Cerebral Cortex November 2007;17:2703–2712
doi:10.1093/cercor/bhl179
Advance Access publication January 30, 2007

Remapping Attentional Priorities: Differential Contribution of Superior Parietal Lobule and Intraparietal Sulcus

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Seeking and selectively attending to significant extrapersonal stimuli in a dynamic environment requires the updating of an attentional priority map. Using functional magnetic resonance imaging, we investigated the role of posterior parietal cortex in such remappings of attentional priorities where the configuration, location, and significance of stimuli were systematically varied. Our data revealed a functional dissociation between 2 juxtaposed posterior parietal regions: one in the superior parietal lobule (SPL) and another in the intraparietal sulcus (IPS). SPL was preferentially activated in all conditions where a spatial displacement occurred in the location of the target, the location of the distracter, or the focus of attention (exogenous and endogenous shifts of spatial attention). Shifts of the attentional focus also activated the IPS but principally if they were guided endogenously by internal rules of relevance rather than stimulus displacement per se (endogenous attention shifts). Only the IPS region was activated by transient resetting of target significance when the stimulus configuration changed but the attentional focus remained spatially fixed (feature attention shifts). These 2 components of the large-scale frontoparietal spatial attention network therefore have common and distinctive functions. In specific, the IPS component is more closely related to the compilation of an attentional priority map, including the endogenous recalibration of attentional weights. The SPL component, on the other hand, is more closely related to the modification of spatial coordinates linked to attentional priorities (spatial shifting). Collectively, these 2 areas allow posterior parietal cortex to dynamically encode extrapersonal events according to their spatial coordinates and valence.

Keywords: endogenous control, fMRI, perietal, shifting

Introduction

Posterior parietal cortex is a major component of a distributed spatial attention network (Mesulam 1981; Corbetta and Shulman 2002; Husain and Rorden 2003). The posterior parietal contribution to spatial attention emanates from multiple areas including the superior parietal lobule (SPL) (Vandenberghe et al. 2001a; Yantis et al. 2002; Pollmann et al. 2003), upper and lower banks of the intraparietal sulcus (IPS) (Corbetta et al. 1993; Nobre et al. 1997; Gitelman et al. 1999; Corbetta and Shulman 2002; Woldorff et al. 2004), angular gyrus (Mort et al. 2003; Husain and Rorden 2003; Hillis et al. 2005), and temporoparietal junction (TPJ) (Corbetta et al. 2000; Corbetta and Shulman 2002; Kincade et al. 2005; Astafiev et al. 2006). SPL and IPS are often activated together, for example, when subjects attentively track moving targets compared with passive viewing (Culham et al. 1998), when subjects attend to motion compared with color (Shulman et al. 2002), or during spatial cueing (Gitelman et al. 1999; Simon et al. 2002). More recently, several attempts have been made to characterize the specializations of these parietal areas, and distinctive roles in endogenous control (Hopfinger et al. 2000; Corbetta and Shulman 2002; Kincade et al. 2005; Vandenberghe et al. 2005), shifting (Corbetta et al. 2000; Vandenberghe et al. 2001a; Yantis et al. 2002), and sustaining attention (Vandenberghe et al. 2001b; Husain and Rorden 2003) have been attributed to these areas.

The current study of selective attention focused on the remapping of attentional priorities. Remapping refers to transitions from one attentional priority map (Koch and Ullman 1985) to another. We studied such transitions against a baseline of sustained attention (Vandenberghe et al. 2001a; Yantis et al. 2002; Liu et al. 2003; Serences et al. 2004; Shomstein and Yantis 2004). This approach departs from a classical trial-by-trial approach with blank intertrial intervals and allows us to subtract out processes related to the maintenance of attention. We also removed effects related to detection and motor responses (Shulman et al. 1999; Woldorff et al. 2004) by temporally separating the occurrence of transient dimmings that had to be detected from the remapping events to which functional magnetic resonance imaging (fMRI) responses were time locked.

In the current study, we attempted to tease apart 2 processes that are involved in remapping attentional priorities. In everyday life, spatial attention is dynamically redistributed in response to changes in the location, perceptual features, and relevance of extrapersonal stimuli. A first process consisted of the recalibration of attentional weights (Bundesen 1990). Within the framework of the theory of visual attention (TVA), an attentional weight is computed for each perceptual unit (object in the visual field) and used for allocation of attention (i.e., visual processing resources) (Bundesen et al. 2005). The attentional weight of a perceptual unit (w_x) is the product of the sensory eidence [$\eta(x, j)$] that object x has a feature j multiplied by the behavioral pertinence of that feature (variable π_j). Within TVA, j is defined broadly and can refer to, for example, a certain color, a shape, a spatial position, or membership of a category (Bundesen et al. 2005). The rate at which a perceptual unit is encoded in visual short-term memory is determined by its attentional weight relative to the attentional weights of the other units (biased competition [Desimone and Duncan 1995]). In a dynamic world, sensory evidence $\eta(x, j)$ or behavioral pertinence π_j continuously change. As a consequence, the attentional weights must be continuously updated. We refer to the updating of weights as the "recalibration of attentional weights." On the basis of previous human brain mapping (Vandenberghe et al. 2005) and monkey electrophysiology studies (Gottlieb and Goldberg 1999; Wardak et al. 2002; Bisley and Goldberg 2003; Treue 2003), we hypothesized that the horizontal segment of the IPS plays a critical role in this process

(Vandenberghe et al. 2005), especially when stimulus selection is under high endogenous control (Corbetta and Shulman 2002).

The second process of interest was spatial shifting. On the basis of previous work (Vandenberghe et al. 2001a; Yantis et al. 2002), we hypothesized that SPL would be activated by the need to shift the spatial focus of attention regardless of what triggered the shift and that, conversely, a feature change would activate SPL more when the feature change triggered a spatial displacement of the attentional focus than when the spatial focus of attention remained locked to the same location.

We used the following strategy to separate these 2 processes. Subjects viewed a display containing 2 stimuli pulled from 2 sets of shapes. Each set contained one relevant and one irrelevant stimulus, and this was defined beforehand. The task was to press a button when the relevant stimulus dimmed but not when the irrelevant stimulus dimmed. By changing either the shape or the spatial location of stimuli, we manipulated the currently attended location. A feature change required endogenous recalibration of attentional weights but did not necessarily change the relevant stimulus site. Conversely, a change of stimulus position to a previously unoccupied location elicited a spatial attentional shift without much endogenous control.

Our purpose was not to compare feature-based with location-based attention: This has already been studied in the past by comparing spatial with feature cueing (Vandenberghe et al. 2001b; Giesbrecht et al. 2003) or interdimensional shifts with a sustained attention baseline (Liu et al. 2003). In our study, shape always defined which stimulus was relevant. The type of spatial shifting we studied also differed from shifts evoked by invalid cueing as studied before (Corbetta et al. 2000). In our study, a shift was not associated with a breach of expectancy (Corbetta et al. 2000; Corbetta and Shulman 2002; Kincade et al. 2005; Astafiev et al. 2006). The position to which a stimulus shifted could not be predicted.

We hypothesized that endogenous recalibration of attentional weights and spatial shifting were dissociable processes that differentially involved IPS and SPL, respectively.

Methods

Subjects

We conducted 4 event-related fMRI experiments. Sixteen subjects (9 women, 7 men) participated in the main experiment, 4 subjects (1 woman, 3 men) in each of 2 control experiments, and 8 subjects (4 women, 4 men) in a second, "auditory switching" experiment. All participants were between 18 and 30 years of age and strictly right handed (Oldfield 1971), free of psychotropic or vasoactive medication, without neurological or psychiatric history, and had a normal structural brain magnetic resonance imaging (MRI) scan. They gave written informed consent in accordance with the Declaration of Helsinki. The ethical commission, University Hospital Gasthuisberg, Leuven, approved the experiment.

Stimuli and Tasks

The fMRI experiments were conducted using Superlab for PC version 2.0 (Cedrus, Phoenix, AR). Visual stimuli were projected from a Barco 6400i LCD projector (1024 × 768 pixels) onto a screen (40 by 30 deg) 36 cm in front of the subjects' eyes.

In the main experiment, 2 stimuli occupied 2 out of 6 possible locations on the horizontal meridian (Fig. 1*A*) at 3.18, 9.46, or 15.5 deg eccentricity to the left or to the right. There were 2 possible, yoked stimulus pairs: A square together with a triangle or a circle together with a diamond (stimulus surface 1.59 deg^2; luminance 89 cd/m^2) (Fig. 1*A*). At any given time, only one pair of stimuli was presented. Each pair

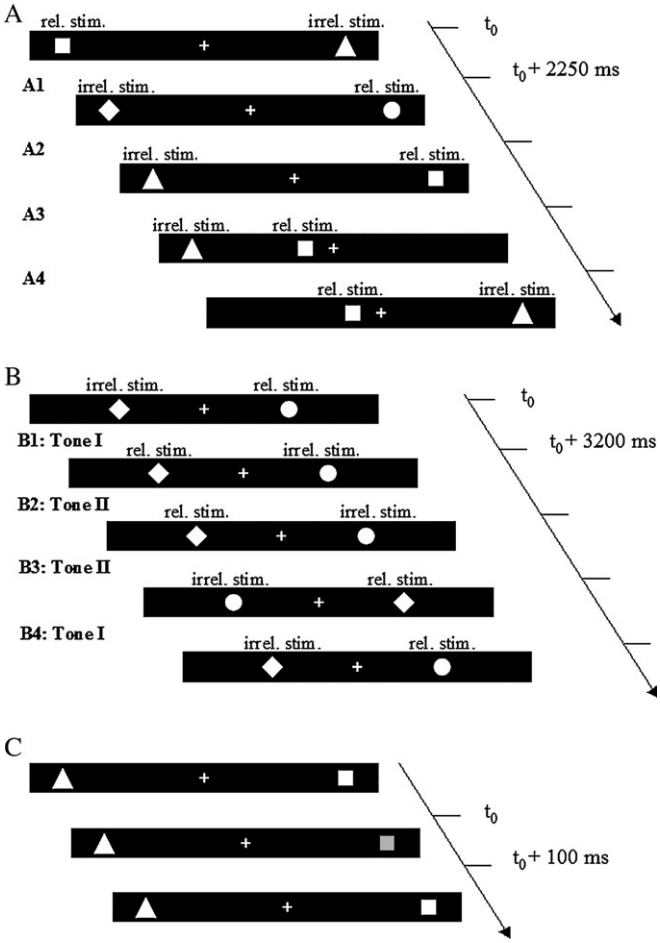

Figure 1. Stimuli and tasks. For each of 2 experiments, we show as an example one randomly chosen segment of an event sequence. In reality, the order of events was pseudorandomized throughout the run. The labels "rel. stim." (relevant stimulus) and "irrel. stim." (irrelevant stimulus) are for clarification only and were not presented to the subjects. (*A*) Main experiment. Which stimulus within each of the 2 pairs was relevant was constant within a subject (in this example, the square and the circle, respectively). (*A1*) Feature change that leads to a spatial attentional shift. (*A2*) Feature change but target and distracter stay in place (no spatial shift). (*A3*) Relevant stimulus moves to a previously unoccupied position. In this example, the stimulus shifts to the opposite hemifield, but throughout a run, the number of between- versus within-hemifield shifts was matched as well as the number of leftward versus rightward shifts. (*A4*) Irrelevant stimulus moves to a previously unoccupied position. Again, the number of between- versus within-hemifield shifts was matched as well as the number of leftward versus rightward shifts. (*B*) Auditory switching experiment. In this example, tone I signals a change in stimulus relevance, tone II signals that stimulus relevance does not change. (*B1*) Auditory tone signals a change in relevance between stimuli. This leads to a spatial attentional shift. No visual changes. (*B2*) Nothing changes. (*B3*) Relevant and irrelevant stimulus swap positions leading to a spatial attentional shift. (*B4*) Relevant and irrelevant stimulus swap positions. Auditory tone signals a change of relevance between stimuli. (*C*) Example of a dimming target. Subjects had to press a key for a dimming of the relevant stimulus but not when the irrelevant stimulus dimmed.

contained a relevant and an irrelevant stimulus. Subjects were instructed and trained beforehand which of the 2 stimuli within each pair was relevant. This was constant within subjects and counterbalanced between subjects. When the relevant stimulus dimmed, subjects had to respond (Fig. 1*C*) but not when the irrelevant stimulus dimmed. A dimming consisted of a change of luminance from 89 to 45 cd/m^2 with a duration of 100 ms. Within each run (duration 8 min 6 s), the relevant stimulus dimmed 30 times (Fig. 1*C*) and the irrelevant stimulus dimmed 30 times. Half of the subjects responded with their left hand, half with their right hand.

This sustained attention baseline was transiently interrupted by stimulus changes of 4 different types (events), 36 of each type. Event

onset asynchrony was 2250 ms. In event types A1 and A2, one pair of stimuli was replaced by the other pair occupying the same positions (Fig. 1*A*). Replacement was immediate, without temporal gap. In event type A1, the "relevant" stimulus of the new pair appeared at the position previously held by the "irrelevant" stimulus of the preceding pair. The irrelevant stimulus of the new pair appeared at the position previously held by the relevant stimulus of the preceding pair. As a consequence, the relevant stimulus site became irrelevant and vice versa. The feature change elicited an endogenous spatial shift (Table 1 and Fig. 1*A1*). In event type A2, the relevant stimulus of the new pair appeared at the position previously held by the relevant stimulus of the preceding pair. The irrelevant stimulus of the new pair appeared at the position previously held by the irrelevant stimulus of the preceding pair. As a consequence, the relevant stimulus site remained relevant and no spatial shift was needed (Table 1 and Fig. 1*A2*). In event types A3 and A4, either the relevant or the irrelevant stimulus changed its position to a location not occupied during the previous trial. Features remained unchanged. In event type A3, the relevant stimulus changed its position. This provoked a spatial shift, without feature changes (Table 1 and Fig. 1*A3*). In event type A4, the irrelevant stimulus changed its position (Table 1 and Fig. 1*A4*). Each run also contained 72 null event trials during which no change occurred. The event sequence was optimized for the contrast of each event type minus the null event (Wager and Nichols 2003). Between event types, we matched the number and amplitude of leftward and rightward shifts, of within-hemifield and between-hemifield shifts, of left- and right-sided attentional allocation, and the positions occupied by the stimuli. We also matched the number of dimmings of relevant or irrelevant stimuli between event types. In order to collect enough behavioral data to detect differential behavioral effects of the different event types, 80% of dimmings occurred between 50 and 500 ms following event onset and 20% between 500 and 1500 ms. In order to determine whether this skewed distribution of dimmings affected results, we conducted a second experiment, the "target timing control" experiment. In this experiment, dimmings were evenly distributed over the entire interstimulus interval. The total number of dimmings was identical to that in the main experiment as were all other experimental parameters.

In all experiments, subjects were instructed to fixate a central cross (1.27 deg) throughout the run. Eye movements were monitored online using the Applied Science Laboratory infrared system (Waltham, MA) and stored for subsequent automatized quantitative analysis. We defined a left- and a right-sided region of interest that covered a rectangular area along the horizontal meridian from 2 to 17 deg eccentricity (height 4 deg). Deviations of eye movements into regions of interest were detected automatically and calculated.

To determine the sensory effect of feature changes and changes of stimulus position, we conducted a sensory control experiment. In this experiment, the same peripheral stimuli were presented as in the main experiment, with the same types of peripheral sensory changes marking the events (event types C1, C2, C3, and C4 corresponding to A1, A2, A3, and A4, respectively). In contrast with the main experiment, subjects always had to attend to the central fixation cross and not to the peripheral stimuli. At irregular intervals, a central arrow (100 ms duration) appeared that pointed upwards or downwards. The central arrow never appeared within the first 1000 ms following an event or within 500 ms preceding an event. Subjects had to press a left or right hand key depending on the direction of the arrow (Vandenberghe et al. 2005). The target occurred with an average frequency of 1 per trial, with a range from 0 to 3, spread evenly across the entire intertrial interval. As the peripheral stimuli were irrelevant, event types C1 and C2 were indistinguishable from each other as were event types C3 and C4.

In the main experiment, events were always associated with a visual change, either of features or of extrapersonal stimulus locations. In a fourth experiment, the "auditory switching" experiment, we studied attentional shifts in the absence of any visual change (Fig. 1*B*). Only one stimulus pair was used (a circle and a diamond). At the start of the experiment, subjects were instructed which was the relevant stimulus within the stimulus pair. As in the main experiment, subjects had to respond when the relevant stimulus dimmed (100 ms duration) but not when the irrelevant stimulus dimmed. The 2 stimuli were shown on the horizontal meridian at 10.5 deg eccentricity, one stimulus to the left and one to the right. This sustained attention baseline was transiently interrupted by 4 types of events. Each event started with an auditory tone (100 ms duration). Its pitch, high or low, signaled whether or not relevance changed between stimuli. In event type B1, the auditory cue signaled that what had previously been the relevant stimulus became irrelevant and what had previously been the irrelevant stimulus became relevant (Table 1 and Fig. 1*B1*). This led to a feature attentional shift from one shape to another as well as an endogenous spatial attentional shift, in the absence of any visual changes. In event type B2, the auditory cue signaled that the relevant stimulus remained relevant and the irrelevant stimulus remained irrelevant (Table 1 and Fig. 1*B2*). Neither spatial or feature attentional shift nor visual changes occurred. In event type B3, the auditory cue signaled that stimulus relevance remained unchanged. Stimuli swapped positions immediately after the tone had ended (Table 1 and Fig. 1*B3*). This led to a spatial shift. In event type B4, the auditory tone signaled that what had previously been the relevant stimulus became irrelevant and what had previously been the irrelevant stimulus became relevant. Immediately after the end of the tone, stimuli swapped positions (Table 1 and Fig. 1*B4*). This led to a shift in feature attention together with spatial shifts between changing stimulus positions. Whether a low or a high pitch signaled a change of stimulus relevance was held constant within subjects and was counterbalanced between subjects.

Table 1
Commonalities & differences between conditions

	Feature change	Positional change of target	Positional change of distracter	IPS	SPL
A1	+	+	+	High	High
A2	+	−	−	**High**	**Low**
A3	−	+	−	**Low**	**High**
A4	−	−	+	**Low**	**High**
	Auditorily cued change in stimulus relevance	Swap in stimulus positions		IPS	SPL
B1	+	−		High	High
B2	−	−		Low	Low
B3	−	+		High	High
B4	+	+		High	High

Event onset asynchrony was 3200 ms. We presented 24 trials per event type plus 24 null event trials. Within each run (duration 6 min 24 s), there were 24 dimmings of the relevant stimuli and 24 of the irrelevant stimuli, divided evenly over the 4 experimental event types. In the auditory switching experiment, dimmings always occurred at 400 ms following event onset.

On the day before the fMRI session of the main experiment, subjects sitting at a distance of 114 cm from a computer screen practiced the experiment in 3 runs. The same experimental parameters were used as in the fMRI session. Eye movements were monitored using ViewPoint Eye Tracker (Arrington Research, Scottsdale, AZ) with a head and chin restraint. In the auditory switching experiment and the 2 control experiments, prior to image acquisition, subjects received one training run while lying under the scanner.

The behavioral data were analyzed by means of a 2-by-2 repeated measures analysis of variance. In the main experiment ($n = 16$), the first factor had 2 levels: Relevant stimulus position changes (event types A1 and A3) versus relevant stimulus stays in place (event types A2 and A4). The second factor also had 2 levels: Feature change (event types A1 and A2) versus change of stimulus position to a previously unoccupied location (event types A3 and A4). Given the low number of subjects in the other 3 experiments (auditory switching experiment: $n = 8$, sensory control and target timing control experiment: $n = 4$), we treated for behavioral analysis as a single data point the average for each event type per run rather than per subject (6 runs per subject, resulting in 47 and 23 degrees of freedom, respectively). Otherwise the behavioral analysis was similar to that of the main experiment. In the auditory switching experiment, the first factor had 2 levels: Auditorily cued change of stimulus relevance (event types B1 and B4) versus no change in stimulus relevance (event types B2 and B3). The second factor also had 2 levels: Swap of positions between stimuli (event types B3 and B4) versus no visual changes (event types B1 and B2).

Image Acquisition

A 3-T Philips Intera system (Best, Netherlands) equipped with an 8-channel head volume coil provided 3D T_1 anatomical volume images (time repetition [TR] = 9.6 ms, time echo [TE] = 4.6 ms, turbo field echo shot interval = 1748 ms, in-plane resolution = 1 mm, slice thickness = 1.2 mm) and T_2* echoplanar images (EPIs) with blood oxygenation level–dependent (BOLD) contrast. EPIs (TR = 2 s, TE = 30 ms, SENSE parallel imaging factor = 2) comprised 36 axial slices acquired continuously in ascending order (voxel size = 2.75 × 2.75 × 3.75 mm^3). In the main experiment and the 2 control experiments, we acquired a total of 250 volumes per run and in the auditory switching experiment 198 volumes per run. The first 6 volumes were discarded to allow the MRI signal to reach steady state. In the main experiment and the 2 control experiments, each subject underwent 6 runs each of 216 trials. In the auditory switching experiment, each subject underwent 6 runs each of 120 trials.

Image Analysis

Image processing analysis was performed using Statistical Parametric Mapping version 2002 (Wellcome Department of Imaging Neuroscience, London, UK). All experiments were preprocessed in the same way. Following correction for differences in timing of slice acquisition within a volume, EPI volumes were realigned and resliced using sinc interpolation. A mean EPI volume was obtained during realignment, and the structural MRI was coregistered with that mean volume. The structural scan was normalized to the Montreal Neurological Institute T_1 template in Talairach space (Talairach and Tournoux 1988; Friston et al. 1995) using nonlinear basis functions. The same deformation parameters were applied to the EPI volumes. The EPI volumes were spatially smoothed using a 5 × 5 × 7 mm^3 filter. Data from different runs were proportionally scaled to a grand mean of 100 arbitrary units to account for overall differences in the intensity of whole-brain volumes across the time series. The time series for each voxel were high-pass filtered to (1/128) Hz. The event-related response, synchronized with the acquisition of the top slice, was modeled by a canonical hemodynamic response function (HRF) consisting of a mixture of 2 gamma functions that emulate the early peak at 5 s and the subsequent undershoot (Friston et al. 1999). The temporal derivative of the HRF was also included in the model. Statistical inference was corrected for intrinsic autocorrelations. A statistical parametric map of the t statistic for the parameter estimates was generated and subsequently transformed to a Z map. Data were analyzed using a random effects general linear model. One contrast image per individual was calculated. At the second level of analysis, we examined for each of the contrasts whether, on average, the contrast images revealed significant differences (1-sample t-test).

The significance map for the group random effects analysis was thresholded at $P < 0.001$ for voxel-level inference with a cluster-level threshold of $P < 0.05$ corrected for the whole brain search volume.

The auditory switching experiment and the 2 control experiments were analyzed by means of a fixed-effects analysis due to the low number of subjects. We restricted the analysis of the auditory switching experiment and of the 2 control experiments to volumes of interest that were defined on the basis of the main experiment. These volumes of interest consisted of the clusters that were significantly activated in the main experiment. The significance threshold in the control experiments and the auditory switching experiment was set at $P < 0.05$ corrected for the volume of interest.

Results

Behavioral Data

Performance parameters are listed in Tables 2 and 3. When subjects pressed for a dimming of an irrelevant stimulus, this was counted as a false alarm.

In the main experiment, subjects responded significantly more slowly when the relevant stimulus position changed (A1 and A3) compared with when the relevant stimulus stayed in place (A2 and A4) ($F_{1,15} = 4.21$, $P < 0.05$) (Table 2). Subjects missed significantly more targets when the relevant or the irrelevant stimulus moved to a previously unoccupied position (A3 and A4) than when features changed (A1 and A2) ($F_{1,15} = 17.99$, $P < 0.0001$). There was no interaction effect (reaction times $F_{1,15} = 0.66$, $P = 0.42$; accuracies $F_{1,15} = 0.73$, $P = 0.40$; false alarms $F_{1,15} = 0.07$, $P = 0.79$). The average number of eye movements did not differ significantly between the different event types ($P > 0.9$) (Table 2).

In the target timing control experiment, subjects responded significantly more slowly when the relevant stimulus position changed (A1 and A3) compared with when the relevant stimulus stayed in place (A2 and A4) ($F_{1,23} = 4.25$, $P = 0.043$). Subjects missed significantly more targets when the relevant or the irrelevant stimulus moved to a previously unoccupied position (A3 and A4) than when features changed (A1 and A2) ($F_{1,23} = 11.78$, $P < 0.001$). There were no interaction effects (reaction times $F_{1,23} = 0.00$, $P = 0.996$; accuracies $F_{1,23} = 0.87$, $P = 0.35$; false alarms $F_{1,23} = 0.82$, $P = 0.37$).

In the auditory switching experiment, reaction times ($F_{1,47} = 158$, $P > 0.20$), true hit rate ($F_{1,47} = 0.81$, $P = 0.49$), and false alarms ($F_{1,47} = 0.38$, $P = 0.77$) did not differ significantly between events (Table 3). Subjects tended to respond faster when nothing changed (event type B2) than in any of the other 3 event types (Table 3).

In the sensory control experiment, reaction times ($F_{3,69} = 1.27$, $P = 0.29$) and true hit rate ($F_{3,69} = 1.08$, $P = 0.37$) did not differ significantly between events (Table 3).

Neuroimaging Data

Superior Parietal Lobule

Overall, SPL activity was determined by the occurrence of spatial shifts, regardless of whether they were elicited by

Table 2

Behavioral parameters [mean (standard deviation)]

	A1	A2	A3	A4	Null
Main experiment					
Reaction times (ms)	678 (79)	666 (90)	674 (94)	646 (68)	631 (85)
True hit rate (%)	67.3 (23.2)	66.4 (23.8)	56.4 (22.0)	53.6 (17.1)	64.6 (26.5)
False alarm rate (%)	5.6 (4.9)	4.6 (6.6)	3.9 (4.9)	3.5 (5.2)	3.7 (4.3)
Number of saccades	0.46 (0.31)	0.51 (0.29)	0.58 (0.35)	0.46 (0.30)	0.50 (0.21)
Target timing control experiment					
Reaction times (ms)	590 (140)	545 (117)	596 (182)	551 (149)	525 (93)
True hit rate (%)	77.8 (26.8)	84.0 (19.9)	66.7 (25.1)	64.6 (27.3)	70.8 (21.0)
False alarm rate (%)	1.4 (4.8)	4.9 (10.4)	1.4 (6.7)	2.1 (7.4)	4.2 (10.1)
Number of saccades	0.67 (0.96)	0.58 (0.65)	0.75 (0.74)	0.63 (1.01)	0.50 (0.83)

Note: False alarm rate: number of key responses to dimmings of the irrelevant stimulus divided by total number of irrelevant dimmings.

a feature change (A1), by a change in position of the relevant stimulus (A3), the irrelevant stimulus (A4), or both (B3, B4), or by a change in stimulus relevance (B1, B4) (Table 1 and Figs 2*C* and 3*B*). When features changed but the relevant and irrelevant stimuli stayed in place (A2), SPL was significantly less active (Table 1 and Fig. 2*C*). Conditions of high SPL activity were those associated with a spatial shift (A1, A3, A4, B1, B3, B4), whereas a feature change without spatial shift activated SPL much less (A2). Details are presented below.

In SPL, a feature change led to a strong response if the feature change led to an endogenous spatial shift but not when features changed but the relevant and irrelevant stimuli stayed in place (A1 – A2: 3, –51, 54, $Z = 4.94$, extent 251, corrected $P < 0.001$) (Fig. 2*A*,*C*). When a feature change led to a spatial shift (A1), SPL was as active as when the relevant stimulus moved to a previously unoccupied position without feature change (A3) (A3 – A1: uncorrected $P > 0.05$). Moreover, in SPL, it did not make a difference whether it was the relevant or the irrelevant stimulus that moved to a new position (A3 – A4: uncorrected $P > 0.05$) (Fig. 2*C*): When either the relevant or the irrelevant stimulus moved to a new position, SPL was significantly more active than when target and distracter stayed in place and only the features changed (A3 – A2: 6, –51, 57, $Z = 5.01$, extent 218, corrected $P < 0.001$; A4 – A2: 6, –51, 54, $Z = 5.94$, extent 306, corrected $P < 0.001$). A feature change without spatial shift was associated with lowest activity of all conditions (Fig. 2*C*). In comparison with baseline, however, activity was increased even during that condition (A2 – baseline: 0, –57, 51, $Z = 4.32$, extent 113, corrected $P = 0.043$). To summarize, SPL was predominantly activated when a spatial shift occurred that was triggered either by a feature change or by a change in stimulus positions (A1, A3, A4) (Fig. 2*C*).

We obtained identical results in the target timing control experiment as in the main experiment (A1 minus A2: –3, –60, 57, $Z = 3.54$, corrected $P = 0.040$; A3 minus A2: 3, –48, 45, $Z = 3.50$, corrected $P = 0.046$; A4 minus A2: 3, –45, 51, $Z = 3.63$, corrected $P = 0.031$).

We defined an SPL volume of interest based on the contrast between feature changes with versus without endogenous spatial shift (A1 – A2). Within this volume of interest, we

Table 3
Behavioral parameters of the 2 control experiments [mean (standard deviation)]

	B1	B2	B3	B4
Auditory switching experiment				
Reaction times (in ms)	845 (298)	781 (174)	853 (245)	836 (251)
True hit rate (%)	70.5 (29.0)	73.0 (28.6)	76.0 (27.5)	76.7 (24)
False alarm rate (%)	22.0 (28.7)	19.1 (29.4)	20.5 (30.8)	20.5 (24)
Number of saccades	0.58 (0.79)	0.52 (0.80)	0.60 (0.82)	0.63 (0.87)
Sensory control experiment				
	C1	C2	C3	C4
Reaction times (ms)	514 (44)	522 (38)	512 (27)	530 (39)
True hit rate (%)	84.1 (10.4)	88.4 (9.7)	82.6 (10.5)	85.2 (11.0)
Number of saccades	0.21 (0.41)	0.29 (0.62)	0.25 (0.61)	0.33 (0.56)

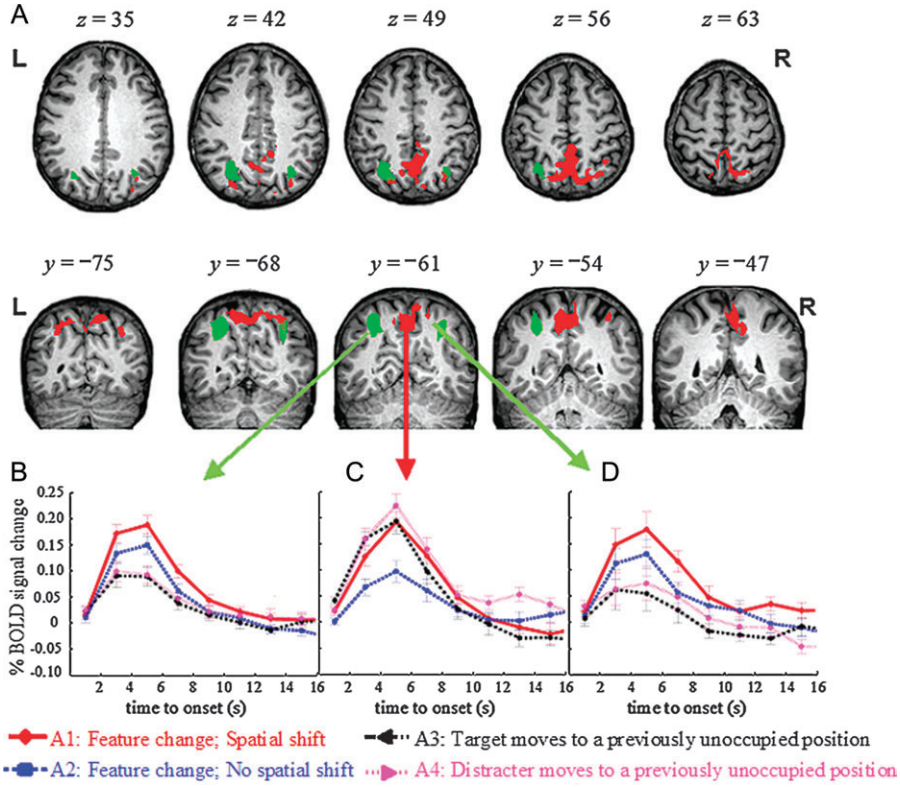

Figure 2. Main experiment. (*A*) Red: contrast between a feature change that leads to an endogenous spatial attentional shift and a feature change that does not lead to a spatial attentional shift (A1 − A2). Green: contrast between a feature change and a change of stimulus positions to a previously unoccupied location [(A1 + A2) − (A3 + A4)]. *Z* maps thresholded at $P < 0.001$ (voxel-level inference) and projected onto transverse and coronal brain sections. (*B*, *C*, *D*) Main experiment. Event-related response averaged over all voxels belonging to the left IPS (*B*) (extent [ext.] 78 voxels), SPL (*C*) (ext. 251), and right IPS (*D*) (ext. 32) cluster, respectively, and over all 16 subjects. *X* axis: time to event onset in seconds. Red: feature change that leads to a spatial attentional shift. Blue: feature change but relevant stimulus stays in place. Black: relevant stimulus moves to a previously unoccupied position. Magenta: irrelevant stimulus moves to a previously unoccupied position.

examined whether, in the main experiment, the direction of a voluntary shift (A1 and A3: leftward vs. rightward) or the hemifield where voluntary shifts took place (A1 and A3: within left vs. within right hemifield) affected SPL responses: In the left hemispheric part of the SPL volume, activity was significantly higher when the shifts occurred within the right hemifield as opposed to the left hemifield (−27, −78, 42, $Z = 3.91$, corrected $P = 0.011$). A trend in the opposite direction was found in the right hemispheric part of the SPL volume (left hemifield shift minus right hemifield shift: 12, −78, 54, $Z = 2.66$, uncorrected $P = 0.004$). The effect of the direction of the shift, leftward versus rightward, remained far below significance (uncorrected $P > 0.01$).

In the sensory control experiment, activity significantly decreased in response to each of the event types. The activity decrease was less pronounced during positional changes than during feature changes [(C3 + C4) − (C1 + C2): −3, −60, 57, $Z = 4.89$, corrected $P < 0.001$] (Fig. 3*E*).

When an auditory tone signaled a change of relevance between stimuli, SPL was significantly more active than when the tone signaled no change (B1 − B2) (15, −75, 57, $Z = 4.69$, corrected $P < 0.001$; −21, −72, 54, $Z = 4.47$, corrected $P < 0.01$) (Fig. 3*B*). The SPL response to a change of stimulus relevance in the absence of visual changes (B1) was as high as when stimuli swapped positions (B3, B4) (Fig. 3*B*).

Intraparietal Sulcus

Overall, IPS activity was high when features changed, and a high level of endogenous control was needed (A1, A2, B1, B3, B4). Obvious changes in the position of target or distracter (A3, A4) activated IPS to a much lesser degree (Table 1 and Fig. 2*B,D*). Details are provided below.

In the main experiment, when features changed (A1 + A2), the IPS was significantly more active than when stimuli moved to a previously unoccupied position (A3 + A4) (Fig. 2*A,B,D*) [(A1 + A2) − (A3 + A4): −30, −57, 45, $Z = 4.11$, extent 78, corrected $P < 0.001$; 33, −66, 42, $Z = 3.96$, extent 32, corrected $P < 0.01$]. This was the case when the feature change led to a spatial shift (A1 − A3: −24, −75, 48, $Z = 4.47$, extent 116, corrected $P < 0.001$; 33, −69, 54, $Z = 3.95$, extent 40, corrected $P < 0.005$) but also when it did not lead to a spatial shift (A2 − A4: −30, −60, 48, $Z = 3.47$, uncorrected $P < 0.001$; 33, −66, 45, $Z = 3.30$, uncorrected $P < 0.001$) (Fig. 2*B,D*). When a feature change led to an endogenous spatial shift, activity was slightly higher than when the feature change did not lead to a spatial shift (A1 − A2: 36, −66, 51, $Z = 3.60$, corrected $P = 0.005$; A1 − A2: −27, −69, 45, $Z = 2.51$, corrected $P = 0.22$).

Stronger IPS activation during feature compared with positional changes was confirmed by the target timing control experiment [(A1 + A2) − (A3 + A4): left IPS: −27, −63, 45, $Z = 5.83$, corrected $P < 0.001$; right IPS: 33, −69, 48, $Z = 2.83$, corrected $P = 0.040$].

Within the left and right IPS volume, we examined whether the direction of a voluntary shift (A1 and A3: leftward vs. rightward) and the hemifield in which a voluntary shift occurred (A1 and A3: left sided vs. right sided) affected responses: The left IPS volume showed higher activity during rightward versus leftward shifts (−30, −57, −54, $Z = 3.22$, corrected $P = 0.048$) and during shifts within the right hemifield versus shifts within the left hemifield (−30, −57, 42, $Z = 3.22$,

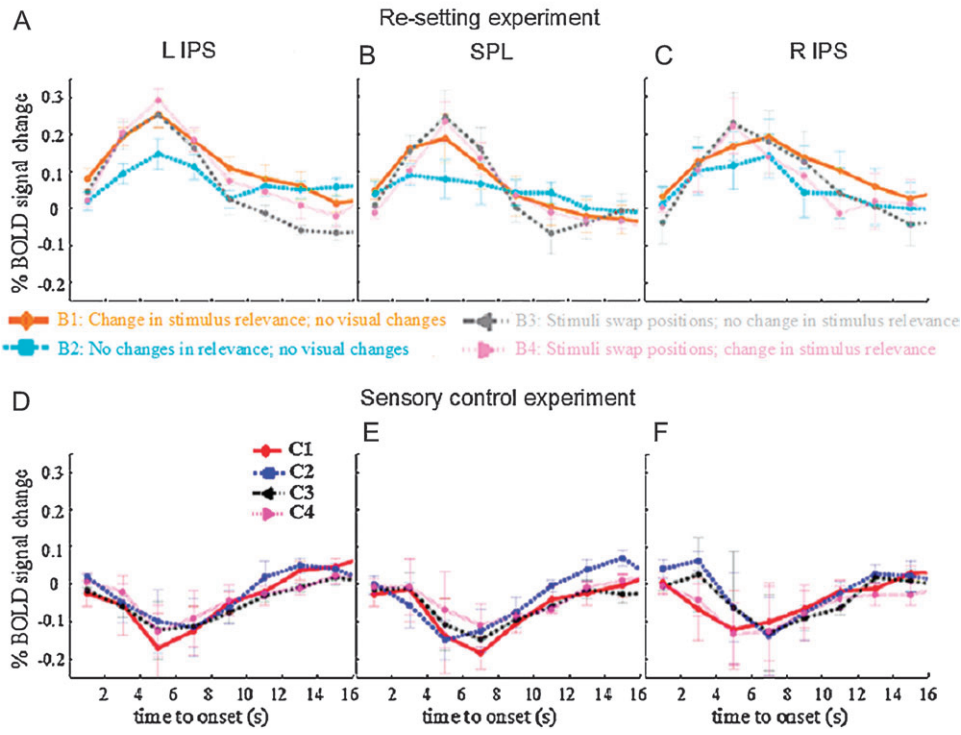

Figure 3. Event-related response averaged over all voxels belonging to the left IPS (*A*, *D*) (ext. 78), SPL (*B*, *E*) (ext. 251), and right IPS (*C*, *F*) (ext. 32) clusters that are shown in Figure 2*A*. (*A*, *B*, *C*) Auditory switching experiment. Responses are averaged over all 8 participants. *X* axis: time to event onset in seconds. *Y* axis: percentage of fMRI signal change. Orange: auditory tone signals a change in stimulus relevance that leads to a feature attention shift and a spatial attentional shift. No visual changes. Cyan: no visual changes, no change in stimulus relevance, or spatial shifts. Gray: stimuli swap positions leading to a spatial attentional shift. No changes in stimulus relevance. Magenta: stimuli swap positions and relevance changes between stimuli. (*D*, *E*, *F*) Sensory control experiment. Responses are averaged over all 4 subjects.

$P = 0.049$). In the right IPS volume, there was no effect of the hemifield where a shift occurred (left-sided or right-sided), and no effect of the direction of shift, even when the threshold was lowered to uncorrected $P < 0.05$.

In the sensory control experiment, responses to each of the event types were significantly decreased compared with baseline (Fig. 3*D*,*F*). There were no differences between feature changes and positional changes, even when the threshold was lowered to uncorrected $P < 0.01$ (Fig. 3*D*,*F*).

When an auditory signal indicated that stimulus relevance changed, in the absence of visual changes, IPS was significantly more active than when stimulus relevance and positions remained unchanged (B1 – B2) (–27, –60, 54, $Z = 4.76$, corrected $P < 0.001$) (Fig. 3*A*). The right IPS showed a trend in the same direction (B1 – B2) (36, –66, 51, $Z = 2.72$, corrected $P = 0.051$) (Fig. 3*C*). The IPS response to a change of stimulus relevance (B1) was as high as its response to a change of stimulus positions (B3, B4) (Fig. 3*A*,*C*).

Other Activations

In the main experiment, apart from IPS, several other areas were significantly activated when stimulus features changed (A1 + A2) than when stimuli moved to a previously unoccupied position (A3 + A4) (Fig. 4): The upper bank of the cingulate sulcus (–3, 12, 54, $Z = 4.36$, extent 163, corrected $P < 0.0001$) (Fig. 4), the crossing between the left inferior frontal sulcus and the precentral sulcus (–48, 6, 39, $Z = 4.41$, extent 143, corrected $P < 0.0001$) (Fig. 4), and the left posterior occipitotemporal sulcus (–45, –72, –15, $Z = 4.31$, extent 113, corrected $P < 0.0001$) (Fig. 4). The right inferior frontal gyrus (36, 27, 0, $Z = 4.00$, extent 40, corrected $P < 0.005$) and the right middle frontal gyrus (36, 51, 18, $Z = 3.77$, extent 26, corrected $P < 0.05$) were also more active during a feature change than when stimuli moved to a previously unoccupied location. This was partially due to a differential activity decrease.

Apart from SPL, no areas showed higher activity in the presence of a voluntary spatial shift compared with its absence [(A1 + A3) – (A2 + A4)].

For each of the contrasts of the main experiment, we specifically probed the TPJ (Corbetta et al. 2000; Kincade et al. 2005). This region is reliably activated during the target phase of invalidly cued trials (Corbetta et al. 2000; Kincade et al. 2005). We defined a spherical volume of interest centered at the coordinates provided by Kincade et al. (2005) (51, –51, 26; 54, –48, 30; –57, –43, 31) and a radius of 3 voxels. In the main experiment, the left TPJ (–54, –42, 30) responded significantly more strongly to positional changes of the relevant or the irrelevant stimulus than to feature changes (–54, –42, 30, $Z = 3.06$, $P = 0.008$). This was mainly due to a differential decrease compared with baseline.

Discussion

Two juxtaposed parietal regions, the SPL (Figs 2*A* [red] and 4) and the horizontal segment of the IPS (Fig. 2*A* green), contribute to the remapping of attentional priorities, each in a different way. Activity in SPL was mainly related to spatial shifting, regardless of what triggered the spatial shift: A feature change, a change in position of relevant or irrelevant stimuli, or a change in relevance of stimuli (Fig. 2*C*). In contrast, activity in IPS was mainly related to feature attention shifts and endogenous control (Fig. 2*B*,*D*), even when the spatial focus of attention remained fixed.

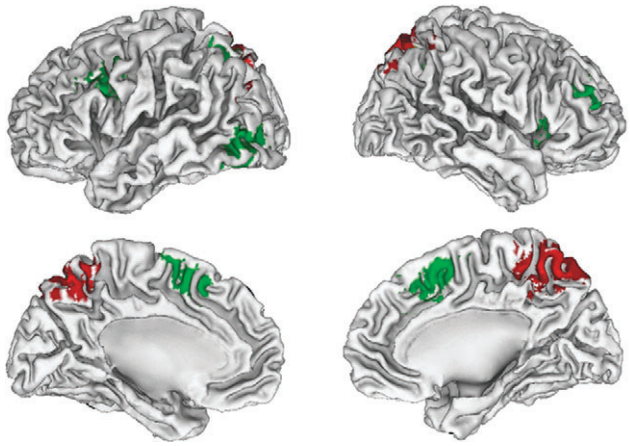

Figure 4. Main experiment. Red: contrast between a feature change that leads to a spatial attentional shift and a feature change that does not lead to a spatial attentional shift (A1 − A2). Green: contrast between a feature change and a positional change [(A1 + A2) − (A3 + A4)]. *Z* maps are thresholded at an uncorrected $P < 0.001$ and superposed onto a standard brain using CARET software (http://brainmap.wustl.edu).

A sensory effect cannot account for our findings. In the main experiment, a significant difference was found in SPL between 2 event types that were strictly matched sensorially: Feature changes with versus without endogenous spatial attentional shifts (Fig. 2*C*). This was not the case for IPS in the main experiment that was more active in response to feature changes versus positional changes. We therefore conducted a sensory control experiment (Fig. 3*D*,*F*): In the sensory control experiment, feature changes did not cause differential activity compared with positional changes, excluding a sensory account for the IPS effect. Third, in the auditory switching experiment, when the relevance of stimuli changed without visual changes, IPS and SPL were as strongly activated as when visual features changed (Fig. 3*A*,*B*,*C*). The source of our SPL and IPS findings must therefore be extraretinal.

SPL was activated not only when the relevant stimulus but also when the irrelevant stimulus moved to a previously unoccupied location (Fig. 2*C*). Activity in SPL actually was highest during that condition. The abrupt onset of a stimulus at a previously unoccupied location is likely to capture attention and trigger an exogenous spatial shift (Jonides and Yantis 1988). When the irrelevant stimulus moves, the exogenous shift may be followed by a corrective endogenous shift back to the relevant stimulus. When the relevant stimulus moves to a previously unoccupied location, the spatial shift to the sudden-onset stimulus most probably has both an exogenous and an endogenous component. Purely endogenous spatial shifts that were elicited by a feature change activated the same SPL region as when stimuli moved to a previously unoccupied location (Fig. 2*C*). Our data provide strong evidence that SPL is involved in spatial shifting, both exogenous and endogenous. The common condition that led to SPL activation was a spatial displacement in the location of stimuli or in the spatial focus of attention (Fig. 2*C*). When stimulus features changed but attentional priorities kept their locations (Fig. 2*C*), SPL was significantly less active. Our findings concerning the SPL are in keeping with previous observations (Vandenberghe et al. 2001a; Yantis et al. 2002) (Fig. 5). Involvement of SPL in spatial shifting may also explain why SPL is activated during visual marking in a visual search

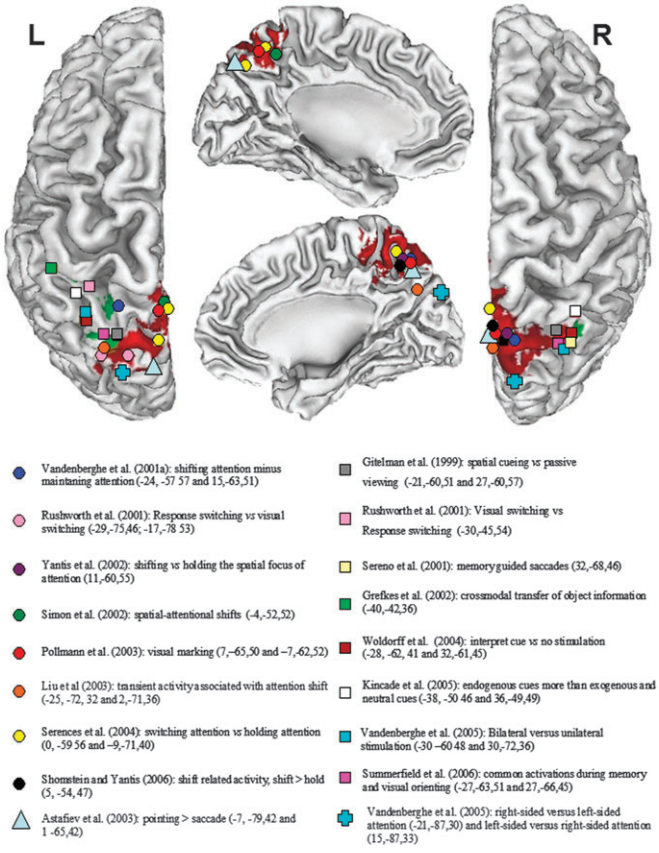

Figure 5. Superposition of activity peaks obtained in previous imaging studies onto the SPL (red) and IPS (green) activations obtained in our experiment. *Z* maps and peaks are projected onto the lateral and medial surface of a human standard brain using CARET software (http://brainmap.wustl.edu).

paradigm (Pollmann et al. 2003). Visual marking is a process that keeps old stationary items out of search and favors processing of new items coming up at previously unoccupied locations (Pollmann et al. 2003) (Fig. 5). Under all these circumstances (Vandenberghe et al. 2001a; Yantis et al. 2002; Pollmann et al. 2003) spatial coordinates associated with attentional weights have to be modified within the attentional priority map.

SPL activation was stronger in the presence of a spatial attentional shift than when features changed without spatial shift. At first sight, our findings seem to be at odds with a set of previous studies implicating SPL in shifts not only between locations but also between feature dimensions (Liu et al. 2003) or between overlapping objects (Serences et al. 2004). In our experiments, SPL was also activated by feature shifts in the absence of spatial shifts (Fig. 2*C*), but its response to a spatial shift was much stronger comparatively (Fig. 2*C*). When a feature shift caused a spatial shift or when a spatial shift occurred without feature shift, responses more than doubled that obtained when a feature shift occurred without spatial shift. Because of this substantial difference in response, we put forward that SPL is particularly involved in spatial rather than feature attention shifts. Second, in our experiments, the feature attention shifts were always within the same dimension, that is, a change in which shape was relevant. It is possible that shifts between feature dimensions, such as color versus motion (Liu et al. 2003), activate SPL more strongly than intradimensional feature shifts. Third, in previous studies, it is hard to exclude that subtle spatial shifts may possibly have confounded the contrasts used to isolate feature attention shifts, especially because online eye monitoring was not always used (Liu et al. 2003). At the moment when subjects shift between color and direction of motion of a moving dot pattern, it is possible that subjects refixate new elements of the random dot pattern (Liu et al. 2003). Likewise, when they shift between overlapping faces and houses (Serences et al. 2004) or male and female voices (Shomstein and Yantis 2006), the strategies applied by the brain to solve these unusual problems may be partly spatial. For instance, the stimuli may be processed as distinct spatial layers. We demonstrate within the same study a much stronger responses to spatial shifts in SPL than to feature shifts. For this reason, we propose that SPL is more closely related to spatial shifting than to feature attention shifts.

In monkeys, the dorsal bank of IPS and SPL has been implicated in visuomanual coordination, for example, during delayed reach paradigms (Galletti et al. 1996; Snyder et al. 1997; Eskandar and Assad 1999; Battaglia-Mayer et al. 2000; Ferraina et al. 2001). In humans, SPL is activated during reversal of conditional-associative manual responses (Rushworth et al. 2001) (Fig. 5) and during spatial matching-to-sample trials, with pointing as effector (Astafiev et al. 2003) (Fig. 5). The accuracy of reaching movements in a dynamic environment strongly depends on how well an individual adapts to spatial changes within the environment. The robust effect of a change of spatial coordinates is in agreement with SPL involvement in visuomotor coordination and manual reaching.

The decrease in IPS and SPL activity compared with baseline during the sensory control experiment (Fig. 3*D,E,F*) can be explained by the fact that a central target never occurred in the period immediately before or after a peripheral stimulus change (Corbetta and Shulman 2002).

As for IPS, our activity focus overlaps with the activation observed in previous studies of selective attention and endogenous or top–down control (e.g., Woldorff et al. 2004; Kincade et al. 2005; Vandenberghe et al. 2005; Serences et al. 2005; Summerfield et al. 2006) (Fig. 5). It overlaps with a region that is activated by memory-guided saccades in a retinotopic manner, a putative human homologue of the lateral intraparietal (LIP) area in monkeys (Sereno et al. 2001; Silver et al. 2005). Even when the spatial focus of attention remained fixed, feature changes activated IPS more strongly than when stimulus positions changed (Table 1 and Fig. 2*B,D*). This is opposite to the pattern seen in SPL (Table 1 and Fig. 2*C*). It indicates that IPS is involved in endogenous attention shifts and feature attention shifts and less in exogenous shifts. Within the framework of the TVA (Bundesen 1990; Bundesen et al. 2005), we attribute this strong IPS response to the need to recalibrate attentional weights when recalibration needs to be guided endogenously without more obvious changes of external coordinates (Corbetta and Shulman 2002; Vandenberghe et al. 2005). According to TVA, attentional weights depend on sensory evidence $\eta(x, j)$ and on behavioral pertinence π_j. Because in our experiments, shape defines pertinence, the potential effect of a change in shape upon the attentional weights is much stronger than that of a change in location. Interpreting a change of a significance-defining feature demands more endogenous recalibration than when a stimulus moves to a previously unoccupied location and retains its pertinent features. Likewise, in the auditory switching experiment, an auditorily cued change in pertinence of features requires more recalibration than when the auditory

cue indicates that the pertinence of features remains the same. In the auditory switching experiment, IPS was also activated when stimuli swapped positions and an auditory cue indicated whether or not feature relevance changed. Under such conditions, more endogenous recalibration is needed than when a stimulus moves to a previously unoccupied location, keeps its features, and retains its relevance. This higher need for endogenous control is manifested by the longer reaction times when stimuli swap positions in the auditory switching experiment than when a stimulus shifts to a previously unoccupied location in the main experiment (Tables 2 and 3). The IPS profile provides strong evidence for its role in endogenous attention shifts and feature attention shifts rather than exogenous shifts (Corbetta and Shulman 2002).

Spatial selectivity, for example, for direction of shifts (Serences and Yantis 2006) or for attended locations (Sereno et al. 2001; Silver et al. 2005), is present in IPS. Similar effects of shifting direction and hemifield were confirmed in our study, especially in the left hemisphere (Weintraub and Mesulam 1987). In a spatially selective way, the saliency map in IPS can exert a top–down modulation (Pessoa et al. 2003; Kastner and Pinsk 2004) of visual and oculomotor areas to determine the focus of attention and the goal of the next saccade if a saccade is appropriate (Ipata et al. 2006). In response to extrapersonal or internal changes, recalibration of a saliency map is needed regardless of whether or not as an outcome of attentional weights retain their spatial distribution. In both instances, IPS will be more active. In contrast, SPL is specifically activated when the spatial distribution of attentional weights changes.

To conclude, 2 juxtaposed parietal structures, the horizontal IPS segment, and SPL, contribute differently to remapping. IPS is involved in endogenous spatial shifts and feature attention shifts and less involved in exogenous shifts. Within our theoretical framework, we propose that the horizontal IPS segment mediates the recalibration of attentional weights, especially when endogenous control is high, regardless of whether the attentional weights retain their spatial distribution. In contrast, SPL is more closely related to spatial shifting, both exogenous and endogenous. SPL is preferentially involved when spatial coordinates within an attentional priority map are altered during remapping.

Notes

This work was supported by grant G.0076.02 from the Fund for Scientific Research, Flanders, Belgium (RV), KU Leuven Research grant OT/04/41 (RV), and National Institutes of Health grant NS030863. RV is a Clinical Investigator of the Fund for Scientific Research (FW0), Flanders. *Conflict of Interest*: None declared.

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