disentangle the neural correlates of divided spatial attention from more general processes associated with monitoring multiple sensory streams (dual-task performance) when subjects attended two visual streams simultaneously at nonadjacent spatial locations. Operationally, we defined dual-task performance as attending to multiple stimulus categories within a single visual feature dimension (category-based selection). Thus, we manipulated the number of task-relevant positions orthogonally from the number of task-relevant categories, dissociating location- and category-based selective processes during whole-brain fMRI. We found largely overlapping activity in fronto-parietal regions when attention was divided in the location or category dimensions (see Figure 2A). Critically, activity in this network increased nonlinearly when subjects attended different categories at separate locations, suggesting that the same neural substrate is engaged by location-based and category-based attentional selection. On the other hand, in the contralateral occipital cortex, spatially selective attentional modulation of attention to one or other hemifield was unaffected by the number of monitored categories (see Figure 3).

A interplay between spatial and nonspatial selective processes has been postulated by several theories of feature integration and object selection (e.g., Treisman &

Gelade, 1980). For example, the “feature similarity gain model” proposes that both types of selection signals can influence the activity of the same neuron. Thus, the combination of spatial and nonspatial modulatory signals will maximally enhance activity in neurons representing stimuli that are within the attentional focus and that match a currently relevant feature (Liu, Larsson, & Carrasco, 2007; Saenz, Buracas, & Boynton, 2002; Treue & Martinez Trujillo, 1999). Moreover, category-based processing may automatically trigger reorienting of spatial attention, inducing shifts of attention toward stimuli that share some feature with a target (“contingent attentional capture”; Serences et al., 2005; Folk & Remington, 1998; Yantis, 1993; Folk, Remington, & Johnston, 1992).

Our imaging data identify the fronto-parietal cortex as a possible substrate for combining spatial and nonspatial mechanisms of attentional selection. The activity of this network has been associated with high-level cognitive processes such as top-down attentional control and working memory (Pessoa & Ungerleider, 2004; Corbetta & Shulman, 2002; D’Esposito, 2001; Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Hopfinger, Buonocore, & Mangun, 2000; Kastner & Ungerleider, 2000; Corbetta, 1998). Increased activity within this network has been described both for spatial (Hopfinger et al., 2000; Nobre et al., 1997; Corbetta, Miezin, Shulman, & Petersen, 1993) and nonspatial attention (Coull, Frackowiak, & Frith, 1998; Coull & Frith, 1998; Le, Pardo, & Hu, 1998; Rees, Frackowiak, & Frith, 1997). A direct assessment of spatial and nonspatial attention within the same study has been undertaken by Giesbrecht et al. (2003). In a cueing attention task, they tested whether the same cortical network was engaged when attention was directed to a location compared to a stimulus feature. They found that large portions of a fronto-parietal network, including the superior frontal and posterior parietal cortex, were activated by both these tasks (Giesbrecht et al., 2003; see also Shafritz, Gore, & Marois, 2002, who reported functional overlap in the fronto-parietal cortex for spatial attention and color/shape conjunction).

Altogether, these findings suggest a shared neural substrate for spatial and nonspatial mechanisms of selective attention. Nevertheless, the question remains whether such functional overlap relates to some general-purpose attention mechanism subserving different forms of selection (Giesbrecht et al., 2003; Wojciulik & Kanwisher, 1999). Here we tackled this issue using a divided-attention task with subjects monitoring one or two stimulus categories at the same or on opposite sides of space. Thus, we assessed the relative contribution of nonspatial selective processes (here, monitoring multiple categories) when attention was divided between different spatial locations. As already mentioned in the Introduction, Nebel et al. (2005) also investigated possible contributions of nonspecific nonspatial factors to brain activation associated with divided visuospatial attention. In this study, the authors matched attentional demands in a

focused- and divided-attention task. They found that both these tasks engaged a similar, distributed network comprising the anterior cingulate, the right dorsolateral prefrontal cortex, and the parietal cortex, plus the bilateral ventrolateral prefrontal cortex. Our results are in agreement with these findings, showing that both spatial and nonspatial factors contribute to fronto-parietal activation for divided compared to focused attention. We extend these results, highlighting the specific contribution of location versus category selection within the same experiment. We show that activity in the fronto-parietal cortex increases nonlinearly in the Div2 condition (monitoring two categories at different locations). This finding suggests that both types of attentional selection involve the same neuronal populations, yielding to supra-additive effects when the two processes are engaged by the same condition (i.e., Div2; see also Beauchamp, 2005; Calvert, 2001 for related viewpoints about supra-additive effects in neuroimaging data).

A trivial account for the functional overlap of divided spatial attention and monitoring of multiple features or categories (dual-task performance) could be that both these conditions result in an overall increase in task difficulty (see also Nebel et al., 2005). We directly addressed this concern by including behavioral performance as a covariate of no interest in our fMRI analyses. The results showed that the interaction of location-based and category-based attention in the fronto-parietal cortex remained significant even when the variance associated with behavioral performance was accounted for (see Table 2B). This does not imply that task difficulty does not affect the level of activation within this network (in fact, fronto-parietal activity did covary with the RTs), but rather that differences in behavioral performance were not sufficient to fully account for the observed pattern of activation in these regions (i.e., interaction between location- and category-based selection).

Our current findings have relevant implications for models of divided spatial attention, showing that fronto-parietal activation during these tasks also involves nonspatial components, such as the concurrent monitoring of multiple streams of information. Our results suggest that spatial and nonspatial processes jointly cooperate to manage high levels of workload associated with divided-attention tasks, and possibly minimizing the behavioral costs of these challenging conditions. Indeed, although the behavioral cost of performing the four attention tasks increased linearly, the activity of the fronto-parietal network increased nonlinearly when participants attended multiple locations and categories (Div2 condition). This additional activation may indicate the engagement of some compensatory mechanism to contain the costs of monitoring multiple streams at different spatial locations. However, we should note that the interaction effect was found in the same regions showing overlapping main effects of location and category, thus suggesting some synergy between the two selection processes

rather than an entirely different process/strategy for the Div 2 condition only.

A compelling extension of this argument may link the pattern of fronto-parietal activation with changes of working memory requirements. When our subjects monitored two different categories in opposite hemifields (Div2 condition), there was an increase in the overall amount of information they had to actively maintain and compare to detect the target shapes. For instance, participants had to retain more task-based rules (i.e., select green rhombus not green square on the left, and red “x” not red “+” on the right), and filter out irrelevant stimuli on two sides (i.e., ignore red shapes on the left side, and ignore green shapes on the right side). Nonetheless, it is important to note that these “rules”—probably stored in working memory—entail a critical spatial component (e.g., green rhombus on the *left*). Thus, also this interpretation would fit our key proposal here, namely, that spatial and nonspatial processes interact in these regions.

In recent years, the relationship between attention and working memory has been investigated extensively, in particular, with regard to the role of attention and memory in the control of capacity-limited processes (Olivers, 2008; Awh, Vogel, & Oh, 2006; Awh & Jonides, 2001). Accordingly, both cognitive processes deal with selecting relevant and ignoring (or preventing interference from) irrelevant visual information. There is now evidence that these processes rely on a common capacity-limited mechanism—working attention—sharing a common neural substrate (Baddeley, 1993; Cowan, 1988). Many examples of interaction between working memory and space-based (or feature-based) attention have been described. For instance, in rapid serial visual presentation tasks, subjects typically fail to report the second of two successive targets (attentional blink). This has been interpreted as a capacity limitation in the formation of durable traces in working memory (Jolicoeur, 1999; Chun & Potter, 1995). Further, it has been shown that memory performance declines when shifts of attention are prevented (attention-based rehearsal hypothesis, i.e., Mayer et al., 2007; Awh, Jonides, & Reuter-Lorenz, 1998; Smyth, 1996; Smyth & Scholey, 1994). These findings suggest a link between cognitive processes involved in the memorization of locations and the focusing of spatial attention. Physiologically, a large-scale cortical overlap between memory and attention systems has been also described (D’Esposito, 2001; Cohen et al., 1997; Courtney et al., 1997). Accordingly, some synergy between attention- and memory-related processes in the fronto-parietal cortex could be required for maintaining adequate levels of behavioral performance when monitoring multiple sensory streams simultaneously, as in our experimental paradigm. Future investigations could assess this further, looking for possible interactions between spatial attention and working-memory demands during divided-attention tasks. Furthermore, the interaction between location- and

category-based attentional selection might be tested “within” rather than “between” visual hemifields. Previous studies that investigated divided visuospatial attention within and between hemifields reported some advantage for splitting attention between opposite hemifields (bilateral field advantage; see Sereno & Kosslyn, 1991). This benefit has been attributed to increased resources availability when the attentional systems of both hemispheres are active (Castiello & Umiltà, 1992), although this advantage disappears when subjects have to monitor complex stimuli (Kraft et al., 2005; see also Lavie, 1995 for a model suggesting that irrelevant information is not processed beyond early sensory stages). Future studies may ask whether also the interactive cooperation of spatial and nonspatial attentional selection is affected by hemifield/hemisphere factors, or instead only the spatial components can take advantage of bilateral presentation.

Although location-based and category-based selection interacted in high-order fronto-parietal regions, side-specific attentional modulation in the visual occipital cortex was unaffected by the category factor. The same level of activation for attention to the contralateral versus ipsilateral hemifield was found irrespective of whether subjects monitored one or two categories at the attended side (see Figure 3). The modulatory role of spatial attention in the visual cortex is well established (McAdams & Reid, 2005; Hopfinger et al., 2000; Gandhi, Heeger, & Boynton, 1999; Martinez et al., 1999; Somers, Dale, Seiffert, & Tootell, 1999; Heinze et al., 1994; Motter, 1993) and is generally linked to mechanisms of early attentional selection (Treue, 2001; Posner & Gilbert, 1999). Feature-based selection has also been shown to modulate activity in the visual cortex, according to target-defining relevant features (Liu, Slotnick, Serences, & Yantis, 2003; Saenz et al., 2002). However, unlike location-based selection, these modulatory effects can operate throughout the visual field, enhancing activity of neurons that code for any task-relevant feature, even if the target stimulus is outside the neuron’s receptive field (Treue & Martinez Trujillo, 1999; also Serences & Boynton, 2007; Saenz et al., 2002). However, in our experiment, we did not manipulate attention of one or another elementary visual feature (e.g., color vs. motion; Liu et al., 2003; Chawla, Rees, & Friston, 1999; Corbetta et al., 1991), but rather, we varied the number of task-relevant categories within the same feature. This may explain why we failed to demonstrate any main effect of category or any interaction between category and spatial attention in the visual cortex. The target stimulus was defined by a combination of color, orientation, and position (e.g., “green rhombus on the left side”), possibly triggering some object-based selection process (Egley, Driver, & Rafal, 1994; Duncan, 1984). In this context, our spatially specific but category-independent results in the occipital cortex may suggest some segregation between “early” location-based versus “late” object-based selection. Accordingly, the mechanism would be to first

select in the occipital cortex (see modulation of visual activity by spatial attention, irrespective of category, Figure 3), then involve higher-order fronto-parietal regions (see conjoint effects of spatial and nonspatial selective attention in Figure 2) for target identification requiring integration of several features (e.g., color, orientation, and position).

In conclusion, our fMRI data highlight a dorsal fronto-parietal network that is engaged by monitoring of multiple visual streams. The factorial manipulation of number of attended locations and attended categories indicate that both spatial and nonspatial processes contribute to this pattern of activation. Critically, we demonstrated significant interactions between the two types of selection mechanism, suggesting a possible common neural substrate. On the other hand, side-specific modulation of activity in the visual cortex during focused attention to one or the other hemifield was unaffected by category, suggesting space-based specific selection mechanisms in the visual cortex.

Acknowledgments

The Neuroimaging Laboratory is supported by The Italian Ministry of Health. We thank R. Frackowiak for his help with this manuscript.

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