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SHORT COMMUNICATION
Visuospatial reorienting signals in the human temporo-parietal junction are independent of response selection

Serguei V. Astafiev,[1] Gordon L. Shulman[2] and Maurizio Corbetta[1,2,3]

[1]Department of Radiology, Washington University School of Medicine, Rm. 2127 A, East Building, 4525 Scott Ave., St. Louis, MO 63110, USA

[2]Department of Neurology and Neurological Surgery, Washington University School of Medicine, Rm. 2127 A, East Building, 4525 Scott Ave., St. Louis, MO 63110, USA

[3]Department of Anatomy and Neurobiology, Washington University School of Medicine, Rm. 2127 A, East Building, 4525 Scott Ave., St. Louis, MO 63110, USA

Abstract

This study contrasts visuospatial reorienting and response selection signals in the right temporo-parietal junction (TPJ) with functional magnetic resonance imaging. The overall goal was to investigate whether spatial orienting signals and motor signals interacted or were independent in TPJ. The right TPJ showed a greater response to targets at invalidly rather than validly cued locations, but no significant modulation from the effector used to respond. We suggest that TPJ may work as a modality-independent 'circuit breaker' for the dorsal fronto-parietal attention system, directing attention to salient events and enabling a variety of responses to those events.

Introduction

A novel anatomical model of human attention (Corbetta & Shulman, 2002) identified two partially segregated networks of brain areas that carry out different attentional functions. One system, which includes parts of the intraparietal cortex (intraparietal sulcus, IPS) and superior frontal cortex (frontal eye field, FEF), is involved in preparing and applying goal-directed (top-down) selection for stimuli and responses (dorsal frontoparietal network). This system is also modulated by the detection of stimuli. Previously we demonstrated that parts of this system (FEF and some parts of IPS) are differentially active when subjects plan and perform visually guided hand movements, as compared with eye movements or covert detection (Corbetta, 1998; Astafiev *et al.*, 2003). The other system, which includes the temporo-parietal junction (TPJ) and ventral frontal cortex (VFC) and is largely lateralized to the right hemisphere, is not involved in top-down selection. Instead, this system is specialized for the detection of behaviorally relevant stimuli, particularly when they are salient or unexpected (Corbetta *et al.*, 2000; Corbetta & Shulman, 2002; Kincade *et al.*, 2005).

Many studies suggest that TPJ is activated by stimuli across modalities. A recent study recorded evoked potentials from subdural electrodes placed over the TPJ cortex, and showed that parts of this region respond to visual, auditory and tactile sensory stimuli (Matsuhashi *et al.*, 2004). Functional magnetic resonance imaging (fMRI) studies also demonstrated that TPJ is more strongly activated by infrequent than frequent stimuli across different modalities (auditory, visual, tactile) (Downar *et al.*, 2000). Similarly, the TPJ is more strongly activated by invalidly cued targets, as compared with

valid targets, regardless of target modality (vision or touch) (Macaluso *et al.*, 2002). Finally, the TPJ is more strongly activated by stimuli containing infrequent features across a range of perceptual dimensions (e.g. spatial location, visual form) (Marois *et al.*, 2000).

While these studies indicate that TPJ responds to salient or unexpected stimuli over a wide range of stimulus types, it is unknown if these activations depend on the response to the stimulus. The main aim of our study was to test whether blood oxygenation-level-dependent (BOLD) responses in the TPJ depend on the performance of an overt response or on the effector used to make the response (arm, foot, eye movements). We examined both the overall effect of the response variable on TPJ activation and whether this variable modulated the effects of target validity on attentional reorienting.

Material and methods

Experimental subjects

Fifteen subjects (six females and nine males; ages 19–24 years, mean 22 years) participated in Experiment 1, and 10 subjects (eight females and two males, ages 19–25 years, mean 21.7 years) participated in Experiment 2. All subjects were strongly right-handed as measured by the Edinburgh Handedness Inventory, had normal or corrected-to-normal vision, and a normal neurological history. Informed written consent was obtained in accordance with procedures approved by the local human studies committee.

Task and procedures

The analyses presented here are based on data from experiments that have been previously published (Astafiev *et al.*, 2003, 2004) and will be only briefly described. Stimuli were generated with an Apple G4

Macintosh computer (Apple Computers, Cupertino, CA, USA) using PsyScope 1.2.5 PPC software (Carnegie Mellon University, Pittsburgh, PA, USA). In the magnetic resonance scanner, stimuli were projected using an Epson PowerLite 703c liquid crystal display projector (Epson America, Long Beach, CA, USA) onto a small Plexiglas screen that was positioned within reaching distance in front of the subject and viewed through a periscope mirror attached to the head coil. The periscopic mirror did not introduce any distortion or scaling of the visual field. Eye position was monitored with an ASL 504 (Applied Science Laboratories, Bedford, MA, USA) eye-tracker during both behavioral and fMRI sessions. During the behavioral session of Experiment 1, electromyographic (EMG) activity was recorded from surface electrodes positioned on the right arm deltoid muscle using a BIOPAC MP100 system (BIOPAC Systems, Santa Barbara, CA, USA). A videocamera was used to verify that subjects performed the tasks (pointing with hand or foot) inside the scanner in Experiment 2.

A fixation cross-hair was displayed inside a grey diamond (size 1.6 °) on a black background at all times. A change in the color of the fixation point from red to green indicated the start of a trial. Simultaneously, one side of the diamond was illuminated for 100 ms indicating either a left or right location (cue stimulus). After a random delay (4.76–5.86 s in Experiment 1 and 2.6–3.7 s in Experiment 2), a white asterisk (target stimulus) was flashed for 100 ms 7.3 ° to the left or right of fixation. The stimulus occurred at the cued location in 73% of the trials (75% in Experiment 2) (valid trial), and at the opposite location in 27% (25% in Experiment 2) of the trials (invalid trial). In the attention condition, a random digit (1–9) was occasionally presented (either 0, 1 or 2 times in a block of trials) instead of the asterisk (only in Experiment 1). After another interval (0.44–1.54 s), which yielded a fixed trial (cue + test) duration of 6.50 s (4.33 s in Experiment 2), the fixation point changed color from green to red to indicate the end of the trial. Trials were separated by a random intertrial interval (ITI) of 2.16–6.50 s, in which the fixation point remained red. In 21% (20% in Experiment 2) of the trials, only the cue stimulus was presented, followed by a fixed interval of 4.23 s (2.07 s in Experiment 2) before the start of the ITI. The presentation of cue-only trials was necessary to separate cue and target fMRI responses within a trial without assuming a hemodynamic response function (Shulman *et al.*, 1999; Ollinger *et al.*, 2001a, b).

In Experiment 1, three different tasks were performed. In the 'right-hand pointing' task, subjects used the cue to prepare a pointing movement to the left or right with their right index finger. After the target was flashed, subjects pointed as quickly as possible in the direction of the target location (without touching the screen), and then returned to the starting position. Some subjects, because of their body size, could see their finger during the execution of the pointing movement. In the 'saccade' task, the cue was used to prepare a saccadic eye movement to the left or right. After the target was flashed, subjects looked at its location and then quickly looked back at the fixation point.

In the 'attention' task, subjects covertly shifted and maintained attention at the cued location, covertly detected the target, and returned attention to the center after the presentation of the target. A random digit was also occasionally presented at the target location instead of the target. Subjects reported at the end of a trial block how many times the digit was presented. The mean accuracy of the digit report was 97% correct. Trials in which the digit appeared were not included in the analysis. Each subject performed 15 scans, five scans per task, and each scan/block involved 28 trials.

In Experiment 2, three different tasks were performed: right-hand pointing, attention and right-foot pointing. The right-hand pointing task was the same as in Experiment 1. The attention task was similar to the task in Experiment 1, except that no digits were presented. The right-foot pointing task was similar to the right-hand pointing task, but subjects pointed with their right foot instead of their right hand. Each subject ($n = 10$) performed 15 scans, five scans per task, and each scan consisted of 30 trials. In Experiment 2, vision of the hand and foot was occluded.

fMRI scan acquisition and data analysis

A Siemens whole-body 1.5T Vision MRI scanner (Siemens AG, Germany) and asymmetric spin-echo, echo-planar sequence were used to measure BOLD contrast over the whole brain [TR (volume repetition time), 2.165 s; TE (echo time), 37 ms; flip angle, 90 °; 16 contiguous 8 mm axial slices; 3.75×3.75 mm in-plane resolution]. Anatomical images were acquired using a sagittal MP-RAGE sequence (TR, 97 ms; TE 4 ms; flip angle, 12 °; inversion time T1, 300 ms). Functional data were realigned within and across runs to correct for head motion using six-parameter rigid-body realignment.

In each subject, hemodynamic responses were estimated without any shape assumption at the voxel level using the general linear model. Random-effects analyses were performed by entering the individual time-points of each estimated hemodynamic response into voxel-level and regional ANOVAs. We focused our analysis only on the target period. In Experiment 1, ANOVAs were run on the time-courses from the target period with MR frame (1–8), Response Condition (right-hand pointing, saccade, attention), target Visual Field (left, right) and target Validity (valid, invalid) as factors. These analyses were based on about 2100 trials per task over the 15 subjects. Experiment 2 was analysed in a similar fashion, with three levels on the Response Condition factor (right-hand pointing, right-foot pointing, attention). Analyses were based on about 1500 trials per task over the 10 subjects.

Group-average anova F-maps were transformed to z-maps

The coordinates of responses in *z*-maps were identified by an automated algorithm that searched for local maxima and minima, and localized according to a stereotactic atlas (Talairach & Tournoux, 1988). Group-average *z*-maps were projected on the Colin-brain atlas(Van Essen *et al.*, 2001).

Results

Behavioral data

Behavioral responses, EMG and eye movement data from these experiments have been previously presented and will be briefly discussed here (Astafiev *et al.*, 2003, 2004). In Experiment 1, subjects were studied in separate behavioral and fMRI sessions. During the behavioral session, central fixation, measured with an infrared eye tracker, was similar during the cue period in all three conditions and during the target period in the attention and pointing tasks. Also, there was no differential EMG activity from the arm across tasks during the cue period or in the saccade and attention tasks during the target period. Eye position was also monitored during the fMRI sessions. The results from the analyses of all 15 subjects in Experiment 1 were confirmed in sub-analyses on the 11 subjects with acceptable eye movement records that included only trials in which accurate fixation (±1.5 °) was maintained during the right-hand pointing or attention tasks, and with execution of instructed saccades in the saccade task.

In the behavioral session of Experiment 1, we measured the efficacy of the central cue in speeding the response to a target at the attended location. Reaction times were faster to valid targets than invalid targets, both during the pointing (388 vs. 423 ms; $t_{14} = -4.28$; $P = 0.001$) and attention tasks (301 vs. 332 ms; $t_{14} = -4.86$; $P < 0.0001$). Therefore, a validity effect was demonstrated in the behavioral version of the attention task, confirming the use of the cue. However, because overt speeded responses were not collected during the MR version (instead subjects were instructed to covertly detect the targets and the digit-counting task was added), the MR version did not provide behavioral evidence for the use of the cue.

MRI data

First, we compared the BOLD signal in regions that were differentially modulated by performing a response, or by responding with a specific effector, with regions that were modulated by reorienting of spatial attention to an unattended (invalidly cued) location during the target period. Figure 1A shows group-average data from Experiment 1. All z-maps were thresholded at a low threshold ($z = 2.81$, $P = 0.005$ uncorrected) to reveal possible overlap between regions. Supplementary Fig. S1a (see Supplementary material section below) presents the same data, but corrected for multiple-comparisons. 'Response' regions, which are colored in red, showed a significantly different time-course of the BOLD response for the three response conditions (right-hand pointing, saccade, attention), as demonstrated by the significant Response Condition × Time interaction (time-points 1–8) in a voxel-wise ANOVA. 'Reorienting' regions, which are colored in green, showed a different BOLD time-course for valid and invalid targets, as demonstrated by the significant interaction of validity (valid/invalid) and time. Black and pink outlines represent the location of similarly defined reorienting regions in the right TPJ from two previously published studies (Corbetta et al., 2000; Kincade et al., 2005). Supplementary Fig. S1 (c and e) presents multiple-comparison-corrected z-maps for the Response Condition × Time and Validity × Time interactions to verify that each effect produced significant activation.

There was a good correspondence between the reorienting activation in the current and previous experiments. Regions of activation in the TPJ (supramarginal gyrus, SMG; superior temporal gyrus, STG) demonstrated strong 'reorienting' activations, but were not modulated by Response Condition, even at low threshold. To avoid possible bias and compensate for the different localization of the peak activation across experiments, we presented time-courses from regions defined on the basis of the current experiment as well as from regions defined independently from a previous experiment (Kincade et al., 2005) that measured the effects of target validity. Time-courses were extracted from the right SMG region (pink outline) centered at $x, y, z = 51, -51, 26$ (Kincade et al., 2005), and from all significantly active voxels ($n = 59$) within 25 mm of the peak TPJ activation (53, −48, 16) in the Validity × Time z-map from the current experiment. The right SMG (region from Kincade et al., 2005) demonstrated a significant Validity × Time interaction ($F_{7,98} = 2.57$, $P = 0.018$), using data from the present experiment, indicating the robustness of validity effects in the TPJ. However, neither this region nor the TPJ region defined from the voxel-wise map for Experiment 1 demonstrated a Response Condition × Time interaction (for the right SMG, $F_{14,196} = 1.6$, $P = 0.08$; for the right TPJ, $F_{14,196} = 1.42$, $P = 0.14$). The Response Condition × Validity × Time interaction was also not significant in either TPJ region, indicating that effects of reorienting on BOLD activation in the TPJ were not modulated by the nature of the response (for the right SMG, $F_{14,196} = 1$, $P = 0.46$; for

the right TPJ, $F_{14,196} = 1.03$, $P = 0.42$). The Response Condition × Validity interaction, measured using the average of time-points 4 and 5 (6.5–8.7 s, representing the peak magnitude of the BOLD signal), was also not significant in either TPJ region (for the right SMG, $F_{2,28} = 0.6647$, $P = 0.52$; for the right TPJ, $F_{2,28} = 1.866$, $P = 0.17$). Finally, a whole-brain voxel-level analysis did not reveal any voxels near the TPJ area showing a significant Response Condition × Validity × Time interaction (see Supplementary Fig. S2). A time-course analysis showed that the BOLD signal was higher in invalid than in valid trials in all three conditions, and that the size of the difference was similar irrespective of whether the target was covertly detected (attention) or detected by a saccadic or hand movement.

Similar results were observed in Experiment 2 (Fig. 1B). Supplementary Fig. S1b presents the same data, but corrected for multiple-comparisons. In this experiment subjects also performed the attention and right-hand pointing tasks of Experiment 1, but instead of the saccade task subjects pointed to the target using their right foot. As in Fig. 1, red voxels define 'response' regions that were differentially activated by the Response Condition (right-hand pointing, right-foot pointing or attention), and green voxels define 'reorienting' regions that were differentially activated by target validity. Black and pink outlines are identical to those in Fig. 1. Supplementary Fig. S1 (d and f) presents multiple-comparison-corrected maps of the Response Condition × Time and Validity × Time interactions to verify that each effect produced significant activation. There was some overlap (voxels colored in yellow) between response and reorienting activations in the right FEF and the ventral part of the right IPS, but no overlap in the TPJ. As for Experiment 1, time-courses were extracted from the right SMG region defined from our previous experiment (Kincade et al., 2005) (pink outline) and from all significantly active voxels ($n = 424$) within 25 mm of the peak TPJ activation (52, −51, 15) from the voxel-wise Validity × Time z-map for Experiment 2.

Time-courses for the SMG region defined from our previous experiment again demonstrated a significant Validity × Time interaction ($F_{7,63} = 2.99$, $P = 0.009$). Again, neither this region nor the region from within the current experiment demonstrated a significant Response Condition × Time interaction (for the right SMG, $F_{14,126} = 1.08$, $P = 0.38$; for the right TPJ, $F_{14,126} = 1.07$, $P = 0.39$). The Response Condition × Validity × Time interaction was also not significant in either TPJ region (for the right SMG, $F_{14,126} = 1.02$, $P = 0.43$; for the right TPJ, $F_{14,126} = 1.74$, $P = 0.055$). The Response Condition × Validity interaction, measured using the average of time-points 4 and 5 (6.5–8.7 s, representing the peak magnitude of response), was also not significant in either TPJ region (for the right SMG, $F_{2,18} = 0.2196$, $P = 0.8$; for the right TPJ, $F_{2,18} = 0.2265$, $P = 0.8$). Finally, a whole-brain voxel-level analysis did not reveal any significant Response Condition × Validity × Time interaction. Once again, the time-course analysis revealed a significantly higher response for targets presented at the unattended location (invalidly cued) irrespective of response or effector.

To determine whether the activation in the TPJ was affected by the addition of the digit-counting task to the attention condition in Experiment 1, we compared the magnitude of the BOLD response during the attention condition in the independently localized region in the right SMG (Kincade et al., 2005). In the right SMG there was no difference in signal magnitude during the attention condition between Experiment 1 and Experiment 2 (Time × Experiment, $F_{7, 161} = 0.9218$, $P = 0.49$).

We also analysed modulations due to reorienting and responding in another part of the ventral frontoparietal attention system, right VFC. In Experiment 1, no VFC voxel from the Validity × Time interaction
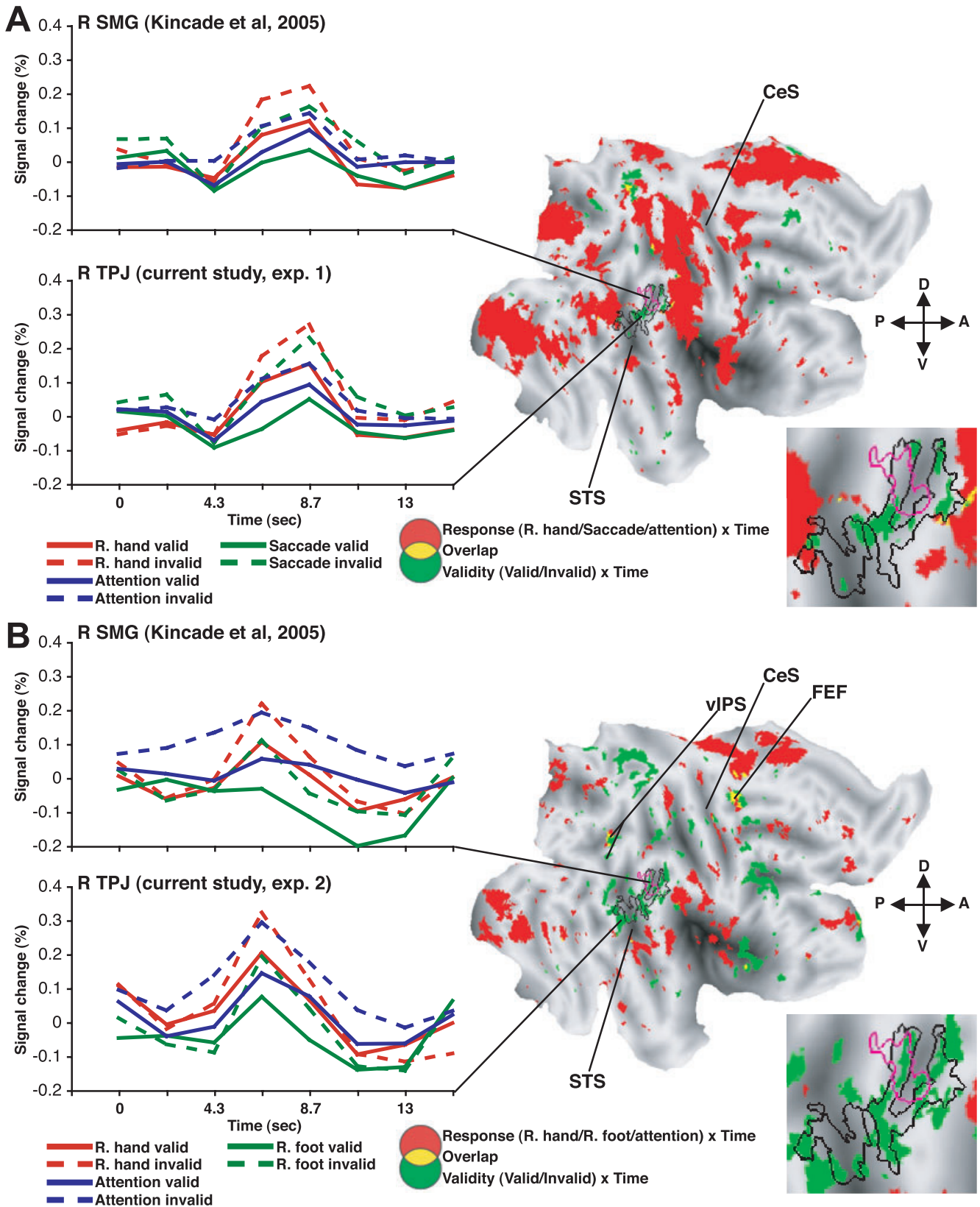
FIG. 1. 'Response' and 'reorienting' regions from Experiment 1 (A) and Experiment 2 (B). Data are projected on the flattened surface of the right hemisphere of the Colin brain (Van Essen *et al.*, 2001). The insert shows a magnified view of the area around temporo-parietal junction (TPJ). The black and pink outlines represent the locations of the right TPJ, from two previously published studies (Corbetta *et al.*, 2000; Kincade *et al.*, 2005). Graphics indicate group-average BOLD time-courses averaged over the target direction for valid and invalid targets across three tasks. Time-courses were extracted from the right SMG (supramarginal gyrus) region (pink outline; top), and from the TPJ region defined from the current experiments (A: from Experiment 1; B: from Experiment 2) (bottom). R, right; CeS, central sulcus; STS, superior temporal sulcus; vIPS, ventral intraparietal sulcus; FEF, frontal eye field.

map passed the multiple-comparison correction significance threshold, although VFC activity was present with a lower threshold. In Experiment 2, a region of interest (ROI) was constructed from all significantly active voxels within 25 mm of the peak VFC activation (33, 11, 12) in the Validity × Time z-map (see Supplementary Fig. S3). We also applied an ROI to both experiments in the right inferior frontal gyrus (IFG) that was defined from the Validity × Time z-map from (Kincade et al., 2005), x, y, z = 48, 12, 12 (black outline).

The right IFG ROI from Kincade et al. (2005) demonstrated a significant Validity × Time interaction in both experiments (in Experiment 1, $F_{7,98}$ = 2.5776, P = 0.018; in Experiment 2, $F_{7,63}$ = 2.3635, P = 0.033), but the Response Condition × Time interaction (in Experiment 1, $F_{14,196}$ = 1.3325, P = 0.19; in Experiment 2, $F_{14,126}$ = 0.5524, P = 0.9) and the (Response Condition × Validity) × Time interaction was not significant in either experiment (in Experiment 1, $F_{14,196}$ = 0.6112, P = 0.85; in Experiment 2, $F_{14,126}$ = 1.0417, P = 0.42). The right VFC ROI defined from significant voxels in the Validity × Time map of Experiment 2 was further analysed in that experiment and showed a similar result: there was no Response Condition × Time interaction ($F_{14,126}$ = 0.9663, P = 0.49) or Response Condition × Validity × Time interaction ($F_{14,126}$ = 0.9853, P = 0.47).

These results suggest that voxels in VFC or IFG that show validity effects also show a similar effector independence to TPJ. However, there was more variability in both the location of these frontal regions and their time-courses, which precludes us from drawing firm conclusions. Future experiments will be needed to resolve this question.

Discussion

The main aim of our study was to measure the activation of TPJ during the execution of different types of responses (eye movements, limb movements), during covert detection (i.e. the attention condition), and the relationship of these activations to activity related to spatial reorienting. The results from two experiments revealed that the overlap between reorienting and response modulations (i.e. the effects of target validity and response condition) was small (mainly ventral IPS and FEF in one experiment) even at a low threshold. While the response × Time interaction map was different in the two experiments, some of the overt motor tasks in the two experiments were also different. Experiment 1 included an eye condition, while Experiment 2 included a foot condition. Also, in Experiment 1 subjects had partial vision of their finger (discussed in Astafiev et al., 2004), which was completely occluded in Experiment 2. These differences might well have influenced the overall effect of response. We believe that the fact that the overlap between the response effect and the validity effect was minimal in both experiments, even though different response conditions were tested, strengthens our conclusion.

Moreover, visuospatial reorienting signals in the TPJ were independent of response modality, as shown by the absence of any interaction between target validity and response condition. Previous studies (Downar et al., 2000; Macaluso et al., 2002; Matsuhashi et al., 2004) have demonstrated that TPJ receives inputs from different sensory modalities and that reorienting signals in the TPJ are independent of sensory modality. The current results show that activity in TPJ related to reorienting (i.e. the difference for targets at unattended vs. attended locations) is independent of whether a response is made to the target, or of the effector used to respond.

These results extend the observations of Braver et al. (2001) who showed that TPJ response to oddball (low-frequency) targets as compared with standard targets is similar irrespective of whether the detection of the target is signaled by a single key press, by a go- vs. no-go response, or by a two-choice response. Therefore, while some parts of the dorsal frontoparietal attention system show specificity for the nature of the motor response (Andersen et al., 1990; Snyder et al., 1997; Astafiev et al., 2003), the TPJ appears response independent. Our data, taken together with the literature, suggest that TPJ may work as a supramodal 'circuit breaker' for the dorsal frontoparietal attention system, directing attention to salient events and enabling a variety of responses to those events.

Supplementary material

The following supplementary material may be found on

http://www.blackwell-synergy.com

Fig. S1. The same data as presented in Fig. 1, but corrected for multiple-comparisons.

Fig. S2. The multiple-comparison-corrected Response Condition × Validity × Time interaction map for Experiment 1.

Fig. S3. 'Response' and 'reorienting' regions from Experiments 1 and 2 in the VFC.

Acknowledgements

Abbreviations

BOLD, blood oxygenation-level-dependent; EMG, electromyographic; FEF, frontal eye field; fMRI, functional magnetic resonance imaging; IFG, inferior frontal gyrus; IPS, intraparietal sulcus; ITI, intertrial interval; ROI, region of interest; SMG, supramarginal gyrus; STG, superior temporal gyrus; TE, echo time; TPJ, temporo-parietal junction; TR, volume repetition time; VFC, ventral frontal cortex.

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