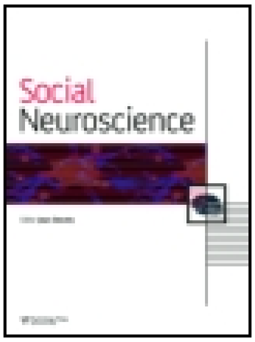

Social Neuroscience

ISSN: 1747-0919 (Print) 1747-0927 (Online) Journal homepage: http://www.tandfonline.com/loi/psns20

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To cite this article: Ceylan Özdem, Marcel Brass, Laurens Van der Cruyssen & Frank Van Overwalle (2016): The Overlap between False Belief and Spatial Reorientation in the Temporo-Parietal Junction: The role of Input modality and Task, Social Neuroscience, DOI: 10.1080/17470919.2016.1143027

To link to this article: http://dx.doi.org/10.1080/17470919.2016.1143027

Publisher: Taylor & Francis

Journal: *Social Neuroscience*

DOI: 10.1080/17470919.2016.1143027

The Overlap between False Belief and Spatial Reorientation in the Temporo-Parietal Junction: The role of Input modality and Task

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(“Van der Cruyssen” and “Van Overwalle” are the last names; ‘Van’ is not the middle name)

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Running Head: Overlap between Spatial Reorientation and False Belief
[Ceylan_Overlap]

Keywords: Theory of Mind, Social Mentalizing, Attentional Reorientation, Temporo-parietal Junction, Spatial Attention

Words: 4903

Abstract

Neuroimaging research has demonstrated that the temporo-parietal junction (TPJ) is activated when unexpected stimuli appear in spatial reorientation tasks as well as during thinking about the beliefs of other people triggered by verbal scenarios. While the role of potential common component processes subserved by the TPJ has been extensively studied to explain this common activation, the potential confounding role of input modality (spatial versus verbal) has been largely ignored. To investigate the role of input modality apart from task processes, we developed a novel spatial false belief task based on moving shapes. We explored the overlap in TPJ activation across this novel task and traditional tasks of spatial reorientation (Posner) and verbal belief (False Belief vs. Photo stories). The results show substantial overlap across the same spatial input modality (both reorientation and false belief) as well as across the common task process (verbal and spatial belief), but no triple overlap. This suggests the potential for an overarching function of the TPJ, with some degree of specialization in different subregions due to modality, function and connectivity. The results are discussed with respect to recent theoretical models of the TPJ.

Introduction

What attracts our attention when we observe social agents and attempt to infer their goals or beliefs? One of the surprising findings during the last decade of social neuroscience research is that inferring the intentions and beliefs of another person activates the same cortical area in humans as reorienting our attention to unexpected stimuli. This area is the temporo-parietal junction (TPJ) in the ventral parietal cortex, particularly in the right hemisphere, which is part of the mentalizing network involved in tracking the mental state of other people (see meta-analyses by Decety & Lamm, 2007; Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Van Overwalle & Baetens, 2009), as well as of the ventral attention network involved in attention allocation (see review by Cabeza, Ciaramelli, & Moscovitch, 2012).

The involvement of the right TPJ in social mentalizing and attention has been confirmed in meta-analyses of neuroimaging research (Decety & Lamm, 2007; Krall et al., 2014; Van Overwalle & Baetens, 2009). More convincingly, in studies using the same participants, Mitchell (2008) found an overlap between these processes in the right TPJ, although Scholz et al. (2009) found less overlap using a higher magnetic field with higher resolution and more individualized statistical analyses.

The functional overlap in the right TPJ, although perhaps limited, has been explained by a number of theoretical accounts. Some theorists put forward an *overarching view* that integrates basic attentional and social processes by referring to an underlying shared process (Krall et al., 2014). Among the proponents of this view, Decety and Lamm (2007) suggested that activation in the right TPJ during social cognition may rely on a lower-level computational mechanism involved in generating, testing, and correcting internal predictions about external sensory events. Van Overwalle (2009) suggested that attribution of intentionality and mental state requires a “where-to” shifting function that is also evident in attention reorientation. Along similar lines, Cabeza, Ciaramelli and Moscovitch (2012) explained the shared role of the TPJ by extending an earlier attention model put forward by Corbetta and Shulman (2002). According to the 2002 model, unexpected stimuli in our environment are captured by a ventral attention network including the TPJ, which reorients attention to these salient stimuli. According to the extension by Cabeza, Ciaramelli and Moscovitch (2012), attention can be allocated not only to unexpected external stimuli, but also to one’s internal memory. For example, attention to a familiar face may give rise to an outpour of recollections from autobiographic memories, involving one’s own intentions and mental states, raising awareness of possibly similar experiences within the other person.

Consequently, reorientation to internal memory and extracting information from it can explain the role of the TPJ in belief reasoning. Indeed, understanding that another person holds divergent or “false” beliefs requires remembering an agent’s behavior in a given context, and the realization that he or she may lack sufficient knowledge about a critical event (see also Van Overwalle, 2010). More recent accounts elaborated on this model. The “nexus” model by Carter and Huettel (2013) suggests that the TPJ is a convergence point of multifunctional areas around it, and so allows crosstalk between information inputs which could support the functions of reorienting attention to salient external stimuli and integration in a social context arising from internal goals, memory and semantic abstraction. Geng and Vossel (2013) proposed a “contextual updating” hypothesis which focuses on the role of the TPJ in updating internal models of the current behavior for the purpose of appropriate actions, which is critical when unexpected stimuli occur.

Taken together, recent theoretical accounts on an overarching function of the TPJ allow for an integration of common (basic reorientation of attention) as well as specific processes (belief updating). Nevertheless, as put forward by Cabeza et al. (2012), their overarching view can also explain differences around the edges of the TPJ under the assumption that the strength of TPJ connectivity with different brain regions that provide input differs gradually across TPJ subregions.

In contrast, other theorists put forward a *fractionation view* stating that there are distinctive subregions in the right TPJ (Krall et al., 2014). Several parcellation results suggest a sharp division between anterior and posterior TPJ subregions based on structural and functional connectivity reflecting distinct functional processes (Bzdok et al., 2013; Kubit & Jack, 2013; Mars et al., 2011). An anterior TPJ cluster functionally associated with attention, and a posterior TPJ cluster functionally associated with social mentalizing. However, one critical limitation of these parcellation techniques is that when a division exists, a sharp boundary is drawn between clusters and voxels are forced into only one cluster. To illustrate, in the approach by Bzdok et al. (2013), “individual voxels … are … successively included into a growing hierarchy by merging the most similar clusters into progressively larger sets of voxels” (p. 384). This may obscure potential overlap and underlying shared processes between distinct functional clusters.

A recent meta-analysis (Krall et al., 2014) suggests a resolution of these two opposing views. It was found that the anterior TPJ is a common area supporting reorientation of attention and false belief, consistent with the overarching view. However, the posterior TPJ was found to support only distinct social belief processes, consistent with the fractionation view.

An important limitation in testing these distinct theoretical positions is that most often, experimental tasks were used that differed in their input modality, even when comparing within the same participants (Mitchell, 2008; Scholz et al., 2009). A spatial modality based on visual input was typically used to investigate attention reorientation by Posner's (1980) cuing task. In this task, a cue (e.g., an arrow) indicates the correct location of the upcoming target stimulus in some trials (valid trials), while in other trials the cue indicates the incorrect location (invalid trials). Invalid trials lead to longer response times and higher activation of the right TPJ (meta-analyses by Decety & Lamm, 2007; Van Overwalle & Baetens, 2009). In contrast, a verbal modality was typically used to investigate another person's mental state using false belief scenario's in which an object is removed in the absence of the protagonist, who thus holds false beliefs about reality (e.g., Saxe & Kanwisher, 2003). False beliefs show increased activation of the right TPJ in comparison with true beliefs (see meta-analyses by Schurz, Radua, Aichhorn, Richlan, & Perner, 2014; Van Overwalle et al., 2009). Likewise, false belief cartoons (Rothmayr et al., 2011; Sommer et al., 2007), although using a visual input, are heavily determined by a narrative content without a critical spatial task component. These different input modalities may have resulted in distinct cognitive subprocesses (e.g., visual versus verbal/narrative), as well as in differences in the complexity, timing and experienced difficulty of the tasks. Consequently, it is possible that prior studies may have underestimated the true amount of overlap of an underlying common process.

The goal of the present study is to provide a more adequate estimation of the functional overlap between attention and belief by controlling more adequately the modality of the task. Specifically, we distinguished the role of (a) input modality and (b) task process, using a within-participants design. To accomplish this, in addition to the classic spatial Posner and the verbal false beliefs tasks, we developed a novel, spatial version of a false belief task. This spatial version was visually and spatially quite similar to the Posner reorientation task, but required participants to resolve false belief issues (Figure 1). Although several studies have used non-verbal animations using simple triangle and circle shapes as in the present task (see meta-analyses by Schurz et al., 2014; Van Overwalle et al., 2009), these studies did not implement false beliefs, but rather social interactions between protagonists, such as chasing, bullying, following etc. The present spatial belief task differs crucially from these earlier studies in that it (a) instantiates the classic false belief task, and no other social or mentalizing processes and (b) its spatial structure and lay-out is made as similar as possible as to the classic Posner task.

Given that attention is an evolutionary more ancient process and a requirement for effective false belief attribution, we predict that the shared process between belief and attention given a spatial modality is located in the anterior right TPJ responsible for attention reorientation (see also Krall et al., 2014). Moreover, in line with the attention reorientation account by Cabeza et al. (2012), we do not expect a total overlap between the three tasks, as there might be some specialization in subregions of the TPJ.

Method

Participants

Twenty-four naive adults took part in this study (twelve women; age range: 18-26 years; mean age: 21.60 years). Three participants were excluded due to excessive head movement (see image processing criteria below) and one participant was excluded due to high error rates (> 50%). Therefore, data of twenty subjects were analyzed. All participants were right-handed as assessed by the Dutch version of the Edinburgh Inventory (Oldfield, 1971). They were paid 10 euro for their participation. Participants reported no history abnormal neurological history, and had normal or corrected-to-normal vision. Participants gave informed consent prior to the experiment in accordance with the guidelines of the Medical Ethics Committee at the Ghent University Hospital (where scanning took place) and the Brussels University Hospital (of the principal investigator).

Stimuli

The experiment consisted of three tasks: spatial reorientation, spatial belief and verbal belief. In the spatial orientation and spatial belief tasks, participants were presented with animated video clips. The animations depicted different geometrical shapes such as a triangle, a circle moving around or in a window subdivided in two adjacent (left-right) rectangular parts. The same geometrical shapes were assigned with different functions according to the tasks (Figure 1). The videos consisted of consecutive scenes which are detailed below for each task (with timing given in Figure 1).

Spatial Reorientation Task

This task involved an adapted version of a Posner cueing task (Figure 1). All trials in this task started with a window consisting of two adjacent rectangular parts, presented at the center of the screen. A triangle that served as a cue for the likely position of the target (i.e., circle) entered the scene from the right or left and stopped at the center of the screen underneath the window. The side from which the triangle entered the scene was counterbalanced across conditions. The triangle indicated the likely position of the target (i.e., circle) by pointing its head to the left or right direction (left 50%, right 50%). In 60% of the trials, the triangle pointed to the correct location of the circle (valid trials), while in the remaining 40% of the trials the triangle pointed to the wrong location (invalid trials). This distribution is comparable to Scholz et al. (2009) who had 55% valid and 45% invalid/no target trials. Then, an occluder appeared and covered the window (this manipulation was introduced for similarity with the spatial belief task). Finally, the occluder disappeared and the circle was shown either on the left or right part of the window. Participants had to indicate as soon as possible whether the circle was located at the left or right part of the window, using the corresponding left or right button on a response box.

Spatial Belief Task

All trials started with a screen showing the same window consisting of two adjacent rectangular parts, presented at the center of the screen, with a target (i.e., circle) positioned either on the right or on the left part of the window (Figure 1). Next, a triangle that served as observer entered the scene either from the same or opposite direction of the circle's location, and appeared at the center underneath the window. The position of the circle and the side from which the triangle entered the scene was counterbalanced across conditions. These movements marked the start of all trials. At the end of all trials, an occluder that covered the window disappeared and participants had to indicate as soon as possible where they thought the triangle would think the circle to appear by pressing the corresponding left or right button on a response box. The following steps between the start and end of the trial changed according to the four conditions:

- True Belief (Target Change - Triangle Present):

The triangle entered the scene and stopped at the center underneath the window. Immediately after, the circle jumped from one part to the other part of the window, and then an occluder covered the window. Then, the triangle moved up and down (to control for the extra movements of the triangle in the false belief condition; see below). Finally, the occluder disappeared and the window was shown again. Given that the triangle was present during the change of the circle's location, it had the same "true" belief about the circle's location as the participant.

- False Belief (Target Change - Triangle Absent):

The triangle entered the scene and stopped at the center underneath the window. Then, it left the scene. In the absence of the triangle, the circle jumped from one part of the window to the other, after which an occluder covered the window. Then, the triangle reentered to the scene from the same side where it left and stopped at the center underneath the window. Finally, the occluder disappeared and the window was shown again. Given that the triangle was not present during the change of the circle's location, it had a "false" belief about the circle's location, while the participant knew the true location of the circle.

- True Filler (No Target Change - Triangle Present):

This condition was created as a filler condition for the true belief condition. Everything was identical, except that the circle did not jump from one part to the other part of the window. Thus, the circle always kept the same location. Consequently, both the participant and the triangle held a true belief.

- False Filler (Late Target Change - Triangle Absent):

This condition was created as a filler for the false belief condition. As before, everything was exactly the same, except that the circle did not jump from one part to the other, but remained on the same location. However, during the last scene, unlike all other three conditions, the circle changed location behind the occluder and hence appeared on the different position when the occluder was removed. Consequently, in this condition, both the participant and the triangle held a false belief.

Verbal Belief Task

This task was translated from Saxe & Kanwisher (2003) into Dutch using typical Dutch names. Participants were presented 20 short vignettes on the screen. Ten belief vignettes described a character's action and required participants to represent his or her (false) belief. Ten photo vignettes required participants to represent the (false) content of a physical representation such as a photograph or map. Each vignette was shown for 20 seconds and followed by a question. Participants had to respond "yes" or "no" using the appropriate response keys. The question remained on screen until the participant responded (this self-pacing response procedure differs from the original task by Saxe & Kanwisher, 2003, because piloting learned that participants complained having insufficient time to respond).

Procedure

Prior to the scanning, participants received instructions and a practice session to ensure that they understood the instructions. For the two spatial tasks in the scanner, they were instructed to keep their eyes focused on the center of the window at all times. They were also asked to respond as fast and accurately as possible after the occluder disappeared from the scene. In addition to this, they had another short practice session in the scanner to make sure that they did not have any problem using the response keypad.

Participants completed all three tasks in the scanner. In the spatial reorientation task, there were 80 trials: 48 valid trials (60 %) and 32 invalid trials (40 %). In the spatial belief task, there were 96 trials: 48 trials (50 %) in the true belief condition, 32 trials (33 %) in the false belief condition, 8 true fillers (8%) and false fillers (8%). We introduced jittering in all tasks. In the spatial reorientation and spatial belief tasks, each trial started with a fixation cross with variable duration between 1.0 – 6.8 s using the pseudo-logarithmic jitter procedure by Hartstra, Kühn, Verguts, and Brass (2010). The duration of the occlusion was also jittered by adding a variable duration between 1.0 - 4.8 s (see Figure 1). In the verbal belief task, each trial began with a fixation cross with variable duration between 0 - 2 seconds. The order of the spatial reorientation and belief tasks was counterbalanced between participants. The verbal belief task is a validated belief localizer (Saxe & Kanwisher, 2003) requiring no speeded responses, and given the length of the whole experiment and potential fatigue of the participants, came always last.

fMRI Data Acquisition

Images were obtained using a 3 T Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany), using a 32-channel radiofrequency head coil. First, a high-resolution anatomical images were collected using a T1-weighted 3D MPRAGE sequence [TR = 2530 ms, TE = 2.58 ms, TI = 1100 ms, acquisition matrix = 256 × 256 × 176, sagittal FOV = 220 mm, flip angle = 7, voxel size = 0.9 × 0.86 × 0.86 mm3 (resized to 1 × 1 × 1 mm^3)]. Second, whole brain functional images were acquired by using a T2*-weighted gradient echo sequence (TR = 2000 ms, TE = 35 ms, image matrix = 64 × 64, FOV = 224 mm, flip angle = 80º, slice thickness = 3.0 mm, distance factor = 17%, voxel size = 3.5 × 3.5 × 3.5 mm^3, 30 axial slices). In the scanner, stimuli were projected onto a screen at the end of the magnet bore and participants viewed the stimuli through an angled mirror located above their eyes on the head coil. Stimulus presentation was controlled by E-Prime 2.0 (www.pstnet.com/eprime; Psychology Software Tools) running under Windows XP. Participants were placed head first and supine in the scanner bore. They were instructed not to move their heads to avoid motion artifacts and foam cushions were placed to minimize head movements.

Image Processing

The fMRI data were preprocessed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK). Prior to the statistical analysis, data were preprocessed to remove sources of noise and artifact. Slice-time correction were applied in order to amend differences in acquisition time between slices for each whole-brain volume, realigned within and across runs for the removal of the movement effects, and co-registered with each participant's anatomical data. The functional data were then transformed into a standard anatomical space (2 mm isotropic voxels) based on the ICBM152 brain template (Montreal Neurological Institute), which approximates Talairach and Tournoux atlas space. Normalized data were then spatially smoothed (6 mm full-width at half-maximum, FWHM) using a Gaussian Kernel. Finally, the preprocessed data were examined, using the Artifact Detection Tool software package (ART; http://web.mit.edu/swg/art/art.pdf; http://www.nitrc.org/projects/artifact_detect/), for excessive motion artifacts and for correlations between motion and experimental design, and between global mean signal and experimental design. Outliers were identified in the temporal differences series by assessing between-scan differences (Z-threshold: 3.0 mm, scan to scan movement threshold: 0.5 mm; rotation threshold: 0.02 radians). These outliers were omitted in the analysis by including a single regressor for each outlier. No correlations between motion and experimental design or global signal and experimental design were identified. Six directions of motion parameters from the realignment step as well as outlier time points (defined by ART) were included as nuisance regressors. We used a default high-pass filter of 128s and serial correlations were accounted for by the default auto-regressive AR (1) model.

Statistical Analyses

In the first level (individual) analysis, the onset regressors were defined and analyzed for each task. Given that each task was run during a separate block, task instructions and participants' processing goals differ greatly between blocks, and as such present a nuisance factor if all tasks would be estimated by a single model. To remove this task effect, we estimated each task by separate models. For all tasks, each condition was modelled as a separate regressor and all trials were modelled with event duration 0. We first estimated this model including only correct trials. Next, we estimated this model, now including separate onset times for correct trials, and for error and filler trials.

In the spatial reorientation task, two onset regressors were defined for the valid and invalid conditions. The onset was defined just after the disappearance of the occluder (and the target circle was shown) in each trial. In the spatial belief task, there were four onsets regressors. For each belief condition, a first onset was defined at the end of the triangle's waiting period under the window and before it changed (or it did not change) location (i.e., about 2 s after the start of the video: when the absence or presence of the triangle becomes evident and a false or true belief can be represented), while a second onset was defined at the beginning of the response phase (i.e., when the occluder disappeared). Thus, the first onset was at the start of the belief formation phase and the second one was right before the response phase. In the belief formation phase, participants would immediately understand whether they had similar or divergent belief when the triangle would stay or leave the screen respectively. At the response phase they would already have formed the belief of the triangle. In the verbal belief task, two onset regressors were defined for the belief and photo conditions. The onset was defined at the beginning of each vignette. A canonical hemodynamic response function was used to model the hemodynamic response to each type of event. The six head movement parameters were also included in the model. Each condition of interest was estimated for each participant, and extracted for the second level analysis using a t-contrast against the implicit baseline.

In the second level (group) analysis, we computed an Invalid > Valid contrast for the spatial reorientation task, a False Belief > True Belief contrast for the spatial belief task, and a Belief > Photo contrast for the verbal belief task. Furthermore, to test whether our experimental tasks activated overlapping areas of the TPJ we computed each of these contrasts masked inclusively with each of the other contrasts. A voxel-based statistical threshold of $p < 0.005$ (uncorrected) was used for all comparisons with a minimum cluster extent of 10 voxels, and comparisons are discussed only when they surpass a peak FWE-corrected threshold of $p < .05$ unless noted otherwise. Statistical comparisons between conditions of interest are reported after correction for multiple comparisons within an a priori ROI of the right TPJ (a sphere of 15 mm around the MNI coordinates 58.5, -39, 16.5) based on the meta-analysis of Bzdok et al. (2013). Note that conventional conjunction analyses across tasks is not possible because we modelled the tasks separately. However, the present inclusive masking procedure is equivalent at the cluster level, and provides only marginal differences at the peak coordinates (one reason is that inclusive masking is asymmetric because it computes one contrast given another contrast as (inclusive) mask. In contrast, a conjunction analysis is symmetric because it computes the two contrasts at once).

Results

Behavioral Results

In each of the tasks, we found significant differences in the accuracy of the responses or the timing of the correct responses (see Table 1). In the spatial reorientation task, t-tests revealed that the responses on the invalid trials lasted significantly longer and were less accurate than on the valid trials.

These significant differences in response times and accuracy reflect the reorienting effect. In the novel spatial belief task, the accuracy of the false belief trials was significantly lower than the true belief trials. In the verbal belief task, the responses on the belief trials lasted significantly longer than on the photo trials. This effect was not reported by Saxe and Kanwisher (2003). No other significant differences were found.

fMRI Results

First, we estimated and analyzed only correct trials. All contrasts of interest (i.e., Spatial Reorientation: Invalid > Valid, Spatial Belief: False Belief > True Belief, Verbal Belief: Belief > Photo) revealed the predicted activation in the right TPJ at a corrected threshold ($p < .05$, FWE corrected; see Table 2). In the spatial belief task, additional activity was revealed in the precuneus which is part of the mentalizing network. The reverse contrasts did not result in any significant activity.

In order to test the overlap between these contrasts of interest, we computed each contrast inclusively masked for every other contrast of interest (see Table 2). This analysis revealed a significant overlap in the right TPJ for the two spatial tasks (Spatial Reorientation and Spatial Belief) and for the two belief tasks (Spatial Belief and Verbal Belief). However, there was no overlap among all three tasks. This analysis is visually represented at an uncorrected threshold of $p < .001$ (Figure 2).

Note that the observed overlap is asymmetric, due to large differences in volume of the clusters of interest (voxel size; Table 2). To illustrate, the overlap among spatial tasks involves 89 % of the spatial reorientation voxels (16 out of 18), but only 2% of the spatial belief voxels (16 out of 990). Likewise, the overlap between mentalizing tasks involves 89 % of the verbal belief voxels (171 out of 193), but only 17 % of the spatial belief voxels (171 out of 990).

Second, we estimated and analyzed all trials, including not only correct trials, but also error and filler trials (Table 3). By fitting all error and filler trials, one might obtain a better statistical fit of the model because leaving these trials unspecified may result in additional noise that is unaccounted for. However, to our surprise, none of the TPJ clusters survived a corrected threshold in this analysis. The Posner task contrast did not reveal any activation, the Spatial Belief (False > True) comparison revealed activation only in the Precuneus, and the Verbal Belief (Belief > Photo) contrast showed activation only in the left hemisphere, including the Sub-Gyral cortex, Precuneus and Postcentral gyrus.

Discussion

The aim of the current study was to investigate the potential overlap in activation in the TPJ during a reorientation and a belief mentalizing task. Past research confounded the role of task process with input modality by comparing reorientation in the spatial modality and mentalizing in the verbal modality (Mitchell, 2008; Scholz et al., 2009). To avoid this, we developed a novel, spatial Posner-like version of the false belief task, so that we could independently compare tasks with the same input modality (spatial reorientation versus spatial mentalizing) as well as tasks from the same task process (spatial versus verbal false beliefs). The data clearly showed right TPJ activation in all three tasks. More importantly, we found an overlap in TPJ activation between the spatial versions of the two distinct tasks (reorientation and mentalizing) and between the mentalizing tasks under different input modalities (spatial and verbal). However, we did not find a “triple” overlap in TPJ activation across all three tasks, contrary to earlier studies that reported an overlap between the spatial Posner task and the verbal mentalizing task (Mitchell, 2008; Scholz et al., 2009).

Before going on, it is important to note that when we modelled not only the correct trails, but also the error and filler trials, the TPJ cluster did not survive the conventional threshold in any task. The reason for the lack of TPJ activation might be that forcing all error responses into a single vector may be inappropriate, because these errors may be caused by many different distractors, leading to a plethora of different underlying error-prone processes. Conversely, fitting all error responses in individual vectors for each error to accommodate this limitation, may underestimate a common underlying process among some of them. In short, we speculate that we do not obtain TPJ clusters because we do not know where each of the error responses come from, so that they are more difficult to estimate adequately than correct trials. Note that it is unlikely that the results presented in the correct-only analysis are false positives, since exactly all three predicted activations are revealed, which drop out when modelled with the additional estimation of error and filler responses. We therefore focus the remainder of the discussion on the analysis with the correct trials.

An important contribution of the novel spatial Posner-like false belief task is that it allowed us to minimize the role of input modality in the overlap of the TPJ, and to focus on the role of task process. We found evidence for an overlap of spatial reorientation with spatial belief, but not with verbal belief. The size of this overlap (128 mm^3 at $p < .001$) suggests that there are reliable similarities in the processes subserving both reorientation and mentalizing, after differences in input modality are removed as much as possible.

Moreover, we found that mentalizing tasks show overlapping activation across verbal and spatial versions, which are distinct from activations resulting from spatial reorientation. The lack of a “triple” overlap across all tasks, demonstrates that there is also some degree of specialization subserving different functional task processes. This is in line with the attention orientation account proposed by Cabeza et al. (2012), which suggests that there should be functional overlap in the TPJ, with “differences around the edges” (p. 345). This view presupposes that the TPJ has a global overarching function but that “different subregions apply this process to different types of information and goals, which vary according to functional connectivity” (p. 345). According to this view, the various subregions of the TPJ mediate different aspects of the same attention function, through connectivity with different inputs (e.g., spatial location of external stimuli in the Posner task; internal memory in a false belief task). Likewise, in line with our distinction of verbal versus spatial modality, Krall et al. (2014) suggested that unexpected false stories may involve high-level disruption of attention, while the classic Posner task (and presumably also our spatial belief task) may involve low-level attention reorientation. They argued that the common mechanism of low-level orientation “might be explained by Corbetta’s breach of expectation (attention shifting), or alternatively Van Overwalle’s concept of where-to shifting” (Krall et al., 2014, p. 9).

The overlap between attentional and belief processes might have been obscured in recent parcellation studies based on functional connectivity (Bzdok et al., 2013; Kubit & Jack, 2013; Mars et al., 2011) by the sharp boundaries imposed between subregions of the TPJ explained earlier. Interestingly, this potential overlap is even evident in the recent parcellation study by Bzdok et al., (2013), who reported briefly on an alternative solution with a third cluster that “behaved more variably” (p. 386) and showed connectivity patterns like the posterior (mentalizing) and anterior (attention) TPJ clusters. The location of the mentalizing and attention subregions in the present study is in accord with the posterior and anterior parcellation division in these earlier parcellation studies, although the present data also show a superior – inferior gradient presumably due to idiosyncratic characteristics of our participants. The fact that input modality may play such an critical role is also important for recent overarching proposals, because they tended to overlook the role of input modality and focused more on integration of functionality (Cabeza et al., 2012; Carter & Huettel, 2013; Geng & Vossel, 2013).

Nevertheless, an important limitation of studies exploring the overlap between tasks, including ours, is that the degree of overlap in neural activity is dependent upon many factors that cannot always be well-determined or specified. The overlap is dependent on the contrasts and control conditions that are used, and that may differ between tasks, as is the case here. Another limitation of the present study is that the accuracy for the Posner reorientation task was quite low (76%) compared to many earlier fMRI studies reporting accuracies beyond 90% and much faster response times. This is probably due to the ratio of 60% valid versus 40% invalid trails in the current study which is less extreme than the typical ratio of 70-80% valid trials and 30-20% invalid trials in earlier research. Hence, the current reorientation task might have been difficult because cueing was relatively unreliable. This may have reduced activity in the TPJ after invalid cueing (see e.g., Giessing, Thiel, Rösler, & Fink, 2006; Vossel, Thiel, & Fink, 2006). This is also evident in the present study and the earlier overlap studies by Scholz et al. (2009) and Mitchell (2008). Under the same whole-brain threshold of $p < .001$, there were increasingly active TPJ clusters in spatial reorientation with a larger validity ratio: cluster volumes went up from 128 mm^3, 144 mm^3, to 675 mm^3 in Scholz et al. (2009; 55% validity), the present study (60% validity), and Mitchell (2008; 75% validity), respectively. Nevertheless, this pattern of increasing neural TPJ activity is not paralleled by an increase in the overlap of attention reorientation with false beliefs, as Scholz et al. (2009) reported a whole-brain overlap of 56 mm^3 at this threshold, while we found no active voxels in the overlap (the overlap in Mitchell, 2008, is unclear as Figure 4 reports it to be larger than the Posner task itself). This is perhaps because the active cluster for the verbal false belief task -- although almost identical in all three studies -- differed greatly using the same threshold (2560 mm^3, 1544 mm^3, and 2673 mm^3 respectively).

Another limitation of the present study, discussed earlier, is that all TPJ clusters disappeared when non-correct trials were included in the model specification and estimation. Future research should explore under which conditions this seemingly profitable statistical procedure may be beneficial or not.

Conclusion

In this study, we developed a novel spatial belief task, in order to unconfound task process and input modality. Our results indicate that the TPJ shows volumes of overlap in activity, across similar task processes (mentalizing across a spatial or verbal input) and input modalities (spatial reorientation and spatial mentalizing), but not across tasks and modalities combined (i.e., no “triple” overlap). These results are in line with an overarching role of the TPJ, with differences and specializations in some subregions as put forward by Cabeza et al. (2012) and Krall et al. (2014).

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Table 1: Accuracy (in %) and Response Time (in ms) for the three Tasks

Task	Condition	Accuracy	*t*(19)	Response Time	*t*(19)
Spatial Reorientation	Invalid	68%	2.09*	969	2.60*
	Valid	76%		952	
Spatial Belief	False	88%	2.31*	881	0.98
	True	93%		877	
Verbal Belief	False	76%	0.83	1131.7	2.69*
	Photo	73%		1048.3	

Note: Response times include correct responses only.

**p* < .05

Table 2: Whole-brain analysis of the task effects (correct trials only)

Comparison and Anatomical Area	*x*	*y*	*z*	*voxels*	*max t*	
Single Contrasts						
Spatial Reorientation (Invalid > Valid)						
R TPJ	56	-42	2	18	3.93	°
Spatial Belief (False > True)						
R TPJ	46	-56	16	990	5.11	***
Precuneus	6	-50	48	1640	7.23	***
Precuneus	-6	-50	56	1640	5.52	***
Verbal Belief (Belief > Photo)						
R TPJ	48	-54	24	193	4.26	*
R Middle Temporal Gyrus	38	-56	22		4.20	*
Overlap in the R TPJ						
Reorientation (Invalid > Valid) inclusively masked with Spatial Belief (False > True)						
R TPJ	56	-42	2	16	3.93	°
Spatial Belief (False > True) inclusively masked with Reorientation (Invalid > Valid)						
R TPJ	54	-44	2	16	3.80	$^{+}$
Spatial Belief (False > True) inclusively masked with Verbal Belief (Belief > Photo)						
R TPJ	46	-56	16	171	5.11	*
Verbal Belief (Belief > Photo) inclusively masked with Spatial Belief (False > True)						
R TPJ	48	-54	24	171	4.25	*
Reorientation (Invalid > Valid) inclusively masked with Verbal Belief (Belief > Photo)						
No activation in TPJ						
Verbal Belief (Belief > Photo) inclusively masked with Reorientation (Invalid > Valid)						
No activation in TPJ						

Note: x, y, and z = Montreal Neurological Institute (MNI) coordinates of the peak values; t = t-score of the peak values; R = Right. Whole brain analysis with $p < .001$ and cluster extent > 10 voxels.

*$p < .05$; **$p < .01$; ***$p < .001$ (whole brain FWE-corrected peaks).

$^{+}$ $p < .07$, ° $p < .05$ (FWE-corrected peaks) after small volume analysis with a ROI sphere with a radius of 15 mm around the peak of the anterior TPJ reported by Bzdok et al. (2013; MNI coordinates: 58.5, -39, 16.5).

Table 3. Whole-brain analysis of the task effects (correct, error and fillers trials)

	x	*y*	*z*	*voxels*	*max t*	
Single Contrasts						
Spatial Reorientation (Invalid > Valid)	No suprathreshold clusters					
Spatial Belief (False > True)						
Precuneus	8	-52	52	191	4.49	**
Verbal Belief (Belief > Photo)						
L Sub-Gyral	-22	-50	60	251	4.26	**
L Precuneus	-18	-60	58	251	4.02	**
L Postcentral Gyrus	-22	-56	72	251	3.74	**

Note: x, y, and z = Montreal Neurological Institute (MNI) coordinates of the peak values; t = t-score of the peak values; L = Left. Whole brain analysis with *p* < .001 and cluster extent > 10 voxels.

*p < .05; **p < .01; ***p < .001 (whole brain FWE-corrected peaks).

Figure Captions

Figure 1: Stimuli and Design of the experiment with the adjusted Spatial Reorientation (Posner) task and novel Belief task. Note that the stimuli are in black and white, while grey arrows show the path of movement of the stimuli.

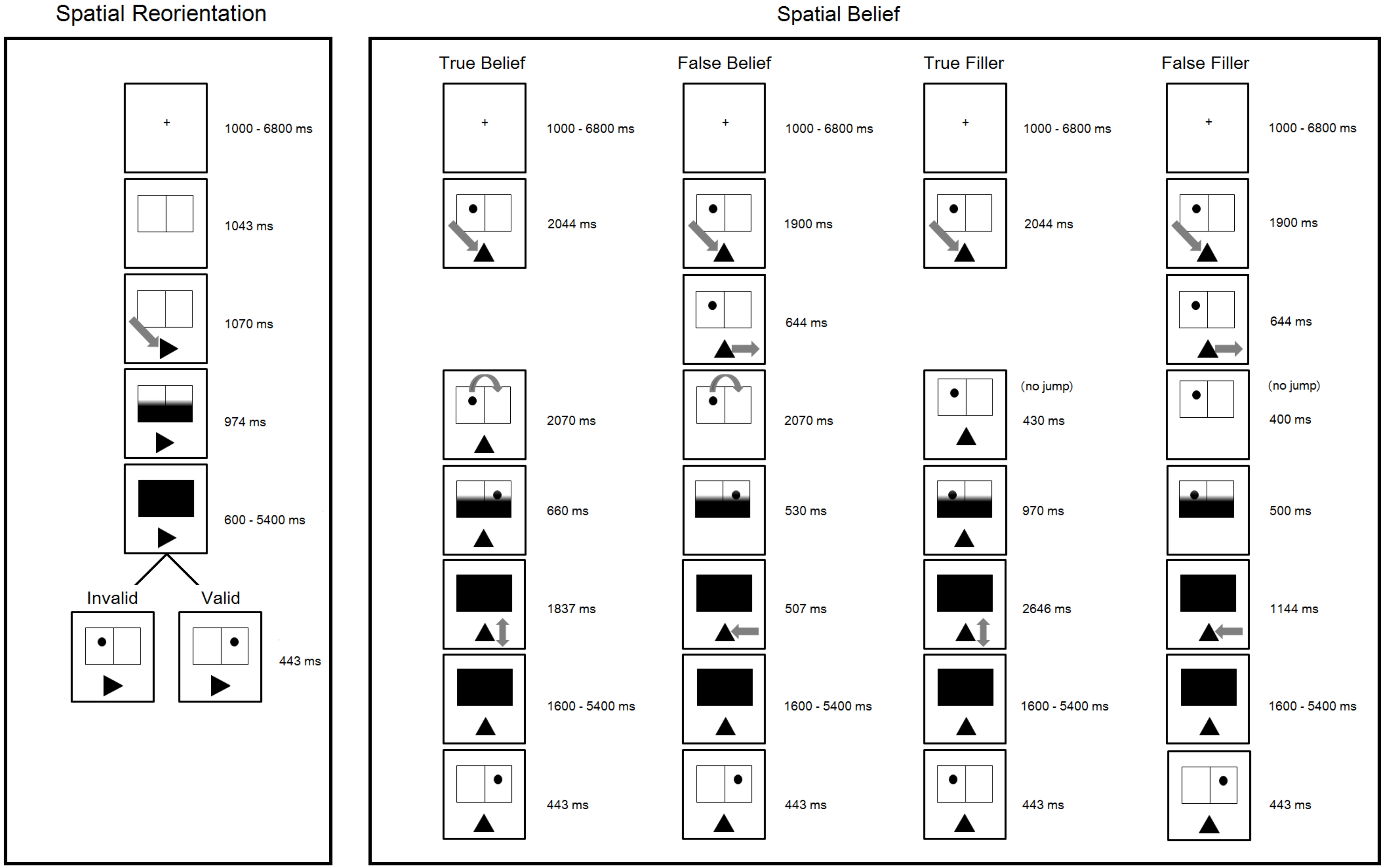

Figure 2: The overlap between Spatial Reorientation (Invalid > Valid), Spatial Belief (False Belief > True Belief) and Verbal Belief (Belief > Photo). The figure was created using MRIcron, with whole-brain activation thresholded at $p < .001$ (uncorrected) with at least 10 voxels.