Rethinking the role of the rTPJ in attention and social cognition in light of the opposing domains hypothesis: findings from an ALE-based meta-analysis and resting-state functional connectivity.

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1 ***Rethinking the role of the rTPJ in attention and social cognition in***
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18   **Abstract**
19

20 The right temporo-parietal junction (rTPJ) has been associated with two apparently disparate
21 functional roles: in attention and in social cognition. According to one account, the rTPJ initiates
22 a "circuit-breaking" signal that interrupts ongoing attentional processes, effectively reorienting
23 attention. It is argued this primary function of the rTPJ has been extended beyond attention,
24 through a process of evolutionarily cooption, to play a role in social cognition. We propose an
25 alternative account, according to which the capacity for social cognition depends on a network
26 which is both distinct from and in tension with brain areas involved in focused attention and
27 target detection: the default mode network. Theory characterizing the rTPJ based on the area's
28 purported role in reorienting may be falsely guided by the co-occurrence of two distinct effects
29 in contiguous regions: activation of the supramarginal gyrus (SMG), associated with its
30 functional role in target detection; and the transient release, during spatial reorienting, of
31 suppression of the angular gyrus (AG) associated with focused attention. Findings based on
32 meta-analysis and resting functional connectivity are presented which support this alternative
33 account. We find distinct regions, possessing anti-correlated patterns of resting connectivity,
34 associated with social reasoning (AG) and target detection (SMG) at the rTPJ. The locus for
35 reorienting was spatially intermediate between the AG and SMG and showed a pattern of
36 connectivity with similarities to social reasoning and target detection seeds. These findings
37 highlight a general methodological concern for brain imaging. Given evidence that certain tasks
38 not only activate some areas but also suppress activity in other areas, it is suggested that
39 researchers need to distinguish two distinct putative mechanisms, either of which may produce
40 an increase in activity in a brain area: functional engagement in the task versus release of
41 suppression.
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Introduction

Research in cognitive neuroscience has implicated cortical regions near the right temporo-parietal junction (rTPJ) in a broad variety of tasks ranging from social interactions (Saxe & Powell, 2006) to attentional interactions with inanimate, visuo-spatial stimuli (Corbetta, Patel, & Shulman, 2008; M. Corbetta & G. Shulman, 2002). The central issue for this paper is how we may best account for observations of rTPJ involvement in attention and social processing.

Anatomical and functional ambiguity at the rTPJ
The rTPJ does not have a distinct anatomical marker, but is considered to lie at the conjunction of the posterior superior temporal sulcus, the inferior parietal lobule and the lateral occipital cortex (Corbetta, et al., 2008). This region of cortex has an unusually high degree of inter-individual variability in gross anatomical structure, as revealed both by careful anatomical observation (Ono, Kubik, & Abernathey, 1990) and quantified measures (Van Essen, 2005). Work on the cytoarchitecture of this region reveals substantial individual variation both in the size of functional regions and in the relationship between cytoarchitectonic borders and macroanatomical landmarks (Caspers et al., 2006). These factors make precise localization of functional regions near rTPJ identified using fMRI and PET challenging. A number of distinct anatomical labels have been used in the literature, including rTPJ, angular gyrus (AG), inferior parietal lobe, supramarginal gyrus (SMG), posterior temporal cortex and posterior superior temporal sulcus. These labels are not always used consistently; hence they cannot be relied upon to discriminate one functional region from another. Here we focus on a putative functional division between more posterior TPJ regions, including the AG, and more anterior TPJ regions, including the SMG.

Attention and the rTPJ
The rTPJ is thought to play a role in reorienting attention to behaviorally salient stimuli. The exact requirements for a stimulus to be considered salient remain unclear (Frank & Sabatinelli, 2012), however, the area has been shown to respond to distractors that share features with the target stimulus (Indovina & Macaluso, 2007) or are spatially informative of a targets' location (Geng & Mangun, 2011). Regions near rTPJ show increased activity in response to breeches of expectation as well as identification of the target stimulus itself (M. Corbetta & G. Shulman, 2002). The most prominent theory integrating the rTPJs' function with other attentional processes suggests the area belongs to a right lateralized ventral attention network (VAN), composed of the TPJ, the middle and inferior frontal gyrus, frontal operculum, and anterior insula (Corbetta, et al., 2008).

Current theory (Corbetta, Kincade, & Shulman, 2002; Corbetta, et al., 2008) suggests the VAN, specifically the rTPJ, plays the role of detecting unexpected but behaviorally relevant stimuli, and acts as a circuit breaker for the dorsal attention network (DAN). The DAN (Corbetta et al., 1998; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Fox et al., 2005) is comprised of the intraparietal sulcus (IPS), superior parietal lobule, and the frontal eye fields (FEF) and is thought to be involved in top-down attentional processes. The DAN maintains visuo-spatial information with regards to the current task-defined goals, such as in response to a directional cue, while the VAN remains inhibited until a target or salient distractor is presented, at which point activity in the VAN interrupts the maintenance of attention in the DAN in order to reorient attention

93   (Corbetta, et al., 2002; Corbetta, et al., 2008). Within the context of the VAN, the rTPJ has been
94   most studied using variations on two tasks: oddball and Posner cue paradigms.
95
96   The standard oddball paradigm presents less frequent stimuli against a stream of frequent stimuli.
97   The key feature is the novel/rare nature of the oddball targets compared to the typical or
98   standard/frequent nature of the baseline stimulus. Visual stimuli are typically presented
99   sequentially at a central fixation point (Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004)
100 and in auditory tasks the stimuli are typically presented through headphones in both ears
101 simultaneously (Stevens, Calhoun, & Kiehl, 2005), although exceptions exist (Linden et al.,
102 1999). As a result, the extent to which the task elicits spatial reorienting is often limited. In most
103 instances participants are instructed to respond with a button press (Downar, Crawley, Mikulis,
104 & Davis, 2001; Kiehl et al., 2005) or keep a mental count (Linden, et al., 1999) of the number of
105 target stimuli presented in the visual, auditory, and tactile sensory modalities (Linden, 2005).
106
107 The Posner cue-type experiment triggers the reorienting of attention in response to invalid cues.
108 During the task the participant is presented with a central cue that more often than not predicts
109 the location of a target stimulus. During invalid trials, the participant is cued to a different
110 location than that of the target stimulus, necessitating a spatial reorienting of attention towards
111 the target. The goal of the task is to detect the target stimulus and respond with a button press
112 upon detection (Macaluso, Frith, & Driver, 2002). The task has been studied in the visual
113 (Corbetta, et al., 2002) and auditory (Mayer, Franco, & Harrington, 2009) sensory modalities.
114
115 The oddball and Posner cue-type designs both involve the detection of unexpected (low
116 frequency) task-relevant stimuli. Since this is a hypothesized function of the VAN, the co-
117 localization of activations associated with both paradigms is consistent with theoretical accounts
118 of the VAN. However, these tasks also differ in at least one important respect. Posner cue-type
119 tasks require the reorienting of attention from one spatial location to another to respond to
120 invalid trials. In contrast, oddball tasks don't require the participant to break their current focus
121 of attention and make a spatial shift to a new location when a low frequency stimulus is
122 presented.
123
124 **Social Cognition and the rTPJ**
125 The rTPJ has also been strongly implicated in social reasoning, specifically theory of mind
126 (ToM) tasks. ToM refers to the ability to understand the intentions of a conspecific, i.e. to predict
127 their actions through the attribution of beliefs and desires (Gallagher & Frith, 2003). ToM studies
128 typically involve short stories followed by questions about the beliefs of one of the protagonists
129 (Gallagher et al., 2000; Saxe & Powell, 2006) or the attribution of intentions to characters
130 depicted in a comic strip (Vollm et al., 2006). The ToM condition is typically contrasted with
131 stories describing human activity without the need for mental state attributions, such as outdated
132 physical representations (Perner, Aichhorn, Kronbichler, Staffen, & Ladurner, 2006).
133
134 The rTPJ is part of a larger network of regions which is consistently activated by a variety of
135 social cognition tasks which involve thinking about internal mental states, often referred to as the
136 mentalizing network (Amodio & Frith, 2006; Denny, Kober, Wager, & Ochsner, 2012; R. B.
137 Mars et al., 2012; Ochsner et al., 2004; Saxe, Moran, Scholz, & Gabrieli, 2006; Schilbach et al.,
138 2012; Schilbach, Eickhoff, Rotarskajagiela, Fink, & Vogeley, 2008; Van Overwalle, 2009). The

139 regions which are most consistently associated with mentalizing are the rTPJ, the medial parietal
140 / posterior cingulate cortex (MP/PCC) and the dorsal medial prefrontal cortex (dMPFC). There is
141 evidence that the these medial mentalizing regions play a relatively general role in social
142 cognition, including emotion processing and introspection (Schilbach, et al., 2012), whereas the
143 function of the rTPJ appears to be more specific to the attribution of beliefs and intentions to
144 others (Saxe, et al., 2006; Saxe & Powell, 2006).
145
146 **Relationship between attention and social cognition in the rTPJ**
147 The current literature remains unsettled as to the extent the locus of activity at the rTPJ for
148 mental state attribution coincides with the locus of activity at the rTPJ region involved in
149 attentional processes. Mitchell (2007) found no topographical distinction between either process
150 at the group or individual level of analysis. A meta-analysis published by Decety and Lamm
151 (2007) found overlapping yet significantly different areas recruited for social and reorienting
152 processes. Decety & Lamm's interpretation of these findings focuses on the overlap. This is
153 curious, since meta-analytic investigations can statistically support the claim that two conditions
154 have distinct spatial profiles, but cannot directly speak to the issue of whether two regions do or
155 do not have functional overlap[1]. Nonetheless, these researchers explain these findings by noting
156 there may be similarities between the process involved in reorienting spatial attention and
157 reorienting to another person's point of view (Corbetta, et al., 2008; Decety & Lamm, 2007;
158 Mitchell, 2007). In contrast, Scholz et al. (2009) find evidence of distinct activation peaks
159 associated with ToM and attention reorienting, using both group and individual level analyses[2].
160 These authors resist the view that attention reorienting and theory of mind tasks share a common
161 neural or psychological mechanism.
162
163 An important finding from work in resting state functional connectivity (rs-fcMRI) is the
164 observation of negative correlations between cortical networks. Fox et al (2005) identify two
165 anticorrelated networks: the default mode network (DMN) and the task positive network (TPN).
166 The DMN includes a region near rTPJ, the angular gyrus (AG). The TPN overlaps the DAN and
167 a second network called the fronto-parietal control network (FPCN) (Vincent, Kahn, Snyder,
168 Raichle, & Buckner, 2008)[3]. The TPN also includes a region near the rTPJ, the supramarginal

[1] This follows from the fact that meta-analytic investigations are based on information about activation peaks, which are not informative about the spatial extent of activation. Further, variations in individual anatomy and in atlas registration for different studies mean that even conditions with distinct peak loci may not be resolved and appear to overlap. On the other hand, if formal meta-analysis reveals a significant difference in location between conditions, then a secure inference can be made that the conditions have spatially distinct activation profiles, because the location of peaks is informative about the spatial distribution of response and random variations in anatomy contribute to the error term.

[2] Scholz et al (2009)'s title might be read as implying the existence of two regions that they demonstrate are functionally distinct. However, their own evidence suggests functional overlap, since their attention reorienting region is modulated by ToM and their ToM region is modulated by attention reorienting. Scholz et al (2009) do not present a statistical analysis that addresses the issue of whether the regions they identify are functionally overlapping or distinct. This would require demonstrating an interaction with spatial location, where the spatial locations are identified on the basis of independent data. They do present a statistical analysis based on individual subject analysis which supports the claim the conditions are associated with distinct peak activations. This finding is consistent with findings we report, and with the view that there is functional overlap between ToM and reorienting.

[3] While the TPN was aligned with the dorsal attention network in Fox et al's initial papers (Fox et al, 2005; Fox et al, 2006) the spatial characterization of the TPN in those analyses was constrained both by negative correlations with seeds in the DMN and by positive correlations with points generated by studies of visual attention. Later studies have more simply identified areas which are negatively correlated with DMN

169   gyrus (SMG) (Fox, et al., 2005; Jack, et al., 2012). Research on the relationship between social
170   and non-social processes in the brain suggests these antagonistic networks support two distinct
171   cognitive domains. The opposing domains hypothesis holds that the mutually inhibitory
172   relationship between the DMN and TPN reflects a cognitive tension between social cognition
173   (including mentalizing and introspection) and non-social cognitive processes (typically recruited
174   by attention demanding non-social tasks) (Jack, et al., 2012). These findings suggest not just that
175   there are at least two distinct regions near rTPJ, but also that they are in tension with each other.
176   This claim is supported not only by resting state functionally connectivity analysis, but also by
177   the finding that the same regions are activated and suppressed (relative to a resting baseline) by
178   different task conditions (Jack et al, 2012). The task-induced activation and deactivation of these
179   regions is important to note, because this evidence cannot be explained away as a potential
180   artifact of methods commonly used in functional connectivity analysis (Murphy, Birn,
181   Handwerker, Jones, & Bandettini, 2009). Critically, a broad range of evidence now supports the
182   view that the maintenance of externally-oriented attention in non-social tasks suppresses activity
183   in the DMN below resting levels (Raichle & Snyder, 2007). It follows from this that the breaking
184   of attention may give rise to a relative increase in activity in regions associated with social
185   cognition, even in the absence of any social processing demands and purely as a result of the
186   termination of suppression - allowing activity to return to resting levels.
187
188   rs-fcMRI has also been used as a data-driven tool to identify the borders of distinct functional
189   regions on the basis of changes in connectivity. Initial work on this application indicates
190   considerable variability in the degree to which clear boundaries between regions can be defined
191   (Cohen et al., 2008), however, some areas contain very clear boundaries between contiguous
192   regions with highly disjoint patterns of functional connectivity. One such boundary occurs in the
193   TPJ, between the AG and SMG, in the immediate vicinity of activation foci associated with ToM
194   tasks and with the VAN. These findings support the existence of two distinct functional
195   networks, including a more posterior region incorporating the AG and a more anterior region
196   incorporating the SMG, which are contiguous at the TPJ (see figure 3 in ref Cohen, et al., 2008).
197   The existence of more than one region in this area is also supported by work in a distinct
198   modality, diffusion tensor imaging, which identifies distinct regions near the rTPJ using
199   tractography–based parcellation (R. Mars et al., 2012).
200
201   **An alternative account**
202   The opposing domains hypothesis holds that regions involved in non-social attentional
203   processing and social cognition are not only distinct, but also tend to suppress each other. How
204   might this theory account for observations of the rTPJ's involvement in both attention and social
205   processing? We suggest extending the opposing domains hypothesis with an additional auxiliary
206   hypothesis: the breaking of attentional set that occurs during reorienting of attention leads to an
207   increase in activity in social regions as a result of the release of suppression associated with the
208   maintenance of focused attention. If both the opposing domain hypothesis and this auxiliary
209   hypothesis are correct, then several predictions follow: (1) There should be distinct loci of
210   activation associated with processes which are clearly social in nature (e.g. theory of mind tasks)

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seeds (Chai, Castanon, Ongur, & Whitfield-Gabrieli, 2012; Chang & Glover, 2009; Fox, Zhang, Snyder, & Raichle, 2009; Jack et al., 2012). These regions overlap both the DAN and FPCN.

211 and processes which are clearly non-social (e.g. detection of a non-social target, as occurs in
212 oddball tasks). (2) Invalid trials in Posner-cue type experiments should lead both to an increase
213 in activity in social regions (associated with release of suppression during reorienting) and an
214 increase in activity in non-social regions (associated with detection of a non-social target).
215
216 The opposing domains account suggests distinct rTPJ areas involved in social and attentional
217 processing. Why might researchers have struggled to clearly distinguish between these putatively
218 distinct but adjacent areas? We suggest that the region's inconsistent structural organization and
219 variations across experimental paradigms have resulted in the misattribution of contiguous
220 regions' response profiles to a single region. The response profile of the rTPJ, in the context of
221 the VAN, may be falsely informed by fMRI findings that fail to account for the strong negative
222 correlation, observed both in resting connectivity and due to tasks, between separate areas at the
223 rTPJ. BOLD changes associated with reorienting may reflect the sum of two independent effects
224 which occur in contiguous regions effectively simultaneously (given the temporal resolution of
225 fMRI). The first is activation above resting baseline of the SMG associated with the detection of
226 a low-frequency task-relevant stimulus. The second is release of deactivation in the AG, possibly
227 only a recovery to baseline levels, which may in some paradigms be followed by a rapid return to
228 a suppressed state due to processes involved in target detection (SMG activation) and/or re-
229 engagement of attention (DAN activation). Although these two putative effects would reflect
230 very different cognitive mechanisms, they may nonetheless produce similar event-related
231 responses in immediately contiguous regions.
232
233 If this account is correct, then the "circuit breaker" function which VAN theory attributes to the
234 rTPJ may be best explained by the posterior TPJ's (including the AG) involvement in social
235 cognition, a type of processing which is in competition with focused attention. Such an account
236 would still suggest a possible "circuit breaker" role for the posterior TPJ, however this role
237 would likely be non-specific in nature, involving a tendency to suppress attentional processes in
238 general rather than communicating specific information that might inform the re-orienting of
239 attention. This account holds that the anterior TPJ (including the SMG), in contrast to the
240 posterior TPJ (including the AG), is directly involved in attentional processes.
241
242 **Summary of key hypothesis**
243 The key hypothesis we propose here, and marshal evidence to support, is as follows: Reorienting
244 (unlike oddball) paradigms require the participant to break their attentional set i.e. on invalid
245 trials the participant must release sustained focused attention from its cued location to complete
246 the task. The maintenance of focused attention is (one of) the cognitive process that tends to
247 suppress DMN regions (while activating attention regions). When focused attention is broken,
248 this suppression is (usually only temporarily) lifted. This causes activity in the posterior TPJ (e.g.
249 AG) to increase relative to its suppressed state, just as happens when a compressed spring is
250 released.
251 While this hypothesis is novel and tentative in the context of attention reorienting tasks, there is
252 prior evidence which broadly supports this 'compressed spring' model of DMN network activity.
253 There is clear evidence that DMN regions are more suppressed for higher effort non-social tasks,
254 and that there is return to baseline when participants disengage, either because the task finishes
255 or because of mind-wandering (Mason et al., 2007; McKiernan, Kaufman, Kucera-Thompson, &
256 Binder, 2003). In addition, there is evidence of a 'rebound' effect, such that DMN activity is

257 greater during resting periods the more it has been suppressed by a preceding working memory
258 task (Pyka et al., 2009). We hypothesize that the sudden breaking, and subsequent refocusing, of
259 attention that occurs in reorienting tasks produces a similar pattern, but on a shorter timescale.
260 That is, reorienting produces a transient release of suppression whose BOLD time course looks
261 similar to that of an above-baseline event related response.
262 While this hypothesis is tentative, it nonetheless raises questions about the view that the AG is
263 involved in attentional reorienting in the manner envisaged by VAN theory. In addition to having
264 implications for VAN theory, this idea has quite broad implications for the interpretation of
265 neuroimaging findings. The usual inference that is made from the observation that an area
266 increases in activity concomitant with a task event is that the area plays a direct functional role in
267 the task-related cognitive processes that occur at that moment. This is the basic logic of cognitive
268 subtraction (Price & Friston, 1997). However, this logic has already been implicitly
269 acknowledged as incorrect for cases where an increase in activity can be more simply explained
270 by a decrease in suppression (Mason, et al., 2007; McKiernan, et al., 2003). VAN theory focuses
271 on a region which, similar to other DMN regions, is typically deactivated compared to rest
272 during task performance (Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007). VAN
273 theory interprets activation of this region following the well-established and intuitive logic of
274 cognitive subtraction. Our provocative suggestion is that this logic fails to apply. Specifically, we
275 suggest that transient increases in activity near the AG have been incorrectly attributed to that
276 region playing an active role in attention reorienting, when the observed effect is really due to
277 the transient release of suppression of that region[4].
278
279 **Experimental design**
280 To test our alternative account of rTPJ involvement in attention and social cognition, we sought
281 to localize and investigate the functional connectivity of regions associated with the detection of
282 task-relevant infrequent stimuli, the attribution of intentions to agents, and the reorienting of
283 attention. To do this, we use formal meta-analytic methods to distinguish the localization of
284 activations associated with oddball, ToM and reorienting paradigms. Of particular significance is
285 that, unlike a prior formal meta-analysis which investigated attention and social processes in
286 rTPJ (Decety & Lamm, 2007), we distinguish oddball from reorienting tasks. We predict that
287 oddball paradigms will preferentially recruit the anterior TPJ (e.g. SMG), ToM tasks will
288 preferentially recruit the posterior TPJ (e.g. AG), and reorienting will tend to be localized
289 between the AG and SMG. Next, we examine functional connectivity associated with these
290 distinct foci. In accordance with the opposing domains hypothesis we predict very different
291 cortical networks will be associated with ToM and oddball seeds. The reorienting seed is
292 predicted to lie on the border between these networks, and hence correlations with this seed
293 should reflect some combination of signals associated with the other two seeds.
294
295 **Materials and Methods**
296

[4] A concern the reader may have with this account is that it would appear inefficient for the brain
to expend energy increasing activity in a region whose function is unrelated to task demands.
However, a large body of work indicates the brain is 'inefficient' in this way: DMN activity
typically increases when non-social task demands terminate (Raichle & Snyder, 2007). Hence,
this concern is not specific to the account we give here.

297 **Literature search and coordinate selection**
298 The research articles used as a source of foci for the meta-analyses were identified in two ways.
299 First, we gathered papers referenced in Decetey and Lamm's formal meta-analysis (2007), as
300 well as Corbetta and Shulman's (2002), and Corbetta et al.'s (2008) reviews. Second, additional
301 papers were identified by performing a search on Google Scholar using the terms "fmri" or
302 "pet"; and "reorienting", "posner", "oddball", "target detection", or "theory of mind".
303
304 Once a database of 50 potentially relevant papers was identified, each paper was categorized as
305 containing either a ToM, attention reorienting, or target detection task. ToM tasks were defined
306 as reasoning about beliefs, intentions, or thoughts. Foci of interest contrasted tasks requiring the
307 attribution of mental states to matched tasks that did not require the participant to consider
308 others' beliefs or intentions. Attention reorienting tasks were defined as redirecting attention
309 towards a target stimulus after a breach of expectation. Foci of interest contrasted trials when
310 participants had to redirect attention after being misinformed about the upcoming target
311 stimulus' location to trials when participants were correctly informed. Target detection tasks
312 were defined as the presentation of a distinct and infrequent stimulus during a stream of frequent
313 stimuli. Foci of interest contrasted trials when participants encountered an oddball to non-oddball
314 trials.
315
316 Rather than filtering out papers based on a reported coordinates' proximity to idealized rTPJ
317 coordinates as in a prior metanalysis (Decety & Lamm, 2007), foci tables containing analyses
318 that reflected a given task definition were all included in the meta-analyses. All of the foci from
319 an analysis were extracted from a paper and reported in stereotactic coordinates (x,y,z). If the
320 coordinates were reported in the Montreal Neurological Institute space, they were converted to
321 the Talairach and Tournoux (TAL) space using the Brett transformation (Brett, 1999).
322
323 **Meta-analyses**
324 Separate meta-analyses were performed to localize activation for each task using activation
325 likelihood estimation (Eickhoff et al., 2009), with a full-width-at-half-maximum (FWHM) of 10
326 mm, p-value threshold of $p < .004$, and a false discovery rate (FDR) threshold of $q = .05$. In
327 addition, differences in activation between the three tasks were computed using difference maps
328 (Laird et al., 2005), using 5000 permutations. The thresholded ALE maps from both analyses
329 were visualized on a fiducial representation of a standardized brain atlas (PALS-B12 human
330 atlas) using Caret version 5.612.
331
332 **Resting state functional connectivity analyses**
333 For each task, the results of the meta-analyses were visualized in Caret and the centers of
334 activation near the rTPJ were identified and used as seeds for three separate resting state
335 functional connectivity analyses. Table 1 lists the coordinates used as seeds for the analyses.
336 Resting state data was retrieved from the public database NITRC on February 15, 2010. Two
337 data sets were used: Beijing_Zang (Zang, Y.F.; n = 198 [76M/122F]; ages: 18-26; TR = 2; #
338 slices = 33; # timepoints = 225) and Cambridge_Buckner (Buckner, R.L.; n = 198 [75M/123F];
339 ages: 18-30; TR = 3; # slices = 47; # timepoints = 119). The total combined number of subjects
340 was 396 (245 female), aged 18-30 (mean age 21.1). The data was aligned to 711-2B atlas space.
341 All methods were identical to those reported by Fox et al. (Fox, et al., 2006; Fox, et al., 2005;
342 Fox, et al., 2009; Jack, et al., 2012) and similarly employed a global grey matter regressor,

343 except that statistical contrasts used a random effects method (Jack, et al., 2012), and the
344 resulting statistical images were whole brain corrected for multiple comparisons (z>3, n=17).
345 Contrasts either used one fisher-z transformed correlation image per subject entered into a single
346 sample t-test, or two such images corresponding to the two seeds entered into a paired t-test.
347
348 **Results**
349
350 **Meta-analyses**
351 The studies used in the primary meta-analyses are listed in tables 2-4. In total, the reorienting
352 category contained 14 papers (139 foci), 12 papers (199 foci) were in the oddball category, and
353 12 papers (104 foci) were in the ToM category.
354
355 In response to a reviewer concern that the meta-analysis accurately represented each category, a
356 secondary, post hoc meta-analysis was conducted including foci from an additional four
357 reorienting and 16 ToM papers. A total of 18 reorienting papers (169 foci) and 28 ToM papers
358 (239 foci) were used in the secondary analysis. Papers used in the secondary meta-analysis are
359 listed and indicated in tables 2-4. Figure 1 shows the results from this secondary extended meta-
360 analysis instead of the primary analysis. The results were highly consistent, such that the seed
361 regions originally identified by identifying peak significance did not need to be altered (Figure
362 1). The principle difference between the two meta-analyses was that the secondary analysis
363 produced more extended areas of significance in the expanded categories.
364
365 Figure 1D displays the results of the three single-condition analyses. Each of the three conditions
366 shows areas of activation unique to each task (see figure description for peaks of activation; table
367 5 for whole-brain peaks of activation). The ToM and reorienting ROIs near the rTPJ show some
368 overlap (purple area), with the ToM ROI extending more posterior at the angular gyrus (AG) and
369 the reorienting ROI extending more anterior. While the peak of the reorienting ROI lay dorsal to
370 the TOM ROI, the reorienting ROI extended in a dorsal-ventral direction such that it clearly
371 separated a posterior TPJ region (including the AG) from an anterior TPJ region (including the
372 SMG). Note the clearly distinct peak activation region at the rTPJ for the target detection ROI,
373 located more anterior at the SMG compared to both the ToM and reorienting ROIs. Figure 1A-C
374 displays the results of the difference maps. All three comparisons resulted in distinct areas of
375 peak activation for each task near the rTPJ, conforming to the same spatial distribution suggested
376 by the initial meta-analyses. The peaks of activation clusters for each difference map from the
377 primary analysis are listed in table 6.
378
379 These findings support our hypotheses that the detection of infrequent behaviorally-relevant
380 stimuli is associated with peak activation in the anterior TPJ (SMG), that attributing intentions to
381 others is associated with a distinct locus of peak activation in the posterior TPJ (AG), and that
382 tasks involving spatial reorienting demonstrate peak activation at points intermediate between
383 these areas.
384
385
386 **Resting state functional connectivity analyses**
387 Figure 2 A-C displays the results of the resting state connectivity analyses.

388   Consistent with our view that regions supporting ToM (e.g. AG) and regions supporting target
389   detection (e.g. SMG) have distinct functional roles, the ToM and target detection ROIs show
390   very different patterns of resting connectivity. There was a complete absence of overlap in either
391   their positive or negative connectivity patterns (a direct comparison is illustrated in figures 3 and
392   4). Consistent with our claim that the ToM region is part of the DMN the ToM seed shows
393   positive connectivity with the DMN, particularly MP/PCC and dMPFC regions associated with
394   mentalizing. In addition, consistent with our claim that the ToM region has a reciprocal
395   inhibitory relationship with the DAN, regions anti-correlated with the ToM seed show an
396   excellent correspondence with the DAN as identified in prior publications (Fox, et al., 2006; Fox,
397   et al., 2005).
398
399   The target detection seed demonstrates a positive relationship with the anterior insula,
400   supplementary motor area, and anterior cingulate cortex; regions involved in saliency detection,
401   effort, and task difficulty typically recruited during oddball tasks (Linden, et al., 1999).
402   Consistent with our claim that regions supporting target detection have a reciprocal inhibitory
403   relationship with the DMN, regions anti-correlated with the target detection seed show an
404   excellent correspondence with the DMN as identified in prior publications (Fox, et al., 2005),
405   including rTPJ, MP/PCC and dMPFC regions specifically associated with mentalizing (Denny,
406   et al., 2012; Van Overwalle, 2009).
407
408   Similar to findings reported in Fox et al (2006), our reorienting seed identified positively
409   correlated regions in medial frontal gyrus, inferior frontal gyrus, a region in medial prefrontal
410   cortex posterior to the dMPFC region previously mentioned, and anterior insula. Hence our
411   positive connectivity pattern was broadly equivalent, however the positive correlations we
412   observed appeared relatively weaker, and we identified anti-correlations with DAN regions
413   which were not observed by Fox et al. 2006.
414
415   Visual inspection of Figure 2B indicates that the reorienting seed demonstrates substantial
416   overlap between both the positive and negative resting state correlation patterns of the ToM seed
417   (see figure 3 and figure 4, yellow areas) and target detection seed (see figure 3 and figure 4, light
418   blue areas). To further examine the hypothesis that the reorienting seed involves the combination
419   of signals associated with the other seeds, we examined differences in connectivity between the
420   reorienting seed and the two other seeds. If the reorienting seed corresponds to a region with a
421   distinct functional connectivity pattern, then distinct regions should be observed which cannot be
422   accounted for by the connectivity of the other seeds. However, this was not what we observed.
423   Examining differences between the reorienting and target detection seeds (Figure 2D), we found
424   a pattern very similar to that observed for the ToM seed (Figure 2C). In particular, no areas of
425   positive connectivity were identified which could not be accounted for by hypothesizing that the
426   reorienting seed involves the combination of signals from the ToM and target detection seeds.
427   Examining differences between the reorienting and the ToM seed, we found a pattern very
428   similar to that observed for the target detection seed. There were two areas of positive
429   connectivity which appeared greater than for the target detection seed, in anterior middle frontal
430   gyrus, and inferior frontal/insula. However, these apparent positives could be accounted for by
431   anti-correlations with the ToM seed. No areas of positive connectivity were identified which
432   could not be accounted for by hypothesizing that the reorienting seed involves the combination
433   of signals from the ToM and target detection seeds.

434
435   **Discussion**
436
437   Our goal in this paper is to articulate an alternative account of the involvement of regions near
438   the right temporo-parietal junction in attention and social processing, and provide evidence
439   which is more consistent with our account than with extant theory concerning the ventral
440   attention network (VAN).
441
442   **Challenges to VAN theory**
443   Our findings are consistent with other findings which suggest there are at least two functionally
444   distinct regions near rTPJ (Caspers, et al., 2006; Cohen, et al., 2008; R. Mars, et al., 2012;
445   Scholz, et al., 2009), and that these regions are part of two distinct networks which can be
446   differentiated using rs-fcMRI (Cohen, et al., 2008; Fox, et al., 2005; R. Mars, et al., 2012) and by
447   virtue of their differential engagement in attention demanding social and non-social tasks (Fox,
448   et al., 2005; Jack, et al., 2012). We add to these prior observations by demonstrating that these
449   distinct networks at the rTPJ correspond to distinct loci for target detection and theory of mind,
450   using formal meta-analysis. These findings present three challenges to current theory concerning
451   the VAN (Corbetta, et al., 2008; M. Corbetta & G. L. Shulman, 2002):
452
453   First, contra Corbetta and Shulman (2002), our findings indicate that target detection has a
454   distinct locus from reorienting. Current theory holds that oddball and reorienting paradigms both
455   activate the VAN because both involve the detection of behaviorally relevant unexpected stimuli.
456   However, we suggest this account oversimplifies reorienting of attention by equating it to a
457   purely confirmatory process (i.e. target detection). A target is undoubtedly detected during
458   invalid trials, but in addition, the preceding attentional set is broken and the locus of attention
459   changed to the unexpected location. The existence of this additional process in the Posner cue-
460   type design is supported by highly consistent findings of longer response times for invalid
461   compared to valid trials (Corbetta, et al., 2002; Hopfinger & Ries, 2005; Mayer, et al., 2009). In
462   contrast, there is no need to break attentional set in oddball paradigms. In accordance with our
463   distinction between the two types of task, the meta-analysis identified two separate areas at the
464   rTPJ for reorienting and target detection.
465
466   Second, contra Corbetta et al. (2008), our findings indicate that theory of mind paradigms recruit
467   a neighboring but significantly distinct locus from reorienting and target detection. Our account
468   can explain the seemingly contradictory findings of prior studies which have directly compared
469   theory of mind and reorienting tasks. Importantly, both prior studies included analyses of
470   individual participants, overcoming the problem of inter-individual differences at the rTPJ.
471   Mitchell (2007) found no topographical distinction between either process, whereas Scholz et al.
472   (2009) find evidence of distinct activation peaks associated with ToM and attention reorienting.
473   These differences between the studies may be accounted for by differences in the methods of
474   analysis, or by scanner resolution differences, as Scholz et al. suggest. Alternatively they may be
475   due to differences in the designs of the reorienting paradigms, which are likely to have altered
476   the relative balance of contributions made by the AG and SMG networks to the reorienting
477   event-related signal[5]. In fact, even using high resolution imaging with regions defined in

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[5] Notably Scholz et al (2009) only found a very small area of significant activation associated with attention reorienting in their group analysis, even though they had a relatively large number of participants (n=21).

478 individual participants, Scholz et al. (2009) report modulation of the theory of mind area
479 associated with reorienting and modulation of the reorienting area associated with theory of
480 mind. This finding is difficult to account for on Scholz et al's own model, which holds the
481 regions play wholly functionally distinct roles in reorienting and theory of mind. However, it is
482 consistent with our view that theory of mind and target detection are functionally connected by
483 virtue of a mutually inhibitory relationship (Jack, et al., 2012). A meta-analysis published by
484 Decety and Lamm (2007) also found a significant difference in peak activation location
485 associated with social and attentional processes. Our results are consistent with theirs. However,
486 they did not distinguish reorienting from target detection foci.

488 Third, contra Fox et al. (2006), our findings suggest that rs-fcMRI derivations of the VAN using
489 a reorienting seed may result from the confounding of distinct signals. To allow a meaningful
490 comparison, we used identical rs-fcMRI methods to the prior report (Fox, et al., 2006). The only
491 differences are that: our reorienting seed is based on a larger sample of reorienting foci which we
492 analyzed using formal meta-analysis methods, our functional connectivity findings are derived
493 from a considerably larger sample, we used random rather than fixed effects analysis methods,
494 and we added the use of paired t-tests for the purposes of comparing connectivity associated with
495 different seeds.

497 The contrast between the reorienting and target detection connectivity produced a correlation
498 pattern almost identical to that of the ToM seed, whereas the contrast between the reorienting
499 and ToM connectivity produces a correlation pattern almost identical to that of the target
500 detection seed. The logic of our analysis is straightforward. If the reorienting seed corresponds to
501 a distinct functional network, then the paired t-tests should have revealed evidence of
502 connectivity to regions which could not be accounted for by correlations with the ToM and target
503 detection seeds. We do not deny the possibility that there is a distinct functional network
504 interposed between the AG and SMG, as suggested by some recent reports (e.g. (Yeo et al.,
505 2011)). However, we do not believe that the methods used in these reports are able to clearly
506 distinguish between correlations which arise due to the summing of signals from contiguous
507 regions and correlations which genuinely reflect the existence of a distinct network. Further, we
508 note very low confidence estimates for networks in this region (see figures 8 and 10 in (Yeo, et
509 al., 2011)). Since it is more parsimonious to assume two networks are present in this region, as
510 opposed to three (figure 7 in (Yeo, et al., 2011)) or six (figure 9 in (Yeo, et al., 2011)), we
511 suggest this should be the null hypothesis pending the development of independently validated
512 methods that can unequivocally distinguish between these possibilities.

514 **Circuit breaking**
515 VAN theory and our account are both consistent with a circuit breaking role for rTPJ regions
516 which are suppressed during visual search. However, our account suggests a different type of
517 circuit breaking. VAN theory holds that suppressed regions are involved in the filtering of
518 unexpected stimuli and, when a task relevant unexpected stimulus is detected, send information
519 about that stimulus to the DAN to guide the reorienting of attention (Corbetta, et al., 2008;
520 Shulman, et al., 2007). Our account sees filtering and sending information about salient stimuli
521 as potential functions of the anterior TPJ (e.g. SMG). The posterior TPJ (e.g. AG) is the primary

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This suggests that their implementation of the attention reorienting paradigm was different from other groups, who have identified more extensive activations.

522   locus of suppression, and is dedicated to tracking the intentions of perceived agents. Nonetheless,
523   since the AG is in tension with the DAN, our account is consistent with its playing a more
524   general circuit breaking role.
525
526   One possibility is that transient activation of the AG sends a non-specific reset signal to the
527   DAN, akin to adding noise to a dynamic system so that it can settle into a new global minimum.
528   However, we note that theoretical explanations proposing the role of the rTPJ as a circuit-breaker
529   (Corbetta, et al., 2008) lack confirmation of the area's purported beneficial role in resetting top-
530   down influences from the DAN. The existing evidence shows increases in activity at rTPJ to be
531   detrimental to target detection (Shulman, et al., 2007), and a negative relationship between
532   behavioral performance and a measure of the VAN's causal influence on the DAN (Wen, Yao,
533   Liu, & Ding, 2012). Research on the time course of the rTPJ and DAN, while not conclusive,
534   suggests the rTPJ's activity follows transient activity in the DAN (DiQuattro & Geng, 2011);
535   results contrary to the circuit-breaker hypothesis of rTPJ function. Instead, the anterior TPJ
536   (SMG) may be involved in updating attentional sets by working in concert with the IFG, which
537   in turn modulates activity in the DAN (DiQuattro & Geng, 2011; Sridharan, Levitin, Chafe,
538   Berger, & Menon, 2007; Vossel, Weidner, Driver, Friston, & Fink, 2012; Weissman & Prado,
539   2012). Hence, we remain neutral concerning the potential circuit breaking role of the posterior
540   TPJ (e.g. AG), awaiting evidence which more clearly distinguishes the roles of these regions. An
541   alternative to the circuit breaker hypothesis, which is equally consistent with our account, is that
542   disruption of a suppressive signal that originates either in the DAN or a third region such as the
543   IFG causes the posterior TPJ (e.g. AG) to be temporarily released.
544
545   Published maps of the VAN obtained using rs-fcMRI are variable. There are notable
546   discrepancies between two papers with overlapping authors (Fox, et al., 2006; Mantini, Corbetta,
547   Perrucci, Romani, & Del Gratta, 2009), most notably with regard to whether or not anti-
548   correlations are seen with the DMN, but also to regions of positive connectivity. One of the VAN
549   maps coheres well with our SMG target detection map (Mantini, et al., 2009), the other is more
550   similar to our reorienting seed map (Fox, et al., 2006). Our account can readily explain such
551   discrepancies, which may result from small variations in the location of the seed near the border
552   between discrete functional networks. However, another possible explanation is the presence of a
553   third, more dorsal region at the rTPJ, in-between the AG and SMG. Recent work has emphasized
554   the role of additional networks other than the VAN and DAN in attention (Petersen & Posner,
555   2012). One such network, the frontoparietal control network (FPCN), is involved in moment-to-
556   moment aspects of executive control, often associated with cue-onset activity within trials, and
557   includes an area more dorsal than the rTPJ node of the VAN. However, the extent to which this
558   region is distinct from DAN (Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008) and VAN
559   (Dosenbach et al., 2006) areas near the rTPJ remains unclear. Outside of standard attentional
560   control tasks, the FPCN is also hypothesized to support executive control in tasks that
561   specifically recruit the DMN (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010).
562   Spreng et al. (2012) argues that the network supports goal-directed cognition, whether it be
563   social or visuo-spatial in nature, pointing to the mediatory connectivity profiles between the
564   FPCN and DAN, as well as the FPCN and DMN, as evidence.
565
566   The overlap between our reorienting connectivity areas and the FPCN is unclear, nonetheless,
567   our connectivity contrasts are potentially congruent with such an account. The FPCN's high

568 degree of interconnectivity with both the TPN and DMN may be reflected in our finding that
569 separately subtracting reorienting connectivity from AG and SMG connectivity leaves no regions
570 left over that could not be explained by correlation with the AG and SMG seeds.
571 In summary, the number of attention networks has increased and evolved into a more complex
572 account than simply the DAN and VAN (M. Corbetta & G. Shulman, 2002). Such a view is
573 consistent with our account that reorienting is a complex process, however, our explanation does
574 not require the addition of a network to explain reorienting-related activity at the rTPJ. If
575 reorienting does rely on a third attentional network including a more dorsal rTPJ region, then our
576 challenge to VAN theory would be restricted to the identification of a distinct region at the rTPJ
577 involved in attention but dissociable from target detection (Corbetta & Shulman, 2011).
578
579 **Empirical limitations**
580 We acknowledge limitations to our empirical findings. First, our meta-analytic findings rely on
581 the anatomical alignment of studies conducted using different scanners whose images have been
582 co-registered to different atlases. Given that our sample was of a reasonable size, these
583 differences should have led an increase in randomly distributed noise and thus greater difficulty
584 resolving distinct localizations. Nonetheless, the possibility of systematic error remains. Second,
585 we have postulated that two factors contribute to reorienting responses. However, we have not
586 directly manipulated these factors in order to establish this claim. Ideally, future work will
587 employ high resolution imaging and paradigms that parametrically modulate these factors in
588 order to distinguish their effects on different cortical areas. Third, we acknowledge that careful
589 anatomical work suggests a number of distinct functional regions near rTPJ (Caspers, et al.,
590 2006) and that our group-based methods may have failed to capture important aspects of this fine
591 grained structure. Although our work is at a similar anatomical resolution to work that has
592 guided VAN theory, we acknowledge that higher resolution work on individual subjects may
593 confirm the existence of a region specific to reorienting between the AG and SMG. Hence, our
594 account of rTPJ involvement in reorienting in terms of the combination of signals from
595 contiguous regions associated with two wide-scale functional networks may turn out to be
596 wrong. In that case, our challenge to VAN theory would be restricted to noting the need to
597 differentiate between regions involved in reorienting, target detection (M. Corbetta & G. L.
598 Shulman, 2002) and theory of mind (Corbetta, et al., 2008).
599
600 **Novel methodological claims**
601 Our theoretical account of reorienting relies on two relatively novel claims. The first is that
602 event-related BOLD effects with positive going waveforms can be attributed to the transient
603 disengagement of suppression in a paradigm. The second is that positive connectivity maps
604 derived from standard rs-fcMRI methods may, in some cases, fail to identify coherent functional
605 networks. We acknowledge that further work is wanted to establish these claims. At the same
606 time, we point to considerations which support the plausibility of these claims.
607
608 First, there is now a substantial body of work which establishes that activity levels of the default
609 network can, in some cases, be best accounted for by the suppressive effect of task demands
610 which are positively associated with functions instantiated in entirely distinct cortical networks
611 (Andrews-Hanna, 2011; Buckner, Andrews-Hanna, & Schacter, 2008; Mason, et al., 2007;
612 McKiernan, et al., 2003). If this view is accepted, it represents a relatively minor step to presume

613 that the transient event-related release of these suppressive effects could give rise to a positive
614 going BOLD waveform.

616 Second, we note that the methods of rs-fcMRI are relatively novel, and to date have only been
617 partially validated. It has already been shown, both mathematically and in practice, that they can
618 produce artifactual results, in particular in relation to negative correlation maps (Murphy, Birn,
619 Handwerker, Jones, & Bandettini, 2009)[3]. Although we don't know of validated examples of
620 spurious positive correlations, they are no less mathematically plausible. The unusually high
621 degree of inter-subject variability in anatomy and functional organization at the TPJ (Caspers, et
622 al., 2006; Van Essen, 2005) further increases the potential for signals from neighboring but
623 functionally distinct areas to be confounded when deriving rs-fcMRI maps of this area.

625 **Implications for theory**
626 A natural assumption which has guided some prior accounts has been the view that attentional
627 reorienting is an evolutionarily basic process which has been coopted to play a role in social
628 cognition (Corbetta, et al., 2008; Decety & Lamm, 2007). However, it is important to remember
629 that the parsing of the cognitive operations involved in tasks is a complex and partially
630 speculative process. Reorienting may not be a basic cognitive process, but may instead be a
631 complex process which involves contributions from different regions with computationally
632 distinct roles. Recent accounts of the evolution of the human cortex suggest that social
633 processing demands have played an important role in the massive evolutionary expansion of
634 cortex, which is evident from comparisons between humans and our nearest evolutionary
635 neighbors. Our view is guided by this work, and suggests that some observations which propose
636 a putative role for the rTPJ in attention may be best explained by an alternative hypothesis.
637 Namely, the view that social processing is accomplished by basic cognitive processes which
638 evolved specifically for that purpose, which are not only distinct from but also in tension with
639 basic attentional processes.

641 While a synthesis of the attention literature lies beyond the scope of this paper, we suggest that
642 some current ambiguities may be resolved by distinguishing between the functions of the
643 anterior TPJ (e.g. SMG) and the posterior TPJ (e.g. AG). For example, a recent review on
644 neglect proposes that the attentional deficits are a result of damage to VAN regions, disrupting
645 communication between the left and right DANs (Corbetta & Shulman, 2011), however, the
646 authors admit the neural mechanisms explaining interactions between the VAN and DAN are
647 poorly understood. Research has demonstrated deficits in sustained attention in patients with
648 posterior parietal cortex lesions (Malhotra, Coulthard, & Husain, 2009) and target detection from
649 TMS over the AG, not the SMG (Chambers, Payne, Stokes, & Mattingley, 2004). The AG region
650 of the DMN has demonstrated abnormal functioning in patients with a variety of neurological
651 disorders (Broyd et al., 2009; Zhou et al., 2007) as well as traumatic brain injuries (Bonnelle et
652 al., 2011) characterized by low sustained attention. In light of our results, we suggest that the

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[3] This represents an important methodological concern, however the reader should note that the negative correlations we report are validated by other methods. First, a number of laboratories have observed anti-correlations using conservative methods that don't employ mean signal regression (Chai, et al., 2012; Chang & Glover, 2009; Fox, et al., 2009; Jack, et al., 2012). Second, Jack et al (2012) validate anti-correlations derived from resting connectivity by demonstrating that they correspond with task related activations and deactivations seen in both the DMN and TPN. Finally, it is important to note that conservative methods which do not use a global regressor likely underestimate the degree of true anti-correlations, and that findings using a global regressor appear more accurate when compared to independent evidence:- The methods of Fox et al (2005) using global normalization, which we also use here, demonstrate good correspondence with regions that are consistently deactivated during cognitively demanding non-social tasks (Raichle & Snyder, 2007).

653 attentional deficits characteristic of neglect patients with damage to the rTPJ region may not be
654 explainable unless the focus of neglect research is widened to include the effects of brain
655 networks whose primary function is not attention.
656
657 In terms of social cognition, the alternative accounts we focus on here have emphasized the
658 notion that mechanisms for external attention have been evolutionarily coopted to play a role in
659 social cognition (Corbetta, et al., 2008; Decety & Lamm, 2007). In contrast, we hypothesize that
660 mentalizing (i.e. our capacity to represent the internal mental states of conspecifics) was built
661 upon a system for internal attention, e.g. whose original functions were those of interoception
662 and self-regulation. According to our account, this system evolved to be in tension with a system
663 for representing the physical and mechanical properties of inanimate objects, which are built
664 upon systems for external attention, e.g. perception and the manipulation of objects. Our account
665 of mentalizing as coopting mechanisms for internal attention fits best with the anatomy of medial
666 parts of the DMN associated with mentalizing (dMPFC and MP/PC). The evidence from rs-
667 fcMRI and activation studies strongly suggests the AG is part of the same network as these
668 medial regions, however it's anatomical location is less congruent with a connection to internal
669 attention. Instead, the right AG lies near to a right lateralized system of occipital and temporal
670 regions involved in the sensory processing of socially relevant information (Kanwisher,
671 McDermott, & Chun, 1997; Peelen, 2004; Pelphrey, 2005). In other words, the posterior TPJ
672 may represent a critical junction box where different types of social information are integrated,
673 namely information that derives from internal attention (medial DMN regions) and external
674 attention (right lateralized regions for social perception). This fits well with the posterior TPJ's
675 more specific functional role in representing the intentions of perceived agents (Saxe, et al.,
676 2006; Saxe & Powell, 2006).
677
678 This raises an interesting question: might there be an evolutionary reason for the tension between
679 posterior and anterior TPJ regions? While such an account would be speculative, it does seem
680 that there are good reasons for a region with the function of posterior TPJ to have an inhibitory
681 connection with regions involved in visual search, and for its activity to increase when an
682 unexpected stimulus is detected. Outside the laboratory, suddenly appearing unexpected stimuli
683 are often animals or conspecifics, which might pose a survival threat. Attempting to find one
684 more apple is not so important as attending to the danger posed by a predator. In this scenario,
685 there is not only an advantage to breaking the current attentional set, there is also an advantage to
686 expediting the processing of social cues and rapidly generating a model of the agent's intentions.
687 Hence, while there is no obvious feature of laboratory reorienting tasks which calls for the
688 engagement of social processing; this may nonetheless occur because the engagement of social
689 processing upon detection of a salient unexpected stimulus is adaptive as a general rule.
690 Consistent with this speculative account, there is evidence that animate motion captures attention
691 more rapidly than inanimate motion (Pratt, Radulescu, Guo, & Abrams, 2010). If this account is
692 borne out, then it may be that information is indeed passed from social processing areas in the
693 posterior TPJ to the DAN in order to reorient attention. Our hypothesis is that this information
694 would derive from active anticipation of the likely actions of a perceived agent using theory of
695 mind. Hence, surprisingly, many of the functions attributed to the rTPJ by the VAN account are
696 consistent with the account offered here. The major difference is that we hypothesize these
697 reorienting functions evolved because of evolutionary pressure for more sophisticated social

698 processing, and our accounts predicts these function will be most profitably investigated using
699 realistic social paradigms.
700
701 Distinguishing between these accounts is clearly theoretically significant for our understanding
702 of cortical function. In addition, it has implications for therapeutic approaches. If it is correct that
703 attentional reorienting represents a basic process which is coopted for social cognition, then this
704 would suggest that early intervention by training attention might be an effective treatment for
705 individuals with social deficits, such as individuals with Autism Spectrum Disorders. On the
706 other hand, if our account is correct, then non-social attention training programs are not likely to
707 be effective for improving social function, and may even be detrimental.
708
709 **Conclusions**
710 For more than a decade, the theory of the ventral attention system has played a leading role in the
711 interpretation of findings which implicate the rTPJ in attention and social processing. In this
712 paper we propose an alternative account which appeals to the interplay between two distinct
713 regions at the rTPJ which are associated with antagonistic functional networks involved in social
714 and non-social processing. We present empirical evidence which is more consistent with this
715 alternative account than prior accounts, identifying distinct loci and functional connectivity maps
716 associated with target detection, reorienting and theory of mind. We acknowledge this evidence
717 is limited in scope, relying entirely on meta-analysis and rs-fcMRI. It does not make use of
718 experimental manipulation of the processes under investigation, high-resolution imaging, or
719 analysis of individual participants, all of which we expect to be critical to establishing a
720 definitive account. However, these findings do motivate further consideration of our account,
721 which has significant implications. First, it has the potential to make sense of a large and
722 confusing literature on the role of the rTPJ in attention and social processing. Second, it suggests
723 an alternative view of the evolution of brain function, in particular functions associated with
724 social cognition. Third, our account emphasizes attempts to understand neural activity not just by
725 reference to the immediate demands of the experimental task, but also by reference to constraints
726 which our neural structure places on cognition. Task analysis of attention reorienting paradigms
727 does not suggest any role for social processing. Nonetheless, we suggest that activation patterns
728 associated with these paradigms cannot be fully understood without reference to an inbuilt neural
729 tension between focused attention and social processing.
730

740

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1021 **Figure legends**
1022 **Figure 1. Meta-analyses results with connectivity seeds.**
1023 Results from the difference maps comparing (A) ToM and target detection, (B) reorienting and target detection, (C)
1024 ToM and reorienting tasks. All three tasks show regions near the rTPJ that survived the pairwise difference maps
1025 (D) Results from the individual meta-analyses. Each panel shows the peaks of activation clusters near rTPJ in the
1026 analysis shown in figure 2. ToM (50, -55, 23), reorienting (54, -47, 21), and target detection (55, -37, 18). Note:
1027 color key applies to activations in D and foci colors in A-C, activation in A-C are colored based on T-statistics. This
1028 figure reflects the secondary extended meta-analysis (see results).
1029
1030 **Figure 2. Resting state connectivity results.**
1031 Results from the resting state connectivity analyses for each seed showing distinct patterns of connectivity for the
1032 (A) target detection, (B) reorienting, and (C) ToM seeds. The target detection seed shows a positive relationship
1033 with the TPN and a negative relationship with areas of the DMN. The ToM seed shows the opposite pattern, a
1034 positive relationship with the DMN and a negative relationship with TPN areas. Results from the resting state
1035 connectivity contrasts showing the comparison of (D) reorienting and target detection connectivity and (E)
1036 reorienting and ToM connectivity. The contrast shown in (D) yields a pattern of connectivity highly similar to the
1037 ToM seed connectivity (C), while the contrast shown in (E) yields a pattern highly similar to the target detection
1038 seed connectivity (A). Left hemisphere connectivity patterns were very similar to right hemisphere connectivity
1039 patterns.
1040
1041 **Supporting Figures**
1042 Figure 3. Positive connectivity results for all three seeds. The ToM and target detection seeds demonstrate a
1043 complete lack of overlap between their positive resting state correlation patterns (purple areas). All three seeds show
1044 minimal overlap in positive connectivity (white areas).
1045
1046 Figure 4. Negative connectivity results for all three seeds. The ToM and target detection seeds demonstrate a
1047 complete lack of overlap between their negative resting state correlation patterns (purple areas). All three seeds
1048 show minimal overlap in negative connectivity (white areas).
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Table 1. Connectivity Analysis Coordinates

	X	Y	Z
Reorienting	54	-47	21
Target Detection	55	-37	18
ToM	50	-55	23

1052
1053 Coordinates used as seeds for each task in the resting state connectivity analyses
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Table 2. Target Detection Meta-Analysis Studies

Authors	*Analysis*
Bledowski, C., Prvulovic, D., Goebel, R., Zanella, F. E., & Linden, D. E. J. (2004). Attentional systems in target and distractor processing: a combined ERP and fMRI study. NeuroImage, 22(2), 530–540. doi:10.1016/j.neuroimage.2003.12.034	regions activated during target condition versus baseline
Braver, T., Barch, D., Gray, J., Molfese, D., & Snyder, A. (2001). Anterior cingulate cortex and response conflict- effects of frequency, inhibition and errors. Cerebral Cortex, 1–12.	regions showing consistent response to low-frequency events in conjunction analyses
Downar, J., Crawley, A. P., Mikulis, D. J., & Davis, K. D. (2001a). The Effect of Task Relevance on the Cortical Response to Changes in Visual and Auditory Stimuli: An Event-Related fMRI Study. NeuroImage, 14(6), 1256–1267. doi:10.1006/nimg.2001.0946	relevant stimulus changes minus irrelevant stimulus changes
Downar, J., Crawley, A., Mikulis, D., & Davis, K. (2001b). A cortical network sensitive to stimulus salience in a neutral context across multiple sensory modalities. J Neurophysiol, 1–7. doi:10.1152/jn.00636.2001	greater response to novel than familiar stimuli across all sensory modalities
Fichtenholtz, H. M., Dean, H. L., Dillon, D. G., Yamasaki, H., McCarthy, G., & LaBar, K. S. (2004). Emotion–attention network interactions during a visual oddball task. Cognitive Brain Research, 20(1), 67–80. doi:10.1016/j.cogbrainres.2004.01.006	attentional targets (shape oddballs & emotional pictures)
Kiehl, K. A., Stevens, M. C., Laurens, K. R., Pearlson, G., Calhoun, V. D., & Liddle, P. F. (2005). An adaptive reflexive processing model of neurocognitive function: supporting evidence from a large scale (n = 100) fMRI study of an auditory oddball task. NeuroImage, 25(3), 899–915. doi:10.1016/j.neuroimage.2004.12.035	detection of target stimuli minus standard stimuli
Kiehl, K., Laurens, K., Duty, T., Forester, B., & Liddle, P. (2001). Neural sources involved in auditory target detection and novelty processing - an event-related fMRI study. Psychopysiology, 1–10.	target stimuli minus nontarget baseline condition
Liebenthal, E., Ellingson, M. L., Spanaki, M. V., Prieto, T. E., Ropella, K. M., & Binder, J. R. (2003). Simultaneous ERP and fMRI of the auditory cortex in a passive oddball paradigm. NeuroImage, 19(4), 1395–1404. doi:10.1016/S1053-8119(03)00228-3	Peaks of BOLD activation correlated with the magnitude of the ERP negativity during the MMN range
Linden, D., Prvulovic, D., Formisano, E., Vollinger, M., Zanella, F., & Gobel, R. (1999). The functional neuroanatomy of target detection-An fMRI study of visual and auditory oddball tasks. Cerebral Cortex, 1–9.	response to targets versus response to non-tragets
Melcher, T., & Gruber, O. (2006). Oddball and incongruity effects during Stroop task performance: A comparative fMRI study on selective attention. Brain Research, 1121(1), 136–149. doi:10.1016/j.brainres.2006.08.120	color-oddballs vs oddball control
Stevens, M. C., Calhoun, V. D., & Kiehl, K. A. (2005). Hemispheric differences in hemodynamics elicited by auditory oddball stimuli. NeuroImage, 26(3), 782–792. doi:10.1016/j.neuroimage.2005.02.044	right hemisphere minus left hemisphere; oddball detection
Watkins, S., Dalton, P., Lavie, N., & Rees, G. (2006). Brain Mechanisms Mediating Auditory Attentional Capture in Humans. Cerebral Cortex, 17(7), 1694–1700. doi:10.1093/cercor/bhl080	singleton trials compared with no singleton trials

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Table 3. Reorienting Meta-Analysis Studies

	Authors	*Contrast*
	Arrington, C., Carr, T., Mayer, A., & Rao, S. (2000). Neural Mechanisms of Visual Attention - Object-Based Selection of a Region in Space. Journal of Cognitive Neuroscience, 1–12.	invalid minus valid
*	Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2006). Visuospatial reorienting signals in the human temporo-parietal junction are independent of response selection. Eur J Neurosci, 23(2), 591-596. doi: 10.1111/j.1460-9568.2005.04573.x	peak TPJ activation in Validity x Time
	Corbetta, M., Kincade, J., & Shulman, G. (2002). Neural Systems for Visual Orienting and Their Relationships to Spatial Working Memory. Journal of Cognitive Neuroscience, 1–16.	invalid minus valid
*	Giessing, C., Thiel, C. M., Rosler, F., & Fink, G. R. (2006). The modulatory effects of nicotine on parietal cortex activity in a cued target detection task depend on cue reliability. Neuroscience, 137(3), 853-864. doi: 10.1016/j.neuroscience.2005.10.005	validity main effect
*	Giessing, C., Thiel, C. M., Stephan, K. E., Rosler, F., & Fink, G. R. (2004). Visuospatial attention: how to measure effects of infrequent, unattended events in a blocked stimulus design. Neuroimage, 23(4), 1370-1381. doi: 10.1016/j.neuroimage.2004.08.008	event and block-related validity effects
	Indovina, I., & Macaluso, E. (2006). Dissociation of Stimulus Relevance and Saliency Factors during Shifts of Visuospatial Attention. Cerebral Cortex, 17(7), 1701–1711. doi:10.1093/cercor/bhl081	invalid minus valid
	Kincade, J. M. (2005). An Event-Related Functional Magnetic Resonance Imaging Study of Voluntary and Stimulus-Driven Orienting of Attention. Journal of Neuroscience, 25(18), 4593–4604. doi:10.1523/JNEUROSCI.0236-05.2005	endogenous condition validity by time
*	Konrad, K., Neufang, S., Thiel, C. M., Specht, K., Hanisch, C., Fan, J., . . . Fink, G. R. (2005). Development of attentional networks: an fMRI study with children and adults. Neuroimage, 28(2), 429-439. doi: 10.1016/j.neuroimage.2005.06.065	invalid minus valid (adults only)
	Lepsien, J., & Pollmann, S. (2002). Covert reorienting and inhibition of return - an event-related fMRI study. Journal of Cognitive Neuroscience, 1–20.	validity effects within SOA of 100 msec
	Macaluso, E., Frith, C., & Driver, J. (2002). Supramodal Effects of Covert Spatial Orienting Triggered by Visual or Tactile Events. Journal of Cognitive Neuroscience, 1–13.	invalid minus valid
	Mattler, U., Wüstenberg, T., & Heinze, H.-J. (2006). Common modules for processing invalidly cued events in the human cortex. Brain Research, 1109(1), 128–141. doi:10.1016/j.brainres.2006.06.051	invalid minus valid
	Mayer, A. R., Franco, A. R., & Harrington, D. L. (2009). Neuronal modulation of auditory attention by informative and uninformative spatial cues. Human Brain Mapping, 30(5), 1652–1666. doi:10.1002/hbm.20631	invalid > valid (100ms SOA)

* denotes additional papers included in the secondary meta-analysis

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Table 3 cont. Reorienting Meta-Analysis Studies

Authors	*Contrast*
Mayer, A. R., Harrington, D., Adair, J. C., & Lee, R. (2006). The neural networks underlying endogenous auditory covert orienting and reorienting. NeuroImage, 30(3), 938–949. doi:10.1016/j.neuroimage.2005.10.050	invalid minus valid
Mayer, A., Harrington, D., Stephen, J., Adair, J., & Lee, R. (2007). An event-related fMRI study of exogenous facilitation and inhibition of return in the auditory modality. Journal of Cognitive Neuroscience, 1–13.	invalid > valid (100ms SOA)
Mitchell, J. P. (2007). Activity in Right Temporo-Parietal Junction is Not Selective for Theory-of-Mind. Cerebral Cortex, 18(2), 262–271. doi:10.1093/cercor/bhm051	invalid minus valid
Natale, E., Marzi, C. A., & Macaluso, E. (2009). FMRI correlates of visuo-spatial reorienting investigated with an attention shifting double-cue paradigm. Human Brain Mapping, 30(8), 2367–2381. doi:10.1002/hbm.20675	invalid minus valid endogenous cues
Thiel, C. M., Zilles, K., & Fink, G. R. (2004). Cerebral correlates of alerting, orienting and reorienting of visuospatial attention: an event-related fMRI study. NeuroImage, 21(1), 318–328. doi:10.1016/j.neuroimage.2003.08.044	invalid minus valid trials
Vossel, S., Thiel, C. M., & Fink, G. R. (2006). Cue validity modulates the neural correlates of covert endogenous orienting of attention in parietal and frontal cortex. NeuroImage, 32(3), 1257–1264. doi:10.1016/j.neuroimage.2006.05.019	reorienting in the 90% validity condition

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Table 4. Theory of Mind Meta-Analysis Studies

Authors	*Contrast*
∗ Aichorn, M., Perner, J., Weiss, B., Kronbichler, M., Staffen, W., & Ladurner, G. (2009). Temporo-parietal Junction Activity in Theory-of-Mind Tasks: Falseness, Beliefs, or Attention. Journal of Cognitive Neuroscience, 1-14.	false belief > photo (question)
∗ Abraham, A., Rakoczy, H., Werning, M., von Cramon, D. Y., & Schubotz, R. I. (2010). Matching mind to world and vice versa: Functional dissociations between belief and desire mental state processing. Soc Neurosci, 5(1), 1-18. doi: 10.1080/17470910903166853	belief-questions > control-questions & desire-questions > control-questions
∗ Bahnemann, M., Dziobek, I., Prehn, K., Wolf, I., & Heekeren, H. R. (2010). Sociotopy in the temporoparietal cortex: common versus distinct processes. Soc Cogn Affect Neurosci, 5(1), 48-58. doi: 10.1093/scan/nsp045	ToM judgments minus appearance judgments
∗ Bruneau, E. G., Pluta, A., & Saxe, R. (2012). Distinct roles of the 'shared pain' and 'theory of mind' networks in processing others' emotional suffering. Neuropsychologia, 50(2), 219-231. doi: 10.1016/j.neuropsychologia.2011.11.008	ToM localizer
∗ Dohnel, K., Schuwerk, T., Meinhardt, J., Sodian, B., Hajak, G., & Sommer, M. (2012). Functional activity of the right temporo-parietal junction and of the medial prefrontal cortex associated with true and false belief reasoning. Neuroimage, 60(3), 1652-1661. doi: 10.1016/j.neuroimage.2012.01.073	salley-ann task (true and false ToM minus reality)
Fletcher, P., Happe, F., Frith, U., Baker, S., Dolan, R., Frackowiak, R., & Frith, C. (1995). Other minds in the brain: a functional imaging study of theory of mind in story comprehension. Cognition, 1–20.	ToM stories vs Physical stories
Gallagher, H., Happe, F., Brunswick, N., Fletcher, P., Frith, U., & Frith, C. (2000). Reading the mind in cartoons and stories: an fMRI study of theory of mind in verbal and nonverbal tasks. Neuropsychologia, 1–11.	ToM vs non-ToM stories
Gobbini, M., Koralek, A., Bryan, R., Montgomery, K., & Haxby, J. (2007). Two takes on the social brain: a comparison of theory of mind tasks. Journal of Cognitive Neuroscience, 1–13.	false belief stories vs physical belief stories
∗ Hartwright, C. E., Apperly, I. A., & Hansen, P. C. (2012). Multiple roles for executive control in belief-desire reasoning: distinct neural networks are recruited for self perspective inhibition and complexity of reasoning. Neuroimage, 61(4), 921-930. doi: 10.1016/j.neuroimage.2012.03.012	false belief minus false photograph
Hynes, C. A., Baird, A. A., & Grafton, S. T. (2005). Differential role of the orbital frontal lobe in emotional versus cognitive perspective-taking. Neuropsychologia, 44(3), 374–383. doi:10.1016/j.neuropsychologia.2005.06.011	Cognitive PT minus Control
∗ Jenkins, A. C., & Mitchell, J. P. (2010). Mentalizing under uncertainty: dissociated neural responses to ambiguous and unambiguous mental state inferences. Cereb Cortex, 20(2), 404-410. doi: 10.1093/cercor/bhp109	mentalizing scenarios > nonsocial scenarios
∗ Kobayashi, C., Glover, G. H., & Temple, E. (2008). Switching language switches mind: linguistic effects on developmental neural bases of 'Theory of Mind'. Soc Cogn Affect Neurosci, 3(1), 62-70. doi: 10.1093/scan/nsm039	ToM > physical (both japanese and english language groups)

* denotes additional papers included in the secondary meta-analysis

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Table 4 cont. Theory of Mind Meta-Analysis Studies

Authors	*Contrast*
* Kobayashi, C., Glover, G. H., & Temple, E. (2006). Cultural and linguistic influence on neural bases of 'Theory of Mind': an fMRI study with Japanese bilinguals. Brain Lang, 98(2), 210-220. doi: 10.1016/j.bandl.2006.04.013	ToM compared with non-ToM-conjunction among language groups
* van der Meer, L., Groenewold, N. A., Nolen, W. A., Pijnenborg, M., & Aleman, A. (2011). Inhibit yourself and understand the other: neural basis of distinct processes underlying Theory of Mind. Neuroimage, 56(4), 2364-2374. doi: 10.1016/j.neuroimage.2011.03.053	ToM high inhibition minus fixation
Mitchell, J. P. (2007). Activity in Right Temporo-Parietal Junction is Not Selective for Theory-of-Mind. Cerebral Cortex, 18(2), 262–271. doi:10.1093/cercor/bhm051	tom minus attention cueing task
Perner, J., Aichhorn, M., Kronbichler, M., Staffen, W., & Ladurner, G. (2006). Thinking of mental and other representations: The roles of left and right temporo-parietal junction. Social Neuroscience, 1(3-4), 245–258. doi:10.1080/17470910600989896	false belief vignettes minus photo vignettes
* Rabin, J. S., Gilboa, A., Stuss, D. T., Mar, R. A., & Rosenbaum, R. S. (2009). Common and Unique Neural Correlates of Autobiographical Memory and Theory of Mind. Journal of Cognitive Neuroscience, 1-17.	ToM photo minus Autobiographical Memory photo
Ruby, P., & Decety, J. (2003). What you believe versus what you think they believe: a neuroimaging study of conceptual perspective-taking. European Journal of Neuroscience, 17(11), 2475–2480. doi:10.1046/j.1460-9568.2003.02673.x	3rd person minus 1st person
* Samson, A. C., Zysset, S., & Huber, O. (2008). Cognitive humor processing: different logical mechanisms in nonverbal cartoons--an fMRI study. Soc Neurosci, 3(2), 125-140. doi: 10.1080/17470910701745858	ToM cartoons minus non ToM cartoons
Saxe, R., & Kanwisher, N. (2003). People thinking about thinking peopleThe role of the temporo-parietal junction in "theory of mind." NeuroImage, 19(4), 1835–1842. doi:10.1016/S1053-8119(03)00230-1	ToM inference minus mechanical inference
Saxe, R., & Powell, L. (206). It's the thought that counts: specific brain regions for one component of theory of mind. Psychological Science, 1–8.	false belief minus false photograph
Saxe, R., Schulz, L. E., & Jiang, Y. V. (2006). Reading minds versus following rules: Dissociating theory of mind and executive control in the brain. Social Neuroscience, 1(3-4), 284–298. doi:10.1080/17470910601000446	ToM reference experiment
* Veroude, K., Keulers, E. H., Evers, E. A., Stiers, P., Krabbendam, L., & Jolles, J. (2012). The effect of perspective and content on brain activation during mentalizing in young females. J Clin Exp Neuropsychol, 34(3), 227-234. doi: 10.1080/13803395.2011.630650	others vs self (females only)
Völlm, B. A., Taylor, A. N. W., Richardson, P., Corcoran, R., Stirling, J., McKie, S., Deakin, J. F. W., et al. (2006). Neuronal correlates of theory of mind and empathy: A functional magnetic resonance imaging study in a nonverbal task. NeuroImage, 29(1), 90–98. doi:10.1016/j.neuroimage.2005.07.022	ToM minus physical causality one character

* denotes additional papers included in the secondary meta-analysis

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Table 4 cont. Theory of Mind Meta-Analysis Studies

Authors	*Contrast*
∗ Wolf, I., Dziobek, I., & Heekeren, H. R. (2010). Neural correlates of social cognition in naturalistic settings: a model-free analysis approach. Neuroimage, 49(1), 894-904. doi: 10.1016/j.neuroimage.2009.08.060	social minus physical inference (multiple choice and silent)
Young, L., Cushman, F., Hauser, M., & Saxe, R. (2007). The neural basis of the interaction between theory of mind and moral judgment. PNAS, 1–6.	belief minus photo
∗ Young, L., Dodell-Feder, D., & Saxe, R. (2010). What gets the attention of the temporo-parietal junction? An fMRI investigation of attention and theory of mind. Neuropsychologia, 48(9), 2658-2664. doi: 10.1016/j.neuropsychologia.2010.05.012	mental > physical sentences
∗ Zaitchik, D., Walker, C., Miller, S., LaViolette, P., Feczko, E., & Dickerson, B. C. (2010). Mental state attribution and the temporoparietal junction: an fMRI study comparing belief, emotion, and perception. Neuropsychologia, 48(9), 2528-2536. doi: 10.1016/j.neuropsychologia.2010.04.031	belief sentences > control sentences

* denotes additional papers included in the secondary meta-analysis

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Table 5. Meta-Analyses Results

Category	Area	Ceneter (TAL)
Target Detection	L Medial Frontal Gyrus	(0.21,6.66,44.4)
	R Superior Temoral Gyrus	(55.24,-37.47,17.68)
	L Transverse Temporal Gyrus	(-53.09,-24.14,12.42)
	L Postcentral Gyrus	(-34.26,-40.5,58.21)
	R Thalamus	(7.46,-15.03,7.84)
	L Postcentral Gyrus	(-37.76,-24.58,55.43)
	R Middle Temporal Gyrus	(52.69,-25.11,-11.65)
	L Cerebellum	(-25.54,-59.95,-30.56)
	R Inferior Frontal Gyrus	(48.98,6.48,21.1)
	L Inferior Parietal Lobule	(-57.01,-38.69,25.89)
	R Precentral Gyrus	(41.87,9.58,6.36)
	R Cerebellum	(17.26,-49.15,-27.23)
	R Superior Frontal Gyrus	(20.04,45.89,30.96)
	L Thalamus	(-11.39,-19.29,6.59)
	R Middle Temporal Gyrus	(54.91,-53.38,1.45)
	L Superior Frontal Gyrus	(-36.53,36.63,27.94)
	L Superior Temporal Gyrus	(-46.3,10.73,-6.03)
	L Superior Temporal Gyrus	(-53.82,-6.52,-4.32)
	L Middle Temporal Gyrus	(-58.22,-56.83,3.1)
Reorienting	R Supramarginal Gyrus	(54,-47.27,20.51)
	L Precentral Gyrus	(-43.51,3.52,30.65)
	R Inferior Frontal Gyrus	(41.01,9.3,31.32)
	L Superior Frontal Gyrus	(-0.54,9.68,53.26)
	R Premotor Cortex 6	(28.84,-2.38,55.04)
	R Precuneus	(11.66,-65.88,44.92)
	L Inferior Parietal Lobule	(-36.35,-45.52,41.09)
	R Inferior Parietal Lobule	38.11,-45.99,45.29
	L Middle Frontal Gyrus	(-29.54,-5.41,53.56)
	L Precuneus	(-11.62,-66.87,47.38)
	R Cerebellum	(17.41,-57.23,-33.62)
	R Superior Temporal Gyrus	(41.08,-45.25,18.5)
	L Cerebellum	(-9,-38.61,-41.39)
	L Superior Temporal Gyrus	(-56.98,-45,12.64)
	R Inferior Frontal Gyrus	(48.39,13.58,9.13)
	R Superior Occipital Gyrus	(34.04,-78.14,30.68)
	R Insula	(32.9,22.88,-0.07)
	R Precuneus	(31.32,-66.21,32.08)
	L Precuneus	(-6.87,-72.25,34.58)
Theory of Mind	L Superior Temporal Gyrus	(-49.02,-58.44,22.05)
	R Superior Temporal Gyrus	(50.18,-54.58,22.51)
	L Cingulate Gyrus	(-1.26,-54.89,26.65)
	L Medial Frontal Gyrus	(-3.12,51.22,13.82)
	R Medial Frontal Gyrus	(2.91,51.58,33.85)
	R Middle Temporal Gyrus	(58.64,-16.97,-13.44)
	L Middle Temporal Gyrus	(-56.17,-25.21,-8.62)
	R Superior Frontal Gyrus	(8.64,19.56,55.45)
	L Inferior Temporal Gyrus	(-49.79,-4.8,-28.86)
	L Superior Frontal Gyrus	(-17.47,46.57,37.76)
	R Putamen	(24.84,3.96,-8.05)
	L Parahippocampal Gyrus	(-24.58,-2.4,-16.89)

Coordinates of clusters produced by the primary meta-analyses. Anatomical labels produced by GingerALE.

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Table 6. Difference Maps Results

Contrast	Ceneter (TAL)	Category	Subjects Represented (Category)	Authors	Sensory Modality	rTPJ Mentioned
REATTN-ODATTN	(55.02,-31.98,23.81)	ODATTN	42%	Linden et al._1999	auditory/vision	20%
				Downar et al._2002	vision/auditory/tactile	
				Kiehl et al._2005	auditory	
				Liebenthal et al._2003	auditory	
REATTN-ODATTN	(53.3,-47.36,28.86)	REATTN	21%	Mitchell_2007	vision	100%
				Vossel et al._2006	vision	
TOM-ODATTN	(55.63,-37.65,18.44)	ODATTN	54%	Bledowski et al._2004	vision	33%
				Kiehl et al._2001	auditory	
				Linden et al._1999	auditory/vision	
				Downar et al._2002	auditory/vision	
				Downar et al._2001	vision/auditory	
				Kiehl et al._2005	auditory	
				Liebenthal et al._2003	auditory	
TOM-ODATTN	(49.61,-54.86,22.74)	TOM	85%	Saxe et al._2006	vision	89%
				Mitchell_2007	vision	
				Young et al._2007	vision	
				Saxe & Powell_2006	vision	
				Fletcher et al._1995	vision	
				Hynes et al._2005	vision	
				Perner& Aichhorn_2006	vision	
				Saxe & Kanwisher_2003	vision	
TOM-REATTN	(60.48,-36.52,19.64)	TOM	70%	Mitchell_2007	vision	75%
				Young et al._2007	vision	
				Fletcher et al._1995	vision	
				Hynes et al._2005	vision	
				Perner& Aichhorn_2006	vision	
				Saxe & Kanwisher_2003	vision	
TOM-REATTN	(60.48,-36.52,19.64)	REATTN	61%	Mitchell_2007	vision	88%
				Macaluso et al._2002	vision/tactile	
				Vossel et al._2006	vision	
				Mayer et al._2006	auditory	
				Corbetta et al._2002	vision	
				Mayer et al._2009	auditory	
				Mattler et al._2006	auditory/vision	
				Natale et al._2009	vision	

Results from the difference maps from the primary meta-analysis. Centers of activation as reported by GingerALE for each contrast listed with papers containing foci that fell within the areas of activation. Note that a foci does not have to lie within a cluster to significantly contribute to the cluster. 'Subjects represented' is the percent of subjects from the papers within the significant cluster over the total amount of subject in the given task category. 'rTPJ mentioned' is the percent of papers specifically implicating the rTPJ within the significant clusters. REATTN = reorienting; ODATTN = target detection; TOM = theory of mind.
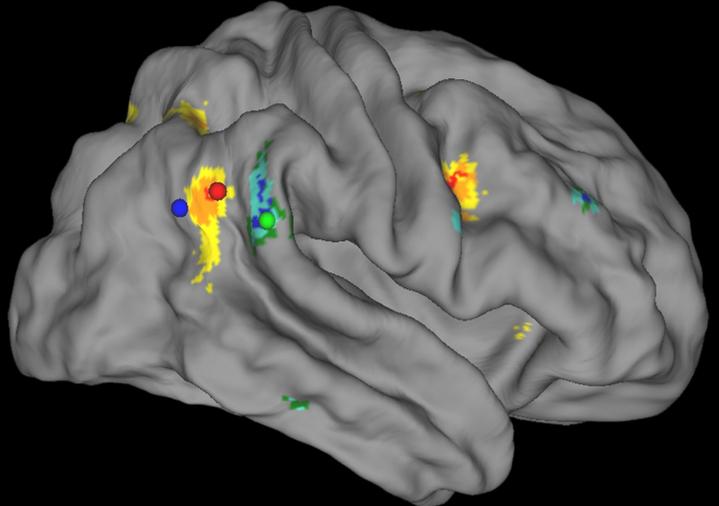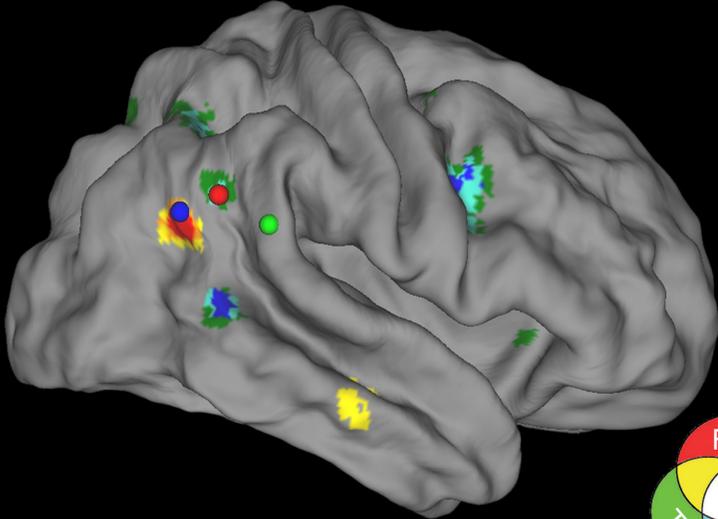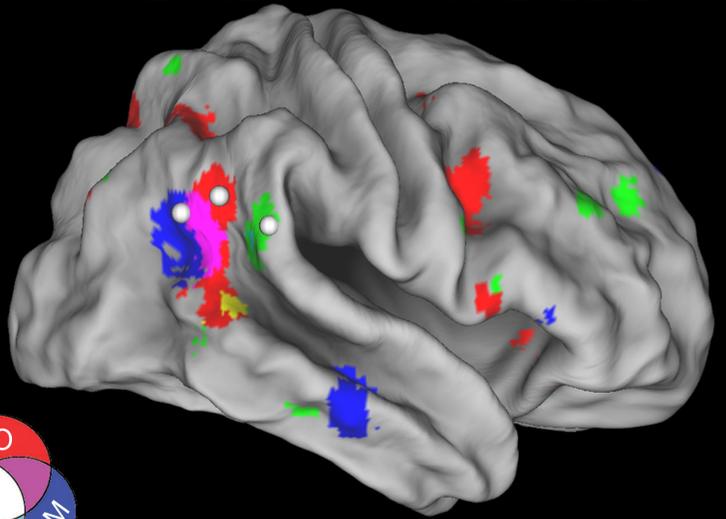
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Figure 1.TIF

A. ToM > TARGET DETECTION
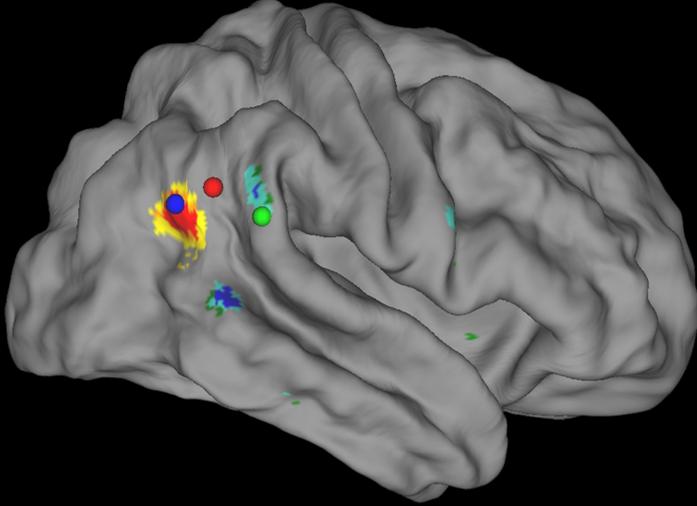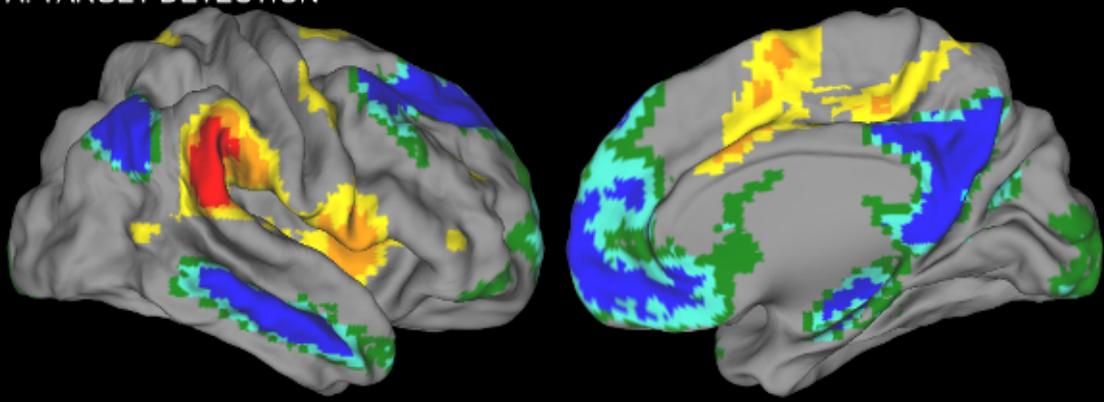
B. REORIENTING > TARGET DETECTION
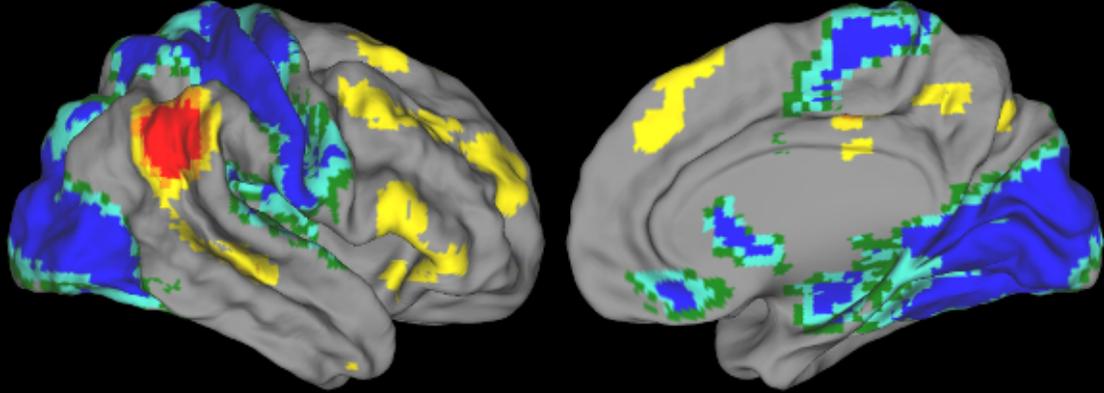
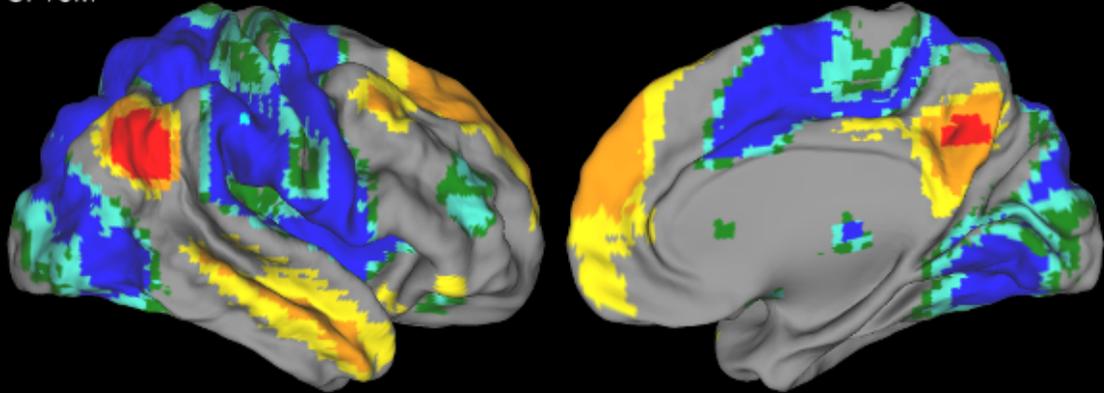C. ToM > REORIENTING

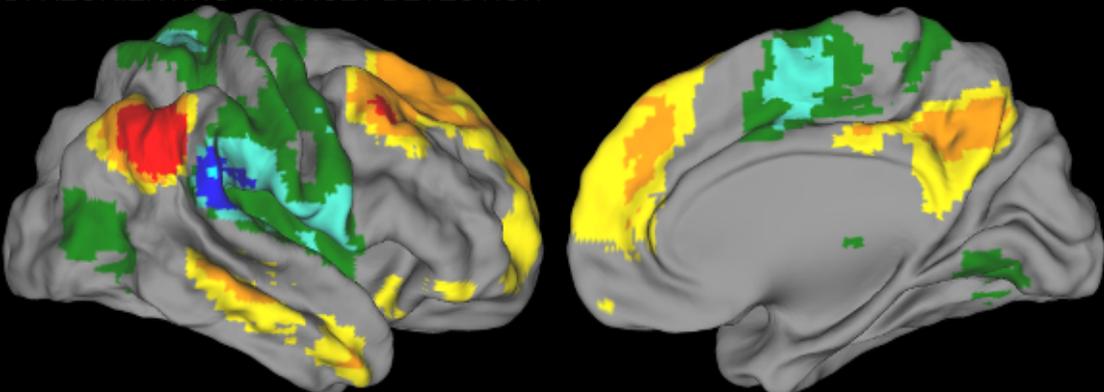D. ToM & REORIENTING & TARGET DETECTION

A. TARGET DETECTION
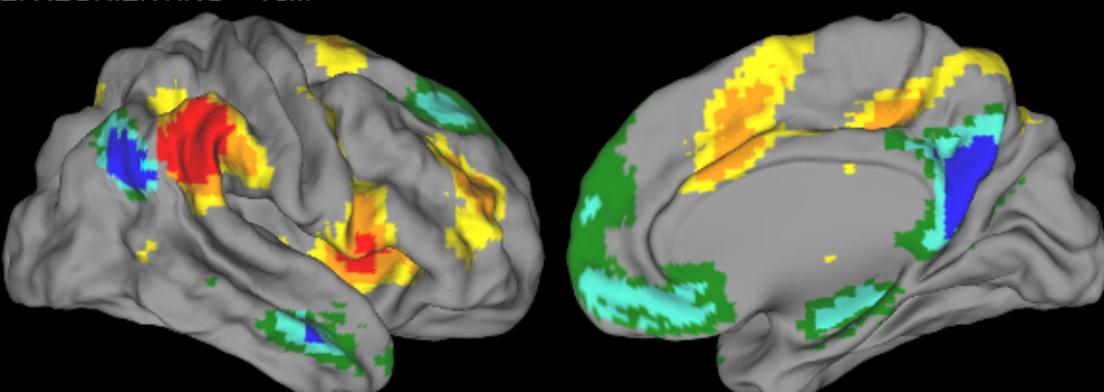
B. REORIENTING

C. ToM

D. REORIENTING > TARGET DETECTION

E. REORIENTING > ToM

-33.1   0.0   34.3

Figure 3.JPEG

Figure 4.JPEG

Theory of Mind

Reorienting   Oddball