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Specific Visual Subregions of TPJ Mediate Reorienting of Spatial Attention

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Abstract

The temporo-parietal junction (TPJ) has been associated with various cognitive and social functions, and is critical for attentional reorienting. Attention affects early visual processing. Neuroimaging studies dealing with such processes have thus far concentrated on striate and extrastriate areas. Here, we investigated whether attention orienting or reorienting modulate activity in visually driven TPJ subregions. For each observer we identified 3 visually responsive subregions within TPJ: 2 bilateral ($vTPJ_{ant}$ and $vTPJ_{post}$) and 1 right lateralized ($vTPJ_{cent}$). Cortical activity in these subregions was measured using fMRI while observers performed a 2-alternative forced-choice orientation discrimination task. Covert spatial endogenous (voluntary) or exogenous (involuntary) attention was manipulated using either a central or a peripheral cue with task, stimuli and observers constant. Both endogenous and exogenous attention increased activity for invalidly cued trials in right $vTPJ_{post}$; only endogenous attention increased activity for invalidly cued trials in left $vTPJ_{post}$ and in right $vTPJ_{cent}$; and neither type of attention modulated either right or left $vTPJ_{ant}$. These results demonstrate that $vTPJ_{post}$ and $vTPJ_{cent}$ mediate the reorientation of covert attention to task relevant stimuli, thus playing a critical role in visual attention. These findings reveal a differential reorienting cortical response after observers' attention has been oriented to a given location voluntarily or involuntarily.

Key words: covert attention, endogenous attention, exogenous attention, fMRI, spatial attention, TPJ

Introduction

Covert attention, the selective processing of visual information in space without directing gaze, enhances visual processing at the attended location and is mediated by several cortical areas (e.g., Reynolds and Heeger 2009; Carrasco 2011). Attention reorienting allows processing at other locations, critical in an ever-changing environment (Corbetta et al. 2008; Dugué et al. 2015, 2016, 2017). Several functional imaging studies have investigated activity in the temporo-parietal junction (TPJ) for exogenous (involuntary) and endogenous (voluntary) covert attention (for reviews see Corbetta and Shulman 2002; Corbetta et al. 2008). The TPJ, proximal to the temporal, parietal, and occipital lobes, extends from the ventral bank of the intraparietal sulcus (IPS) to the dorsal bank of the superior temporal sulcus (STS) (Mars et al. 2012; Igelstrom et al. 2015), and is implicated in a broad variety of cognitive and social functions; for example,

attention, awareness, and theory-of-mind. Thus, it is likely that this region is an aggregate of several specialized subregions (see review Geng and Vossel 2013).

The TPJ is widely considered part of the ventral attentional network known to play a critical role in attentional reorienting of exogenous (Corbetta and Shulman 2002; Scholz et al. 2009) and/or endogenous attention (Kincade et al. 2005; Corbetta et al. 2008). The location and spatial extent of the TPJ varies across studies (see meta-analysis by Geng and Vossel 2013); and, given asymmetrical behavioral deficits in spatial attention following damage to each hemisphere (e.g., spatial neglect; Robertson 1999), more than half of the studies have concentrated on the right hemisphere, which is thought to control attentional shifts to both sides of the space. However, there is no consensus regarding either the hemispheric specialization or the specific subregions that mediate reorienting (Table 1).

Table 1 fMRI studies on the role of TPJ in attention. These studies were the attention studies included in the meta-analytic work from (Geng and Vossel 2013) and updated based on PUBMED literature search (until December 2015). The 4 main sections correspond to the attention manipulation that we identified in each of the studies and are grouped by task (detection or discrimination). For each study, we report the type of attention reported by the authors, the experimental manipulation, when applicable the specific manipulation allowing attentional reorienting (target, appearing as a single stimulus or among distractors, cue or response cue onset), the behavioral measurements (RT, Reaction Time; Hit, Hit Rate; FA, False Alarm Rate; c, criterion; CR, Correct Rejection Rate), whether eye movements were recorded during the scanning sessions (*, eye movements recorded but trials not removed for the fMRI analyses) and the TPJ involved (R, Right and/or L, Left hemisphere). Note that all studies defined the TPJ based on statistical maps from that study or earlier publications. The "Others" category includes a variety of studies using different types of attention manipulations—for example, feature-based attention, temporal attention, induced-blindness—which relate attentional activity to TPJ

Study	Type of attention reported	Experimental manipulation	Reorientation driven by	Measure	Eye	TPJ
Independent endogenous and exogenous cueing						
Detection task						
Peelen et al. (2004)	Endogenous and exogenous attention	2 cue types (separate blocks) Central arrow: 250 ms Validity: 75% Change in peripheral place-holder: 50 ms Validity: 50% Neutral (intermixed): 250/50 ms No ISI	Target onset (single stimulus)	RT	Yes	R
Mayer et al. (2004)	Endogenous and exogenous attention	2 cue types (separate blocks) Central arrow: 100 ms Validity: 70% Change in peripheral place-holder: 100 ms Validity: 50% Neutral (intermixed): 100 ms ISI: 100/800 ms	Target onset (single stimulus)	RT	No	R&L
Discrimination task						
Kincade et al. (2005)	Endogenous and exogenous attention	3 cue types Exo cue and neutral in same block; Endo in separate block Central arrow, neutral or peripheral colored singleton: 100 ms ISI: 2.06 s	Target onset (among distractors)	RT	Yes*	R
Present study	Endogenous and exogenous attention	2 cue types (separate blocks) Central line: 67 ms Validity: 75% ISI: 250 ms Peripheral line: 67 ms Validity: 50% ISI: 57 ms Pre- or postcueing	Response cue onset	d' (RT)	Yes	R&L
Interactive endogenous and exogenous cueing						
Detection task						
Geng and Mangun (2011)	Endogenous orienting and stimulus-driven reorienting	Bilateral stream of visual stimuli and 2 concurrent cue types: Central cue to orient: 12–18 s Validity: 100% peripheral infrequent cue at the unattended location to reorient	Target onset (among distractors)	d' & c (RT)	Yes	R&L
Discrimination task						
Indovina and Macaluso (2007)	Endogenous and exogenous reorienting	2 Concurrent cue types Central arrow to orient: 68 s Validity: 80% Peripheral checkerboard to reorient: 200 ms	Target onset (among distractors)	RT (% correct)	No	R&L
Natale et al. (2009)	Endogenous and exogenous reorienting	2 Concurrent cue types Central arrow to orient: 500 ms ISI: 800 ms Validity: 75%	Target onset (single stimulus)	RT (error rate)	Yes	R

(Continued)

Table 1 (Continued)

Study	Type of attention reported	Experimental manipulation	Reorientation driven by	Measure	Eye	TPJ
		Change in peripheral place-holder to reorient: 100 ms No ISI Validity: 50%				

Endogenous cueing

Detection task

Study	Type of attention reported	Experimental manipulation	Reorientation driven by	Measure	Eye	TPJ
Astafiev et al. (2006)	Visuospatial attentional reorienting	Central arrow: 100 ms ISI: 2.6–5.86 s Validity: ~75%	Target onset (single stimulus)	RT (outside scanner)	Yes	R
Chen et al. (2012)	Endogenous attention	Central arrow: 200 ms ISI: 400/700 ms Validity: 80%	Target onset (single stimulus)	RT	Yes	R
Corbetta et al. (2000)	Voluntary attention and target detection	Central arrow: 2.36 s No ISI Validity: ~75%	Target onset (single stimulus)	RT	No	R
Corbetta et al. (2002)	Voluntary attention and target detection	Central arrow: 2.36 s No ISI Validity: ~75%	Target onset (single stimulus)	RT	No	R
Doricchi et al. (2010)	Endogenous and stimulus-driven attention	Central arrow: 1.4–1.8 s No ISI Validity: 80/50%	Target onset (single stimulus)	RT	Yes	R&L
Giessing et al. (2006)	Visuospatial attention	Central arrow: 100 ms ISI: 400/700 ms Validity: 50/64/100%	Target onset (single stimulus)	RT	No	R&L
Lee and McCarthy (2014)	Attention reorienting	Central arrow: 800 ms ISI: 500–2000 ms	Target onset (single stimulus)	RT	No	R&L
Mitchell (2008)	Attention reorienting	Central arrow: 800 ms ISI: 500–2000 ms Validity: 75%	Target onset (single stimulus)	RT	No	R
Scholz et al. (2009)	Exogenous attention	Central arrow: 2 s Validity: 88%	Target onset (single stimulus)	RT	No	R
Thiel et al. (2004)	Visuospatial attention	Central arrow: 100 ms Neutral cue: 100 ms ISI: 400/700 ms	Target onset (single stimulus)	RT	Yes	R
Vossel et al. (2006)	Covert endogenous orienting	Central arrow: 100 ms ISI: 400/700 ms Validity: 90/60%	Target onset (single stimulus)	RT	Yes	R
Mattler et al. (2006)	Visual attention	Central letter: 100 ms ISI: 2.9 s	Target onset (single stimulus)	RT (error rate)	No	R&L
Silvetti et al. (2015)	Spatial attention	Central arrow: 1.4–1.8 s No ISI	Target onset (single stimulus)	RT (error rate)	Yes	R&L
de Haan et al. (2015)	Top-down and bottom-up attention	Central arrow: 200 ms ISI: 1.99/2.49/2.99 s Validity: 75%	Target onset (single stimulus)	RT (% correct)	Yes	R&L
Vossel et al. (2015)	Visuospatial attention	Central arrow: 200 ms ISI: 600 ms Validity: 88/69/50%	Target onset (single stimulus)	Saccadic response speed	Yes	R&L

Discrimination task

Study	Type of attention reported	Experimental manipulation	Reorientation driven by	Measure	Eye	TPJ
Arrington et al. (2000)	Spatial and object-based attention	Central arrow: 1 s Or object-cue: 1 s No ISI Validity: 80%	Target onset (among distractors)	RT	No	R
Ruff and Driver (2006)	Preparatory visual attention	Central arrow: 1 s ISI: 2–9 s Validity: 100%	–	RT (error rate)	Yes	R

(Continued)

Table 1 (Continued)

Study	Type of attention reported	Experimental manipulation	Reorientation driven by	Measure	Eye	TPJ
Vossel et al. (2009)	Visuospatial attention reorienting	Central arrow: 200 ms ISI: 600/900 ms Validity: 80%	Target onset (single stimulus)	RT (error rate)	Yes	R&L
Vossel et al. (2012)	Spatial attention orienting and reorienting	Central arrow: 200 ms ISI: 400/700 ms Validity: 90/60%	Target onset (among distractors)	RT (error rate)	Yes	R
Endogenous auditory cueing (discrimination task)						
Macaluso et al. (2002)	Covert spatial attention	Auditory cues: 1.7 s No ISI but mask: 100 ms Validity: 80%	Target onset (single stimulus)	RT	Yes	R&L
Mayer et al. (2009)	Endogenous attention	Auditory cue (1000 Hz) ISI: 100/800 ms Validity: 75/50%	Target onset (single stimulus)	RT	No	R
Mayer et al. (2006)	Endogenous auditory covert orienting and reorienting	Auditory cue (1000 Hz) ISI: 100–800 ms Validity: 75%	Target onset (single stimulus)	RT	No	L
Mastroberardino et al. (2015)	Goal-driven and stimulus-driven attention	Audio-visual cue: 400 ms ISI: 0/450 ms	Target onset (among distractors)	Inverse efficiency score (RT & error rate)	Yes	R
Exogenous cueing						
Detection task						
Lepsien and Pollmann (2002)	Covert exogenous attention	Peripheral whitening place-holder: 80 ms ISI: 100/200/500 ms Validity: 50%	Target onset (single stimulus)	RT (error rate)	No	R
Shulman et al. (2010)	Stimulus-driven attention	Peripheral colored square: 160 ms No ISI Validity: 100%	Shift cue (among distractors)	% correct (FA & RT)	Yes	R
Shulman et al. (2009)	Stimulus-driven attention	Peripheral colored square: 160 ms No ISI Validity: 100%	Shift cue (among distractors)	% correct (FA & RT)	Yes	R
Discrimination task						
Konrad et al. (2005)	Reorienting of attention	Peripheral asterisk: 150 ms ISI: 400 ms	Target onset (single stimulus)	RT (error rate)	No	R
Others						
Detection task						
Diquattro et al. (2013)	Feature-based attention	Central arrow: 500 ms ISI: 1.5–6.5 s Target: conjunction of color and spatial location	Target onset (among distractors)	RT (% correct)	Yes	R
Serences et al. (2005)	Voluntary and stimulus-driven attention	*RSVP* Both attention types in the same trial	Target onset (among distractors)	% correct	No	R&L
Asplund et al. (2010)	Goal-directed and stimulus-driven attention	*Surprise-induced Blindness (RSVP)* Both attention types in the same trial	Target onset (single stimulus)	Detection rate (Hit & FA)	No	R&L
Braver et al. (2001)	Attention	*Oddball* Target frequency: 17%	Target onset (single stimulus)	Detection rate (RT)	No	R
Downar et al. (2001)	Involuntary attention	*Oddball* 2 concurrent streams: visual and auditory Block types: attend to visual/auditory modality	Target onset (single stimulus)	Detection rate at ceiling	No	R&L
Shulman et al. (2003)	Visual attention	*Visual search* Motion and digit tasks	–	RT (FA & Hit)	No	R&L
Discrimination task						
Cieslik et al. (2010)		*Visual short term memory and attention*	–	Report rate & RT	No	R

(Continued)

Table 1 (Continued)

Study	Type of attention reported	Experimental manipulation	Reorientation driven by	Measure	Eye	TPJ
Gillebert et al. (2012)	Selective attention	*Visual short term memory and attention*	–	Report rate & RT	Yes	R
Todd et al. (2005)	Stimulus-driven attention	*Visual short term memory and inattentional blindness*	–	Report rate & RT	Yes	R
Tyler et al. (2015)	Temporal selective attention	*Oddball* Central pre- or postcue arrow	–	% correct	Yes	R&L
Pollmann et al. (2014)	Attention	Feature and conjunction searches Search array: 200 ms	–	Hit, CR & RT	No	R
No observable task						
Bray et al. (2015)	Visual attention	*Virtual reality navigation*	–		No	R&L
Downar et al. (2000)	Involuntary attention	*Oddball* 3 concurrent streams: visual, auditory and tactile Block types: attend to visual/ auditory/tactile modality	Target onset (among distractors)		No	R&L
Downar et al. (2002)	Attention	*Oddball* 3 concurrent streams: visual, auditory and tactile Block types: attend to visual/ auditory/tactile modality	Target onset (among distractors)		No	R

Attention is known to alter basic visual processes, such as contrast sensitivity and spatial resolution (reviews by Carrasco and Yeshurun 2009; Carrasco 2011, 2014; Anton-Erxleben and Carrasco 2013; Carrasco and Barbot 2015). Neuroimaging studies dealing with such processes have thus far concentrated on visually responsive cortical areas, in particular striate and extrastriate areas (Liu et al. 2005; Buracas and Boynton 2007; Li et al. 2008; Murray 2008; Herrmann et al. 2010; Pestilli et al. 2011). A recent study has reported a small, right-lateralized subregion of the TPJ that responds to visual stimuli (Horiguchi et al. 2016). In this study, we investigated whether attention orienting and reorienting modulate activity in TPJ subregions that respond to visual stimulation, that is, the visually responsive TPJ subregions.

To do so, here we followed a novel approach, which is commonly used for striate and extrastriate areas. First, we identified regions of interest (ROIs) using a statistically independent localizer; we identified the anatomical location and spatial extent of the TPJ subregions that respond to visual stimulation, that is, the visually responsive TPJ subregions. We identified 2 bilateral and 1 right-lateralized TPJ subregions that responded to visual stimuli presented at the relevant experimental locations in each observer. Second, we measured activity in these subregions to assess whether they are modulated during reorienting of endogenous and exogenous visual attention. We measured fMRI activity while observers concurrently performed a 2-AFC orientation discrimination task, which is contingent upon contrast sensitivity (Nachmias 1967; Carrasco et al. 2000; Pestilli et al. 2009), under 2 independent attention conditions—endogenous and exogenous attentional orienting—and 2 types of cueing—pre- and postcueing (before target onset and after target offset, respectively). Cues presented before and after the stimulus display alter both behavior (Kinchla et al. 1995; Ling and Carrasco 2006; Pestilli et al. 2009; Herrmann et al. 2010; Gazzaley and Nobre 2012; review by Carrasco 2011) and fMRI activity (Liu et al. 2005; Herrmann et al. 2010; Pestilli et al. 2011; Sergent et al. 2013). We manipulated the orienting and reorienting of attention as follows: we optimized the spatial and

temporal parameters of the cues for the orienting of endogenous and exogenous attention (for reviews see Carrasco and Yeshurun 2009; Carrasco 2011, 2014; Anton-Erxleben and Carrasco 2013; Carrasco and Barbot 2015), and we used a central response cue to directly compare reorienting in these 2 cases (Montagna et al. 2009; Herrmann et al. 2010; Barbot et al. 2012; Sergent et al. 2013). We used the same experimental protocol, task, stimuli, and observers, while measuring fMRI responses and concurrently measuring the behavioral consequences of both types of attention on perceptual accuracy. Our results established a link between 2 of the 3 visually responsive TPJ subregions and the reorienting of visual attention.

Materials and Methods

Observers

Five observers (3 females, 24–30 years old) with normal or corrected-to-normal vision participated in the study. Observers provided written informed consent. The University Committee on Activities Involving Human Subjects at New York University approved the experimental protocol. Each observer participated in 10 scanning sessions: 1 session to obtain a set of 3 high-resolution anatomical volumes, 2 sessions for retinotopic mapping, 1 session for MT+ localizer, 3 sessions for the exogenous attention condition and 3 sessions for the endogenous attention condition. Prior to the first scanning session of each attention condition, observers performed several practice sessions outside the scanner.

Stimuli

Stimuli were generated using MATLAB (MathWorks) and the MGL toolbox (http://gru.stanford.edu/doku.php/mgl/overview) on a Macintosh computer. Stimuli were displayed on a flat-panel display (NEC, LC-XG250 MultiSync LCD 2110; resolution: 1024 × 768 pixels; refresh rate: 60 Hz) housed in a Faraday box with an electrically conductive glass front, positioned at the rear of the scanner bore. Observers viewed the display through

an angled mirror attached to the head coil, at a viewing distance of 172 cm. The display was calibrated and gamma corrected using a linearized lookup table. A white fixation cross (0.3°) was present at the center of the screen throughout the experiment. The stimuli consisted of 2 gratings (4 cpd) windowed by raised cosines (3° of diameter; 7% contrast). The stimuli were presented in the bottom quadrants (5° horizontal eccentricity; −2.65° azimuth). Endogenous cues were white rectangles (0.7°), positioned adjacent to the fixation cross indicating one of the 2 lower quadrants (0.35° horizontal eccentricity from the edge of the fixation cross, and 0.35° azimuth). Exogenous cues were also white rectangles (0.7°), but were positioned adjacent to an upcoming grating stimulus, above the horizontal meridian (1° away from the edge of the grating stimulus; and the edge of the cue 4.44° horizontal eccentricity from the edge of the fixation cross) and vertically aligned with the stimulus.

Behavioral Procedure

A single trial lasted 1700 ms for the exogenous attention condition and 1900 ms for the endogenous attention condition (Fig. 1; note that for illustration purposes, the display is not at scale). In 40% of the trials (precue condition), a cue was shown first, followed by the pair the gratings. In 40% of the trials (postcue condition), the order of presentation of the cue and the gratings was reversed. In 10% of the trials, the gratings were not presented ("cue-only" trials). In the remaining 10% of the trials, neither a cue nor the gratings were presented ("blank" trials). For both precue and postcue trials, observers were instructed to report the orientation of a target grating, that is, clockwise or counter-clockwise compared with vertical, by pressing one of 2 keys. For cue-only and blank trials, observers were asked to press a third key.

Cues (both exogenous and endogenous) were presented for 60 ms, indicating either the left or the right grating location. The interstimulus interval (ISI) between the precues and the gratings was 50 ms for exogenous cues and 250 ms for endogenous cues, resulting in stimulus-onset asynchronies (SOA) of 110 ms and 300 ms, optimal delays to manipulate exogenous and endogenous attention respectively and maximize their behavioral consequences (Müller and Rabbitt 1989; Nakayama and Mackeben 1989; Mackeben and Nakayama 1992; Liu et al. 2006, 2007). The behavioral effects of endogenous attention are sustained (Ling and Carrasco 2006) and can thus still be present in later brain activity, as shown in ERP studies (Seiss et al. 2009). Further, the brain responses elicited by exogenous and endogenous cues are different during 300 ms following cue onset. The gratings were shown for 50 ms. For the postcue trials we used the same timings but inverted the order of presentation, so that the cues followed the stimuli (Kinchla et al. 1995; Carrasco and Yeshurun 1998; Liu et al. 2005; Pestilli et al. 2011). A response cue, presented for 800 ms, at the end of the trial indicated which of the 2 gratings was the target (50% of the trials at each location). Note that in all 4 trial conditions (exogenous/endogenous, pre-/postcueing), the response cue appeared
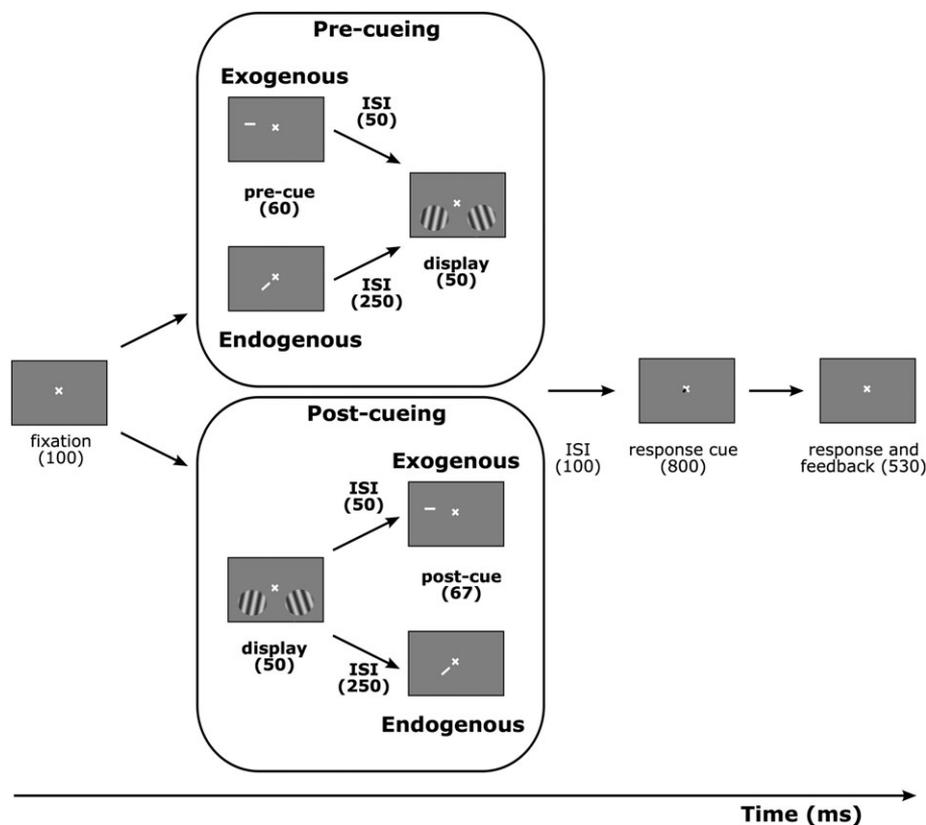
Figure 1. Experimental protocol. Observers performed a 2-AFC orientation–discrimination task. Precues were presented before the gratings. Postcues were presented after the gratings. Exogenous cues appeared in the periphery, above 1 of the 2 grating locations. Endogenous cues appeared at the center of the screen and pointed toward 1 of the 2 grating locations (The display is not at scale for the purpose visibility.). The ISI between the cue and the gratings differed between exogenous (50 ms) and endogenous (250 ms) conditions. A response cue indicated the target location, and instructed the observer to press 1 of 2 keys to indicate whether the target grating was tilted clockwise or counter-clockwise of vertical. The fixation cross turned green for a correct answer, and red for an incorrect answer.

after both the cue and the stimuli had disappeared. The maximum delay between the stimuli offset and the response cue onset was brief (~400 ms max in the endogenous condition). This time interval is less than typically associated with a demand for working memory (>600 ms; Phillips 1974). Visual feedback was provided immediately following each trial. The fixation-cross turned green or red to indicate a correct or incorrect response, respectively. If observers had not pressed any key after 530 ms, the fixation crossed did not change color indicating that they missed the response window.

Exogenous, peripheral cues were not informative regarding the target location or orientation; the cue and the target location matched in 50% of the trials (valid trials), but not in the other 50% of the trials (invalid). Endogenous, central cues were informative of the target location but not its orientation; cues pointed towards the target in 75% of trials (valid trials), but not in the remaining 25% of trials (invalid).

Each of the 3 sessions of the exogenous condition and 3 sessions of the endogenous consisted of 14 runs of 40 trials each, as well as an additional run of stimulus localizer (see MRI Procedure). Prior to the first session of each attentional scanning condition, observers performed 2 practice sessions outside the scanner. The tilt of the grating was adjusted so that each observer would achieve ~80% correct performance in the valid trials. During the scanning sessions, the tilt was adjusted between runs to maintain this overall performance level. Only correct trials were included in the MRI analysis. Eye position was monitored using an infrared video camera system (Eyelink 1K, SR Research, Ottawa, Ontario, http://www.sr-research.com/EL_1000.html). Trials in which the observers blinked or broke fixation (1.5° away from fixation) at any point during the trial sequence (from fixation onset to response cue offset; 13% ± 4% of the trials on average across all observers) were identified and removed from the behavioral analysis (see Results), and regressed separately in the MRI analysis (see below).

MRI Procedure

MRI Scanning

Imaging was conducted on a 3T Siemens Allegra head-only scanner (Erlangen, Germany). Padding was used to minimize observers' head movements. Anatomical images were acquired using a Siemens NM-011 head coil to transmit and receive. In a single scanning session for each observer, 3 high-resolution anatomic images were acquired using a T1-weighted magnetization-prepared rapid gradient echo (MPRAGE) sequence (FOV = 256×256 mm^2; 176 sagittal slices; $1 \times 1 \times 1$ mm^3 voxels). These 3 images were coregistered and averaged. We then used the public domain software FreeSurfer (http://surfer.nmr.mgh.harvard.edu), to segment the gray matter from these averaged anatomical volumes. All subsequent analyses were constrained only to voxels that intersected gray matter.

Functional images were acquired with a receive-only 8-channel surface coil array (Nova Medical, Wilmington, MA). T2*-weighted echo-planar imaging sequence (TR = 1750 ms; TE = 30 ms; flip angle = 90°) measured blood oxygen level-dependent (BOLD) changes in image intensity (Ogawa et al. 1990). One volume contained 28 slices oriented 45° to the calcarine sulcus and covered the occipital and posterior parietal lobes (FOV = 192×192 mm^2; resolution = $2 \times 2 \times 2.5$ mm^3; no gap). In each session, we acquired T1-weighted anatomical images in the same slices as the functional images (spin echo; TR = 600 ms; TE = 9.1 ms; flip angle = 90°; resolution = $1.5 \times 1.5 \times 3$ mm^3). The in-plane images were used to align functional images from different sessions to the same high-resolution anatomical volume for each participant, using a robust image registration algorithm.

Preprocessing of the MRI Data

Imaging data were analyzed using mrTools (http://gru.stanford.edu/doku.php/mrtools/overview) and custom software written in MATLAB. The first 8 volumes of each run were discarded to allow longitudinal magnetization to reach steady-state. The measurements of the B0 static magnetic field performed in each session were used to correct for spatial distortion. Preprocessing of the functional data included motion correction, linear trend removal, and temporal high-pass filtering (cutoff: 0.01 Hz) to remove low-frequency noise and slow drifts in the fMRI signal.

Retinotopic Mapping

Retinotopic mapping procedures followed well-established methods using conventional traveling-wave, phase-encoded methods. Phase maps of polar angle were measured using clockwise and counter-clockwise rotating checkerboard wedges, and eccentricity maps were measured using concentric and eccentric checkerboard rings (Engel et al. 1994, 1997; Sereno et al. 1995; Larsson and Heeger 2006). Borders of visual areas were drawn by hand on flattened surface representations of the brain following published conventions (Engel et al. 1997; Larsson and Heeger 2006; Wandell et al. 2007). The locations of retinotopic visual cortical areas were used as landmarks when defining the visually responsive TPJ subregions, that is, ensuring that none of the TPJ ROIs corresponded to retinotopic ROIs (see below and Fig. 3).

Localization of MT+

For each observer, we performed a functional localizer to delineate visual area MT+ (including both MT and MST). In a separate, dedicated scanning session, observers completed 2 runs (4.7 min each) consisting of a 2-condition block alternation protocol: 14 cycles, each cycle was 20 s (10 s of 100% coherent inward-outward dot motion at 5°/s, 10 s of stationary dots). Observers were instructed to fixate across at the center of the screen throughout each run. We took particular care in defining MT+ (comprising MT and MST) according to criteria in the published literature. In particular, we used 2 primary functional criteria to distinguish MT+. First, MT responds more strongly to coherently moving dots relative to static dots (Tootell et al. 1995a), setting it apart from neighboring areas LO1 and LO2 (Larsson and Heeger 2006). Second, MT is identifiable relative to nearby visual areas by its distinct topographic organization (Huk et al. 2002; Smith et al. 2006): MT is located anterolateral to LO1 and LO2 (Larsson and Heeger 2006), has a representation of the fovea that is different from neighboring visual areas, and has a complete representation of the contralateral hemifield. Applying these criteria enabled us to reliably identify MT in both hemispheres of all observers and to distinguish MT+ from the TPJ subregions.

Localization of Visually Responsive TPJ Subregions

The stimuli were the same size, spatial frequency, and location as those in the main experiment, but they were at full contrast, and their orientation and phase were randomly changed every 200 ms to avoid adaptation. A localizer run consisted of a 2-condition block alternation protocol: 16 cycles, each cycle was 17.5 s (8.75 s with the stimuli on, 8.75 s stimulus off). Observers completed one localizer run in each scanning session

of the main experiment (6 runs overall, 4 min each). Observers were instructed to fixate a cross at the center of the screen throughout each run. Data were averaged across the 6 runs and analyzed using the same methods as for the retinotopic mapping scans, to define the cortical representation of the gratings. Retinotopic regions in striate and extrastriate areas as well as IPS areas were activated by the stimulus (see Results). We also identified additional regions in the TPJ, anatomically defined as the region of cortex from the ventral bank of the IPS to the dorsal bank of the horizontal and main branches of the STS (Mars et al. 2012; Igelstrom et al. 2015). We ensured that none of the visually responsive TPJ subregions corresponded to other nearby previously identified visual areas (e.g., MT+, IPS). Each TPJ subregion was further restricted to voxels that responded positively during the blocks when the grating stimuli were presented. A sinusoid was fit to the fMRI time series from each voxel. To be conservative, voxels were included in the ROI if the best-fit sinusoid had a phase value between 0 and π, and if the correlation (technically, coherence) between the best-fit sinusoid and the time series was greater than 0.2. In addition, we conducted the analysis without restricting the ROI to this coherence level, yielding similar results that supported the same conclusions.

Event-Related Analysis

fMRI time series in the main (attention) experiment were averaged across voxels in each ROI (separately for each hemisphere) and then concatenated across runs. The data were denoised using GLMDenoise (https://github.com/kendrickkay/GLMdenoise; Kay et al. 2013). fMRI response amplitudes were then computed from the denoised data using linear regression, with twelve regressors: right and left valid precue, right and left invalid precue, right and left valid postcue, right and left invalid postcue, right and left cue-only, blank (no cue nor stimulus) and eye-movements (trials in which observers broke fixation or blinked). The resulting fMRI response amplitudes were then averaged across observers, separately for each ROI and separately for each hemisphere.

Statistics

Nonparametric randomization tests for fixed effect statistics were computed to test the difference between valid and invalid trials, in each ROI and in each attentional condition. For each observer, the condition labels were shuffled, and the fMRI response amplitudes were recomputed and reaveraged across observers. This permutation was done 10 000 times to construct null distributions. The null distributions were then compared with the actual fMRI responses (with the correct condition labels). The false discovery rate (FDR) was used to control for multiple comparisons, that is, 2 attentional conditions (exogenous and endogenous attention) and 5 ROIs, 3 in the right hemisphere (vTPJ$_{ant}$, vTPJ$_{cent}$, and vTPJ$_{post}$) and 2 in the left hemisphere (vTPJant and vTPJpost). We performed one-tailed statistical tests given our a priori hypothesis that invalid trials would elicit higher activity than valid trials in those TPJ areas.

Results

Meta-analysis

The precise definitions of the different types of attention and the different methods to manipulate each of them are essential for understanding the underlying neural system(s). There have been a large number of fMRI studies on the role of TPJ in covert attention, and we group them by type of attention manipulation and task (Table 1). But the type of attention discussed in these publications does not always match the experimental manipulation, and the experimental protocols have confounded what could be different processes:

a. Stimulus-driven reorienting to the target stimulus can follow the orienting of both endogenous and exogenous attention, but there is no reason to assume that the reorienting of these 2 attention types have the same neural substrate. So it is critical to investigate the role of TPJ with regard to both endogenous and exogenous attention, which should be precisely defined and operationalized using well-established psychophysics protocols maximizing each type of attention while keeping all other variables constant (Carrasco 2011). However, these ideal conditions have not been met. Only ~1/6 of the studies in Table 1 dealt with both types, ~6/8 exclusively with endogenous attention, and ~1/8 with exogenous attention. Moreover, 2/3 of the studies to manipulate either endogenous or exogenous attention, and all but one of the few studies that investigated both types of attention, assessed their effects on detection tasks using reaction times (RT) as their only or main dependent variable. However, differences in RT can be due to changes in decision criteria or to differences in discriminability (Reed1973; Wickelgren 1977; Carrasco and McElree 2001) and to motor behavior (Correa et al. 2010; Yashar and Lamy 2011), which confound interpretation of results.

b. Only 3 studies used accuracy as their main dependent variable to assess attention effects and all 3 did so with detection tasks, which cannot disentangle attention and decisional processing. Spatial cues should convey only information that is orthogonal to the task at hand (Carrasco 2011). In detection tasks, in which a high-probability cue encourages observers to direct their attention to a given location, it is hard to disentangle whether higher performance is due to facilitation of information coding at that location, probability matching, or a decision mechanism. In contrast, a discrimination task (e.g., orientation discrimination), because the cue conveys no information as to the correct response, can be used to assess whether the cueing effect reflects changes in sensory (d') rather than decisional (criterion) processing.

c. Even though exogenous attention (i.e., involuntary capture of attention) and stimulus-driven reorienting (i.e., reorienting to the target stimulus) refer to conceptually different processes, several authors have treated them indistinctly. Exogenous attention is shifted transiently and automatically to a particular location by either of 2 types of peripheral, salient stimuli: the sudden onset of a single object (a single cue), or the appearance of an array with a single unique element (e.g., capture by a color singleton). Both modulate low-level visual processing, but compared with a single cue, the behavioral effects of a color singleton are less pronounced and more constrained to the precise location of the unique element (White et al. 2014). Moreover, salient but irrelevant stimuli for the task at hand may capture exogenous attention without activating (what has been referred to as) the reorienting network (Chica et al. 2013). All but 2 of the studies summarized in Table 1 assessed attention reorienting as driven by target onset, thereby confounding reorienting with sensory stimulation.

d. In studies with spatial cues, the consequences of differences in stimulus conditions on attentional processing must not be overlooked when interpreting results. For ~75% of the studies, there was only one stimulus. With a valid cue there was a shift to the attended location and engagement (i.e., observers processed the stimulus at that location), whereas following an invalid cue there was no engagement (because there is no stimulus to process) and thus no disengagement prior to reorienting to the target location. Attentional shifting and engagement have been behaviorally dissociated (Folk et al. 2009) and could have distinct neural substrates. In the remaining ~25% of the studies, stimuli appeared at both the attended and unattended locations: with a valid cue there was a decision about the stimulus at the attended location, but in the case of an invalid cue, additionally, there was disengagement prior to reorienting.

e. Finally, most likely due to the difficulty of having an eye-tracking system in the MRI scanner, about half of the studies that manipulated spatial attention using exogenous and/or endogenous cues did not record eye movements. However, controlling for fixation is critical to study the orienting and reorienting of covert attention, which is not accompanied by gaze shifts to the attended location.

For all the studies summarized in Table 1, TPJ was localized based on statistical maps from the average data of ≥10 observers and, as mentioned above, more than half found that only the right TPJ was involved in attentional reorienting. Most studies averaged a weak evoked signal within the TPJ across many participants, complicating the identification of TPJ subregions. A better understanding of the anatomical location and spatial extent of the TPJ subregions is necessary to characterize their functional roles. According to recent TPJ parcellation studies, based on task-free fMRI data, both the left and the right TPJ can be subdivided into several subregions, belonging to distinct functional networks (Mars et al. 2012; Igelstrom et al. 2015). Additionally, a small, right-lateralized subregion within the TPJ, vTPJ, responds robustly to simple visual stimuli (Horiguchi et al. 2016). Hence, it is possible that specific subregions of TPJ may be involved in endogenous and/or exogenous attention.

In sum, many studies concluded that TPJ is a component of the ventral attentional network involved in the reorienting of spatial attention, some of which suggested that specific subregions of TPJ may be activated during reorienting (e.g., SMG, angular gyrus, STS). However, due to the conceptual and methodological shortcomings discussed above, none of the previous studies used an experimental protocol that enabled unambiguous conclusions. Consequently, no clear picture has emerged with respect to the hemispheric specialization, the specific subregions mediating reorienting in endogenous versus exogenous attention, and the degree to which activity in these regions corresponds to sensory processing, decisional processing, or reorienting per se.

Behavior

Observers ($n = 5$) performed a 2-AFC orientation–discrimination task under 2 attentional conditions (i.e., exogenous or endogenous attention), when the cue was presented either before (precue) or after (postcue) the grating stimuli (Fig. 1), and while their brain activity was measured with fMRI. The cue was either valid (50% of the time in the exogenous condition and 75% in the endogenous condition) or invalid. We calculated performance (d') in each condition, for each observer separately (Fig. 2A). We conducted a 3-way repeated measures $2 \times 2 \times 2$ ANOVA (exogenous/endogenous × valid/invalid × pre/postcue). There was better performance for valid than invalid cues ($F_{1,4} = 23.6$, $P = 0.008$). Exogenous versus endogenous cues were statistically indistinguishable ($F_{1,4} < 1$), and there was no evidence for a difference between pre- versus postcues ($F_{1,4} < 1$). None of the 2 or 3-way interactions were significant. RT was also calculated in each condition, for each observer separately (Fig. 2B). The corresponding 3-way ANOVA revealed that RT were faster for valid than invalid cues ($F_{1,4} = 62.3$, $P = 0.001$). There was no evidence for a difference between exogenous and endogenous cues ($F_{1,4} = 2.7$, $P = 0.17$), nor for precues and postcues ($F_{1,4} = 1.7$, $P = 0.27$). There were 2 significant interactions, indicating that the difference between precues and postcues ($F_{1,4} = 8.1$, $P = 0.047$) and between valid cues and invalid cues ($F_{1,4} = 16.2$, $P = 0.02$) were more pronounced for endogenous than for exogenous attention. These results show that attention improved orientation discrimination (both accuracy and RT), and rule out a speed-accuracy trade-off.
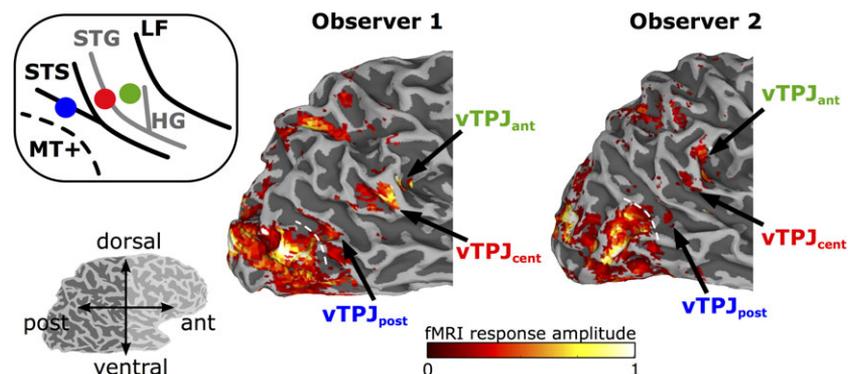
Visually Responsive TPJ Subregions

The TPJ is anatomically defined as the cortical region extending from the ventral bank of the IPS to the dorsal bank of the STS (Mars et al. 2012; Igelstrom et al. 2015). Regarding STS, we
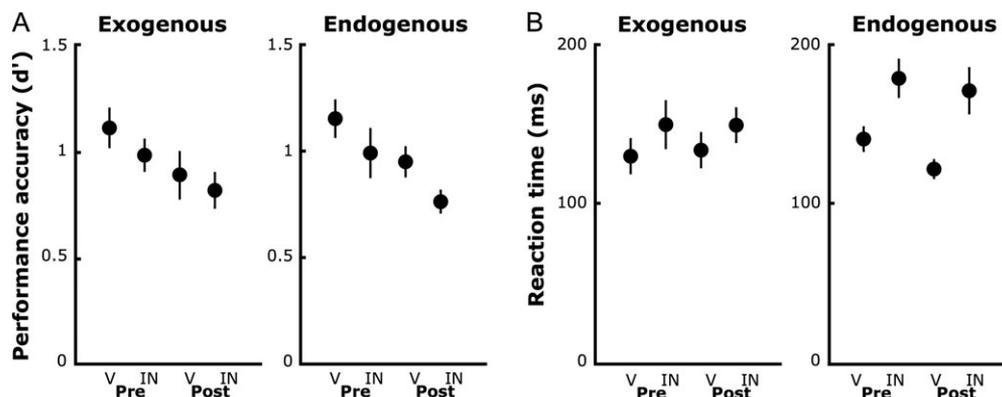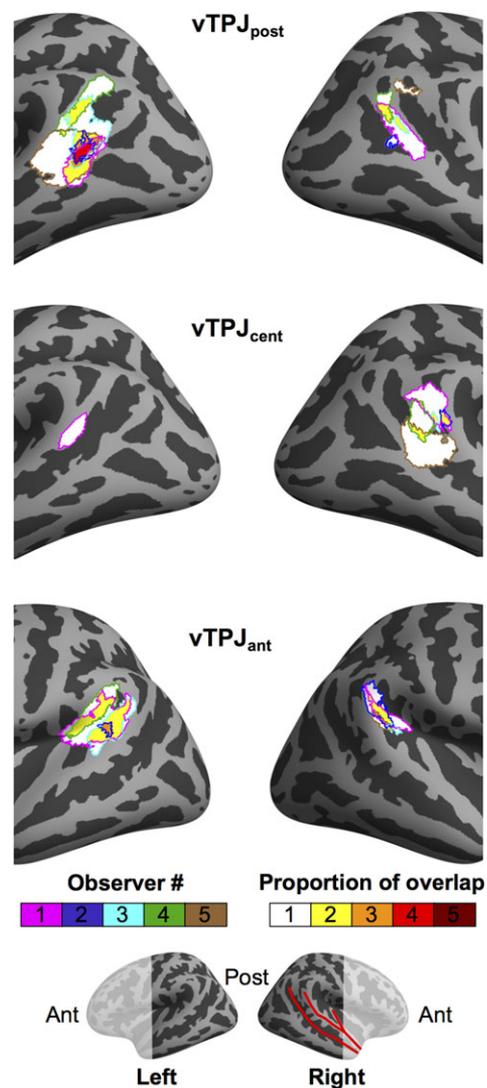
Figure 2. Behavioral performance. (A) Performance accuracy (d') averaged across observers ($n = 5$) as a function of cueing condition. (B) Reaction time. V, valid cue (location of precue/postcue and response cue matched). IN, invalid cue (location of precue/postcue and response cue mismatched). Pre, precue presented before the grating stimuli. Post, postcue presented after gratings. Valid cues led to more accurate and faster responses; there was no evidence for a speed-accuracy trade-off. Error bars on plot are ±1 SEM (standard error to the mean).

further refined this definition as anterior to MT+, within the STS. Within this region, we measured activity evoked by visual stimulation (the stimuli subtended the same size and were at the same location as in the main attention experiment) to identify 3 visually responsive TPJ subregions (Fig. 3). For each observer, we bilaterally defined: vTPJ$_{ant}$, located anterior to the superior temporal gyrus (STG), in the posterior part of the lateral fissure (LF); vTPJ$_{cent}$, located on the STG, just posterior to the Heschl's gyrus (HG); and vTPJ$_{post}$, located in (or posterior to) the horizontal branch of the STS. We defined vTPJ$_{post}$ in both the left and the right hemispheres of all observers; vTPJ$_{ant}$ in the right hemispheres of all observers and in the left hemispheres of 4 out of 5 observers; and vTPJ$_{cent}$ in the right hemispheres of all observers but in the left hemisphere of only one observer. Note that vTPJ$_{post}$ is adjacent to a previously defined multisensory region called STS-MS, localized in the most caudal part of the STS (Beauchamp et al. 2004). However, vTPJ$_{post}$ does not respond to auditory stimulation (Figure S2) suggesting that vTPJ$_{post}$ and STS-MS are 2 distinct regions.

To assess the variability among observers in size and location of the 3 visually responsive TPJ subregions, we performed 2 complementary analyses. In the first analysis, we created ROIs based on thresholded activity maps, using a coherence threshold of 0.2. We then projected these ROIs onto the cortical surface, and aligned each individual's cortical surface to an atlas using FreeSurfer software (Fischl, Sereno, and Dale 1999; Fischl, Sereno, Tootell, et al. 1999). The 3 TPJ subregions varied in location and size across observers. At most 3 out of the 5 observers had overlapping ROIs (Fig. 4). Curiously, there was less overlap in the right hemisphere, even though all 3 regions were identified in the right hemispheres of all observers. Moreover, the ROIs varied substantially in terms of both size (Table 2) and location (Table 3). We also found that vTPJ$_{post}$ and vTPJ$_{ant}$ were larger in the left than in the right hemispheres of each of the 5 observers. In the second analysis, which did not require defining ROIs, we took the fMRI responses from the localizer for each observer and projected the measurements onto the FreeSurfer atlas. We then averaged across observers. This analysis yielded robust responses in visual cortex, in areas that have a highly reliable location with respect to the underlying cortical anatomy. But this analysis did not yield reliable responses in any of the 3 TPJ regions (Figure S1). This second analysis confirms that the TPJ is highly variable in size and location, and is hence best suited to an analysis approach that targets individual observers, rather than group averages.

Figure 4. Inter-observer variability. The cortical surfaces of 5 observers were aligned using FreeSurfer. The outline of each of the 3 vTPJ subregions is represented with a different color for each observer. Colored background, proportion of observers whose ROIs overlapped. In the bottom images are marked in red the 3 main branches allowing vTPJ identification: STS, STG and HG, same convention as in Figure 3.

Figure 3. Visually responsive TPJ subregions. The posterior lateral surface of the right hemisphere in 2 observers. Colors indicate fMRI response amplitudes from the localizer experiment, for those voxels that exhibited reliable responses to the grating stimuli (relative to fixation). Voxels were selected by their signal-to-noise-ratio (coherence > 0.2) and response timing (temporal phase between 0 and π, corresponding to when the grating stimuli were presented). Dashed white curves, anterior edge of MT+ (defined with a motion localizer). The schema in the upper left represents the approximate anatomical location of the 3 regions relative to specific landmarks: MT+, STS, Superior Temporal Sulcus; STG, Superior Temporal Gyrus; HG, Heschl's Gyrus; and LF, Lateral Fissure.

Attentional Reorienting in the TPJ Subregions

We found evidence for reorienting (i.e., significantly higher fMRI activity for invalid than valid cues) in several ROIs (Fig. 5). For each ROI (Figs 3 and 4), that is, $vTPJ_{post}$, $vTPJ_{cent}$, and $vTPJ_{ant}$ in both hemispheres, we measured the fMRI response amplitudes for each attentional condition—exogenous and endogenous—and each cueing condition—pre- and postcueing (Fig. 5). In the case of the right $vTPJ_{post}$, we observed significantly larger responses for invalid trials (regardless of pre- or postcueing) for both exogenous and endogenous attention conditions (exogenous, $q = 0.013$; endogenous, $q = 0.013$); controlling for multiple comparisons using a FDR (Benjamini and Hochberg 1995). For the left $vTPJ_{post}$, we observed significantly larger responses in invalid trials (regardless of pre- or postcueing) for the endogenous condition ($q = 0.04$) but not for the exogenous condition ($q > 0.1$). In the case of the right $vTPJ_{cent}$ (left $vTPJ_{cent}$ was only observed in one participant), significantly larger responses were measured in invalid trials for the endogenous attention condition only ($q = 0.003$), and marginal for exogenous attention ($q = 0.07$). There was no evidence for differences in $vTPJ_{ant}$ activity between valid and invalid cues, for either attentional condition in either hemisphere. Finally, comparing pre- versus postcueing (pooling across valid and invalid conditions) revealed no significant differences.

Discussion

Localization of TPJ Visual Subregions

In the TPJ, a large region of cortex ($\sim 50\ cm^2$), we identified 3 visually responsive subregions exhibiting reliable responses to the onset of a visual stimulus during fixation. Two regions were activated bilaterally, $vTPJ_{post}$ and $vTPJ_{ant}$, whereas one region, $vTPJ_{cent}$, was consistently observed only in the right hemisphere. Activation in the right $vTPJ_{cent}$ is consistent with a recent study that reported a small, right-lateralized subregion of the TPJ that responded robustly to a large visual grating that was presented while observers performed an oddball task (Horiguchi et al. 2016). Our results are also in line with a recent parcellation study

of the TPJ, based on task-free fMRI data, showing that 5 subregions compose the right TPJ, and only 4 subregions compose the left TPJ (Igelstrom et al. 2015). Note, however, that direct comparisons with this study are hard to draw because those data were acquired while observers fixated a central cross and the data were averaged across a large number of observers.

Human neuroimaging studies often combine data from many observers by warping the measurements from each individual's brain to a standard template. Whereas this approach facilitates the identification of brain activity patterns that are common in a population, it is inappropriate when studying regions that are highly variable in size and location across individuals. In particular, all of the previous research on the role of the TPJ region in the orienting and reorienting of visual attention has used this approach, undermining precise localization of TPJ subregions. Instead, we used a simple visual localizer to identify visually responsive TPJ subregions, separately for each individual, and then analyzed the measurements from the main attention experiment in these individually defined subregions. We would have not been able to conduct these analyses, had we used group-averaging methods (Figure S1).

There has been a long-standing debate about the relative merits of ROI-based analysis versus analysis approaches that depend on statistical parametric mapping (Friston et al. 2006; Saxe et al. 2006) to identify parts of the brain that are active during task performance. Whereas both approaches clearly are important for studying brain function, a concern has been recently raised about the statistical validity of statistical parametric mapping (Eklund et al. 2015). We note that our approach is not subject to this concern.

### Reorienting Following Endogenous and Exogenous Attentional Orienting

For each of the 3 subregions that we identified, we measured fMRI responses to the endogenous and exogenous attention, using the same experimental protocol, task, stimuli, and observers. The results revealed that, regardless of the cueing order (i.e., pre- or postcueing), $vTPJ_{post}$ was involved in the reorienting process following both endogenous and exogenous attentional orienting, and $vTPJ_{cent}$ was involved primarily in reorienting following endogenous attentional orienting, whereas $vTPJ_{ant}$ was not involved in reorienting following either endogenous or exogenous attentional orienting. We acknowledge that additional TPJ subregions that we have not identified with our visually responsive localizer may also play a role in attentional reorienting. We cannot rule out the possibility that the other localizers would identify other subregions with different properties. Note that the goal of this study was to investigate whether and how visually responsive TPJ subregions are involved in attention orienting and reorienting, rather than to localize all TPJ subregions involved in attentional reorienting. Figure S3 shows the coordinates reported

Table 2 Size of the visually responsive TPJ subregions. The volume of each ROI is reported in cm^3 for each hemisphere and each observer

Observer #	Left			Right		
	$vTPJ_{post}$	$vTPJ_{cent}$	$vTPJ_{ant}$	$vTPJ_{post}$	$vTPJ_{cent}$	$vTPJ_{ant}$
#1	1.95	–	2.90	1.04	1.05	0.61
#2	1.48	–	1.97	0.27	0.70	1.92
#3	3.59	–	2.46	0.28	0.64	0.33
#4	2.96	1.62	5.70	1.60	3.60	0.78
#5	4.46	–	–	1.06	4.80	0.46

Table 3 Talairach coordinates of each individual ROI. The xyz coordinates of the most active voxel are reported for each ROI

Observer #	LEFT									RIGHT								
	$vTPJ_{post}$			$vTPJ_{cent}$			$vTPJ_{ant}$			$vTPJ_{post}$			$vTPJ_{cent}$			$vTPJ_{ant}$		
#1	−49	−60	7	–			−52	−48	15	49	−60	7	48	−46	10	48	−40	11
#2	−44	−63	9	–			−49	−56	18	40	−58	−6	61	−59	2	52	−55	11
#3	−49	−69	6	–			−43	−47	12	51	−63	7	51	−45	6	42	−41	14
#4	−55	−63	8	−63	−52	6	−57	−44	17	45	−61	9	62	−41	18	53	−38	23
#5	−48	−51	6	–			–			52	−64	29	39	−46	7	51	−36	14
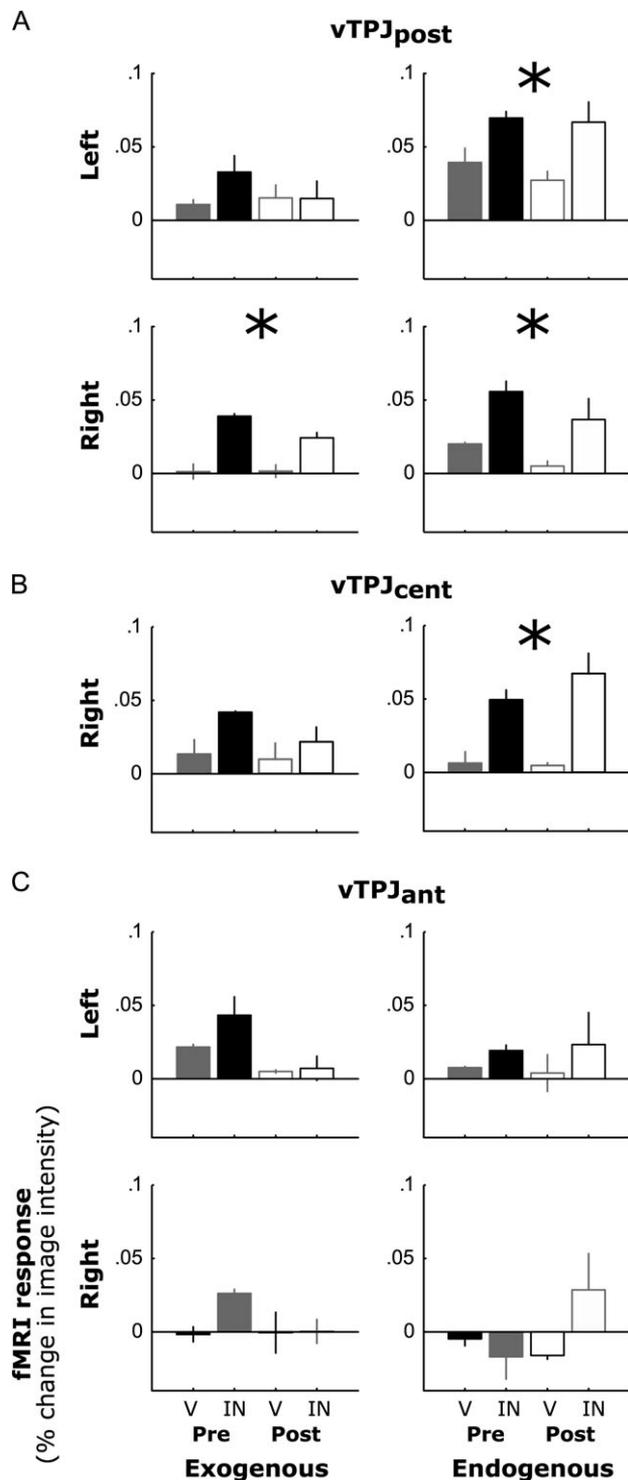
Figure 5. Specificity of each visually responsive TPJ subregion in attentional reorienting. fMRI response amplitudes were measured for each attentional condition, separately in right and left (A) vTPJ$_{post}$ (B) vTPJ$_{cent}$, and (C) vTPJ$_{ant}$. V, valid cue (location of precue/postcue and response cue matched). IN, invalid cue (location of precue/postcue and response cue mismatched). Pre, precue presented before the grating stimuli. Post, postcue presented after gratings. *Statistically significant difference between invalid and valid. Error bars on plot are ±1 SEM.

in Geng and Vossel's (2013) attentional TPJ meta-analysis, as well as the visually responsive TPJ subregions involved in attention orienting and reorienting, vTPJ$_{post}$, vTPJ$_{cent}$.

Our findings go beyond the classic view of a ventral, right lateralized attentional reorienting system (Corbetta and Shulman 2002; Corbetta et al. 2008), because we found differential activity for reorienting following endogenous and exogenous attentional orienting and their effects on basic visual processes. First, right vTPJ$_{cent}$ showed a more consistent response to reorienting following endogenous than exogenous attentional orienting. This result is consistent with the observation that >75% of studies that manipulated endogenous attention (Table 1) found TPJ activity during reorienting elicited by the target onset, and all but one study reported activity in the right TPJ either exclusively or in addition to activity in the left TPJ. Our findings suggest that this asymmetry may be driven by this vTPJ$_{cent}$ subregion.

Second, we found that vTPJ$_{post}$ was bilaterally involved in reorienting following both endogenous and exogenous attentional orienting. This result reveals that this subregion plays a role in attentional reorienting to task relevant stimuli, regardless of the type of attention. Although in our study, for both endogenous and exogenous attention, reorienting was elicited by a central cue presented at fixation (instead of by target onset as in many previous studies), our observation of bilateral activity is in line with studies reporting that both the left and the right hemispheres are active during reorienting endogenous and exogenous attention (Mayer et al. 2004; Doricchi et al. 2010; Silvetti et al. 2015).

Our findings suggest that bilateral activity during attentional reorienting may be driven by this vTPJ$_{post}$ subregion. Bilateral activity has also been reported during an endogenous cueing detection task, in which fMRI responses differed between neutral and invalid cueing (attentional reorienting elicited by the target onset) in both the right and left TPJ, and between valid and neutral cueing in the left TPJ (Doricchi et al. 2010; Silvetti et al. 2015). Because in those studies, the activity in the left TPJ differed from neutral in both valid and invalid cue conditions, a conventional valid/invalid fMRI contrast would not reveal left TPJ activity. Additionally, the location of vTPJ$_{post}$ is similar to that of a region described in a study of functional connectivity of the parietal cortex during temporal selective attention (Tyler et al. 2015). Although the authors reported that their posterior, bilateral TPJ region was connected to nodes within the default mode network, rather than the attention network.

Both pre- and postcueing facilitated behavioral performance in valid trials and evoked greater activity in invalid trials. Some studies have shown that a postcueing manipulation affects perception (Kinchla et al. 1995; Vogel et al. 2005; Sergent et al. 2013) and induces neural modulation even in early visual areas (Vogel et al. 2005; Pestilli et al. 2011; Gazzaley and Nobre 2012; Sergent et al. 2013), whereas other studies have reported that postcues neither affect behavioral performance (Carrasco and Yeshurun 1998; Gobell and Carrasco 2005; Liu et al. 2005), nor modulate neural activity in early visual areas (Liu et al. 2005). The differences may reflect different task parameters allowing the postcue to affect the post-perceptual or readout processes. For instance, in studies in which the postcue did not affect performance, observers knew at the time of stimuli presentation which stimulus they were going to report (e.g., observers had to report the orientation of the tilted stimulus and the other stimulus was vertical). In contrast, in the present study, the identity of the target was known only at the end of the trial sequence, when the response cue appeared (Fig. 1). Our results indicate that the postcue enabled a successful readout and affected behavioral performance by inducing changes in the neural representation of the stimulus after stimulus encoding.

Conclusion

The present results document the location of 3 distinct visually responsive TPJ subregions, and link one subregion to reorienting following endogenous and exogenous attentional orienting (bilateral vTPJpost), and another subregion to reorienting following endogenous attentional orienting (right vTPJcent). These findings go beyond the classic view of a ventral, right-lateralized attentional system. They show that this system is neither only driven by the sensory salience (Corbetta and Shulman 2002) nor only by the target stimulus behavioral relevance (Corbetta et al. 2008), and that the reorienting response is distinct after observers' attention has been oriented to a given location voluntarily or involuntarily.

The lack of definitive conclusions from previous studies about the role of TPJ subregions in orienting and reorienting endogenous and exogenous attention (Table 1) may be due to critical methodological factors: (1) endogenous and exogenous attention were not optimally manipulated and (2) the group-averaging methods generally used to map brain regions in the reorienting of attention were coarse and may have conflated activation from different subregions. We note that some studies have employed an alternative approach, which consists in searching for individual-specific ROIs within an anatomical region in which the group peak resides (Geng and Mangun 2011; Silvetti et al. 2015). The importance of individual observer analysis has been also illustrated in a recent fMRI study that revealed interleaved vision-biased and auditory-biased attention subregions in human lateral frontal cortex, where prior studies using group-averaging methods had reported modality-independent activity (Michalka et al. 2015). Using individual ROI-based analysis is optimal in hypothesis-driven studies in which particular brain regions can be identified a priori and then the modulation brought about by attention or other cognitive states can be measured in those predefined regions.

Future research is necessary to investigate whether the visually responsive regions defined in this study are the same TPJ regions involved in all forms of attentional reorienting (e.g., feature-based attention, object-based attention), whether these 3 regions participate in other cognitive functions (e.g., awareness, memory), and whether other regions that are not visually responsive also play a role in reorienting endogenous and/or exogenous attention.

Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

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Notes

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