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Topographical organization of attentional, social and memory processes in the human temporoparietal cortex

Attention, memory and social cognition in the TPJ

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1 **Abstract**

2 The temporoparietal junction (TPJ) is activated in association with a large range of
3 functions, including social cognition, episodic memory retrieval and attentional
4 reorienting. An ongoing debate is whether the TPJ performs an overarching, domain-
5 general computation, or if functions reside in domain-specific subdivisions. We scanned
6 subjects with fMRI during five tasks known to activate the TPJ, probing social,
7 attentional and memory functions, and used data-driven parcellation (independent
8 component analysis) to isolate task-related functional processes in the bilateral TPJ. We
9 found that one dorsal component in the right TPJ, which was connected with the
10 frontoparietal control network, was activated in all the tasks. Other TPJ sub-regions were
11 specific for attentional reorienting, oddball target detection or social attribution of belief.
12 The TPJ components that participated in attentional reorienting and oddball target
13 detection appeared spatially separated, but were both connected with the ventral attention
14 network. The TPJ component that participated in the theory-of-mind task was part of the
15 default mode network. Further, we found that the BOLD response in the domain-general
16 dorsal component had a longer latency than responses in the domain-specific
17 components, suggesting an involvement in distinct, perhaps post-perceptual,
18 computations. These findings suggest that the TPJ performs both domain-general and
19 domain-specific computations that reside within spatially distinct functional components.

20 **Significance Statement**

21 The temporoparietal cortex (TPJ) is a major communication hub in the human brain. The
22 exact pattern of overlap and separation of function in the TPJ has been difficult to study
23 due to the complexity of its responses during many different kinds of tasks. We studied

24 the activity in the TPJ during five behavioral tasks associated with attention, memory
25 retrieval and social cognition. We found that one zone in the TPJ was active in all five
26 tasks, whereas other zones were active in a more task-specific manner. Our findings
27 suggest that the TPJ is a site where multiple brain networks converge and interact, but
28 that it also contains more functionally specific subregions.

29 **Introduction**

30 Many theories have been proposed to explain the multitude of tasks that activate the
31 temporoparietal junction (TPJ), which involve functions ranging from bottom-up
32 attention to episodic memory retrieval and social cognition. For example, it has been
33 suggested that the episodic memory activity in the TPJ is related to reflexive orienting to
34 information retrieved from memory (Cabeza, 2008; Ciaramelli et al., 2008; Cabeza et al.,
35 2011), and that social cognition in the TPJ might depend on similar low-level information
36 processing (Decety and Lamm, 2007). Other theories have postulated that the TPJ is a
37 zone of convergence and integration, in which internal models of one's environment,
38 social context or attentional state are maintained and updated (Graziano and Kastner,
39 2011; Carter and Huettel, 2013; Geng and Vossel, 2013; Kelly et al., 2014; Webb and
40 Graziano, 2015). Comparisons of activation patterns within single subjects have shown
41 some separation but also zones of overlap. For example, topographic overlap has been
42 reported between theory-of-mind and attentional reorienting activity (Mitchell, 2008),
43 between memory retrieval and attentional reorienting (Cabeza et al., 2011), and between
44 theory-of-mind, attentional reorienting and biological motion (Lee and McCarthy, 2014).
45 However, functional heterogeneity has also been seen in both meta-analyses and within-
46 subject fMRI studies, manifesting as physical separation of processes, an ability of

47 multivoxel pattern analysis to discriminate different tasks within regions of overlap, and
48 distinct connectivity patterns of activation foci (Hutchinson et al., 2009; Scholz et al.,
49 2009; Cabeza et al., 2011; Cabeza et al., 2012; Daselaar et al., 2013; Lee and McCarthy,
50 2014).

51 The great spatial variability of fMRI activations in the TPJ is perhaps not surprising given
52 the inter-subject heterogeneity in the TPJ, the limitations of normalizing individual brains
53 into a common space, and the limitations of voxel-wise analysis. One useful way of
54 addressing TPJ function is careful within-subject analysis of task-related activity in high-
55 resolution fMRI scans (Mitchell, 2008; Scholz et al., 2009; Cabeza et al., 2011; Lee and
56 McCarthy, 2014). Another possibility, explored in this study, is to use multivariate data-
57 driven methods to work around the limitations of voxel-wise analysis. We previously
58 found that localized independent component analysis (local-ICA), which decomposes the
59 fMRI signal in the TPJ into a linear mixture of spatiotemporal source processes, could be
60 used to parcellate the TPJ into 5 to 6 subdivisions per hemisphere (Igelström et al., 2015,
61 2016, in press). These components included bilateral posterior (TPJp), anterior (TPJa),
62 dorsal (TPJd), and ventral (TPJv) regions, and a central right-biased region (TPJc). The
63 time courses of the independent components (ICs) within the TPJ were correlated with
64 distinct resting state networks (Igelström et al., 2015, 2016, in press), indicating that they
65 represented functionally distinct processes. This method of local-ICA was robust across
66 multiple independent subject cohorts (Igelström et al., 2015).

67 We hypothesized that local-ICA, by isolating functional processes from noise and by
68 providing IC time courses that can be analyzed for task-relatedness, may be a powerful
69 approach to study the distribution of processes in the TPJ. A primary goal of this

70 experiment was to test a diversity of tasks that in the previous literature have been shown
71 to evoke robust activity in the TPJ. This diversity of tasks allowed us to ask basic
72 questions, such as: is the TPJ heterogeneous, with subareas that tend to be recruited in
73 different tasks, or is it a site of convergence, with a generalized activity that is similar
74 across a range of tasks? Or does the TPJ have some combination of properties, with some
75 sub-regions showing task-specific activity and other sub regions showing functional
76 overlap? To pursue that goal, five tasks were chosen based on their prominent roles in the
77 TPJ literature and their diversity in terms of behavioral paradigm and cognitive function,
78 although they were not an exhaustive list of all tasks that may be relevant. The tasks
79 included 1) a social attribution of belief task (Dodell-Feder et al., 2011), 2) an Old/New
80 episodic memory retrieval task (Konishi et al., 2000), 3) an attribution of attention task
81 (Kelly et al., 2014), 4) a Posner attentional reorienting task (Mitchell, 2008), and 5) an
82 oddball target detection task (Stevens et al., 2000). We analyzed the fMRI signal during
83 these tasks by using local-ICA to decompose the signal within the temporoparietal cortex.
84 Task-related ICs were identified using multiple regression analysis and their network
85 participation was mapped using functional connectivity analysis. This data-driven
86 approach revealed a functional topography within the temporoparietal cortex that
87 included zones of both task convergence and task specialization.

88 **Materials and Methods**

89 The experimental approach consisted of four main steps. First, fMRI data was collected
90 during behavioral tasks that in prior studies evoked activity in the TPJ (**Fig. 1**). Second,
91 for each task, local-ICA was used on the group level to extract the dominant
92 spatiotemporal TPJ processes in a data-driven manner. Third, the IC time courses from

93 these task-specific ICAs were entered into mixed-effects multiple regression analyses to
94 identify components that were significantly task-related. Fourth, all IC time courses were
95 used for a functional connectivity analysis to map the network participation of each IC.

96 *Theory-of-mind task*

97 The theory-of-mind task was performed by 20 subjects (12 females; 22.6 ± 0.8 years old).
98 The study was approved by the Princeton University Institutional Review Board. All
99 subjects gave informed written consent, had normal or corrected to normal vision, and
100 had no history of psychiatric or neurological disorders.

101 We used a theory-of-mind localizer task from a study by Dodell-Feder et al. (2011),
102 which contrasts brain activations during attribution of beliefs to people (Belief trials)
103 versus activations during judgments about the contents of photographs, maps or signs
104 (Photo trials) (**Fig. 1A**). The stimuli were provided by David Dodell-Feder, Nicholas
105 Dufour and Rebecca Saxe (<http://saxelab.mit.edu/superloc.php>). This task was chosen
106 because of its extensive use in theory-of-mind studies and its popularity as a TPJ localizer
107 task (Saxe and Powell, 2006; Mitchell, 2008; Scholz et al., 2009; Dodell-Feder et al.,
108 2011). In each trial, the story was presented for 10 seconds, followed by a True/False
109 question for 4 seconds and an inter-trial interval of 12 s. Participants responded to the
110 questions using a button box. The task consisted of two runs of 10 trials each, and the
111 order of stories was counterbalanced and equally distributed across the two runs. The
112 BOLD response was modeled with a 14-s boxcar convolved with a standard
113 hemodynamic response function (“waver” function, AFNI). A contrast between Belief
114 trials and Photo trials is known to reveal activation in the TPJ and other theory-of-mind
115 regions (Dodell-Feder et al., 2011). The reaction time was not significantly different in

116 Belief versus Photo trials (2.7 ± 0.10 seconds and 2.6 ± 0.10 seconds, respectively; mean
117 \pm SEM; $P = 0.18$, paired t-test).

118 *Episodic memory retrieval task*

119 The episodic memory retrieval task was performed by 20 subjects, one of whom was
120 excluded due to excessive movement. Subjects had normal or corrected to normal vision
121 and no history of psychiatric or neurological disorders (10 females; 22.3 ± 1.0 years old).

122 The episodic memory task was an Old/New task based on a study by Konishi et al.
123 (2000) (Fig. 1B). The Old/New paradigm was chosen because several studies have found
124 TPJ activation with this contrast and it has been part of meta-studies of functional overlap
125 (Hutchinson et al., 2009; Cabeza et al., 2012; Hutchinson et al., 2014). The task consisted
126 of four runs. Each run comprised a memory encoding phase and a memory retrieval
127 phase. In the encoding phase, subjects were asked to memorize 33 words, which were
128 presented on the screen one at a time (word duration 2 s, trial duration 3 s). In the
129 retrieval phase, a randomized collection of words was presented in the same manner.
130 These included 25 words from the learning phase and 50 new words. Twenty-five
131 fixation trials were also randomly interspersed in each run. Subjects were asked to
132 indicate with a button press whether or not they remembered the word as being from the
133 learning run. There was no overlap of words between the four runs. The contrast between
134 successfully retrieved old words (Old trials) and successfully rejected new words (New
135 trials) has been shown to evoke TPJ activation (Konishi et al., 2000). The word list was
136 derived from the SUBTLEXus 1.00 word frequency database (Brysbaert and New, 2009),
137 and consisted of five-letter words with a frequency of 5–10 per million. The BOLD

138 response was modeled with a boxcar time-course convolved with a standard
139 hemodynamic response function (“waver” function, AFNI). The average accuracy did not
140 differ between the Old and New trials ($81.8 \pm 2.7\%$ and $87.9 \pm 2.9\%$, respectively; mean
141 \pm SEM; $P = 0.13$, paired t-test). The reaction time for New trials was slightly longer than
142 for Old trials (993 ± 27 ms and 927 ± 23 ms, respectively; mean \pm SEM; $P = 0.0013$,
143 paired t-test).

144 *Social attribution of attention*

145 The attribution of attention task was chosen because it was previously found to evoke
146 robust activity in the TPJ even in individual subjects (Kelly et al., 2014) and offers a
147 contrasting approach to testing social cognition from the belief attribution task. In the
148 present study we used the data collected in our previous study (Kelly et al., 2014) and re-
149 analyzed it for the present study. The task (Fig. 1C) required subjects to rate the
150 perceived level of awareness of a cartoon face (“Kevin”) for an object next to it. The
151 direction of gaze of the face was manipulated (toward or away from the location of the
152 object) and the emotional expression of the face either matched the valence of the object
153 (such as a happy face paired with a cup cake or a frightened face paired with a house fire)
154 or mismatched the valence of the object (such as a frightened face paired with a cup cake
155 or a happy face paired with a house fire). Subjects rated Kevin’s level of awareness of the
156 object on a scale of 1 (not aware) to 3 (very aware). When both the gaze and expression
157 cues matched the object, subjects tended to rate Kevin as very aware (rating of 3). When
158 both the gaze and expression cues mismatched the object, subjects tended to rate Kevin
159 as unaware (rating of 1). When the cues to Kevin’s state of awareness were incompatible,
160 one cue suggesting awareness and the other suggesting unawareness, subjects tended to

161 compromise between the two cues and rate Kevin's awareness as intermediate (rating of
162 2). In the previous study, it was found that TPJ activity was significantly higher when
163 subjects compromised between two incompatible cues to Kevin's state of mind,
164 presumably when the computation about Kevin's state of mind was more difficult ("Hard
165 trials"), and activity in the TPJ was significantly lower when the subjects used two
166 compatible cues to Kevin's state of mind, presumably when the computation about
167 Kevin's state of mind was easier ("Easy trials").

168 The details of the paradigm are described in the previous publication (Kelly et al., 2014).
169 Briefly, the behavioral task consisted of eight runs of 48 trials each. Each trial started
170 with a fixation cross for 0.5 s, followed by a picture of an object for 1 s. The fixation
171 cross returned for 0.5 s, and was then replaced by a cartoon face for 2 s. The object was
172 presented either to the left or right and had either positive or negative valence. The gaze
173 of the cartoon figure was either averted from or directed at the object, and the expression
174 was either happy or alarmed. In this way, the gaze could either match (Gaze+) or
175 mismatch (Gaze-) the location of the object, and the expression could either match
176 (Expr+) or mismatch (Expr-) the valence of the object (examples in **Fig 1C**). Subjects
177 were asked to indicate with one of three buttons whether the person was not aware (1),
178 somewhat aware (2) or very aware (3) of the object. For the present study, we used data
179 from the first 20 subjects out of the total of 50 subjects from the previous study (Kelly et
180 al., 2014) (8 females; 19.4 ± 0.4 years old). The reason for analyzing a smaller subset of
181 subjects was a limitation in memory on the compute cluster, which prevented a full 50-
182 subject group-level ICA. Therefore we chose to analyze the first 20 subjects in this task
183 as an unbiased way of decreasing the computing requirements. We used the same

184 regressors and contrast as in the previous study (described above), convolving the Hard
185 and Easy trial types with a hemodynamic response function (“waver” function, AFNI)
186 and testing the contrast Hard versus Easy.

187 *Attentional reorienting task*

188 This task was performed by 20 subjects with normal or corrected to normal vision and no
189 history of psychiatric or neurological disorders (11 females; 21.6 ± 0.6 years old).

190 Attentional reorienting was tested using a Posner task modeled closely on a previous
191 study (Mitchell, 2008) (**Fig. 1D**). This task was chosen to represent reorienting to
192 invalidly cued targets, which is thought to be a major function of the TPJ (Corbetta and
193 Shulman, 2002; Corbetta et al., 2008; Mitchell, 2008; Geng and Vossel, 2013). The task
194 consisted of five runs of 40 trials each. Subjects were given one practice run inside the
195 scanner before the experiment started. The fixation screen consisted of a black
196 background with a red central fixation plus sign and two peripheral square boxes with
197 white outlines. The peripheral boxes were centered 7 degrees from the fixation and were
198 3 degrees across. At the start of a trial, the central plus sign turned green for a fixation
199 period of 700 ms, and was replaced by a central cue consisting of an arrow for 800 ms.
200 The arrow pointed either left or right, in randomized counterbalanced order. After a pre-
201 target period of 0.5–2 seconds, the target (a white asterisk) was presented in one of the
202 two peripheral boxes for 100 ms. The post-target time was selected to make the total trial
203 duration 4 seconds, after which the fixation plus sign turned red again for a randomized
204 inter-trial interval (ITI) of 0.5–7.5 seconds. Subjects responded with a button press to
205 indicate whether the target was on the left or on the right. The direction of the central cue
206 predicted the side of the target in 75% of trials (Valid trials) and was mismatched in 25%

207 of trials (Invalid trials). Subjects were informed that the arrow would predict the target in
208 the majority of trials. A contrast between Invalid and Valid trials has been reported to
209 reveal activity in the right TPJ and the ventral attention network (Corbetta et al., 2000).
210 The BOLD response was modeled by convolving the stimulus timings with a gamma
211 function. The reaction time for Invalid trials was significantly longer than for Valid trials
212 (394 ± 16 and 362 ± 15 ms; mean \pm SEM; $P = 0.00007$, paired t-test).

213 *Oddball target detection task*

214 This task was performed by 20 subjects, one of whom was excluded due to poor
215 performance. The subjects had normal or corrected to normal vision and no history of
216 psychiatric or neurological disorders (10 females; 22.9 ± 1.0 years old).

217 The target detection task was a simple visual oddball task based on Stevens et al. (2000)
218 (Fig. 1E). The oddball paradigm was chosen because it represents a non-spatial form of
219 attentional reorienting that is often reported to cause TPJ activations (Corbetta et al.,
220 2008; Cabeza et al., 2012). It consisted of four runs with 120 trials each. The standard
221 stimulus was the letters “OOOO” presented centrally for 500 ms. The rare target stimulus
222 consisted of the letters “XXXX” (4–7 % of trials in each run) and was made task-relevant
223 by asking the subjects to report on how many targets they had seen after each run. A
224 contrast between the target (Target trials) and the standard stimuli (Standard trials) was
225 reported to evoke TPJ activity (Stevens et al., 2000). The BOLD response was modeled
226 by convolving the stimulus timings with a gamma function.

227 *Distribution of subjects across the five tasks*

228 For reasons of feasibility, every subject did not perform all tasks, which would have
229 required a prohibitive number of hours and sessions for each subject. Instead, each task
230 was analyzed separately. In effect, we performed five independent experiments. All
231 statistical analyses were performed independently for each task, with no between-subjects
232 statistical tests. The results are reported separately for each task and not used to draw
233 conclusions about quantitative differences across tasks in the exact spatial location of ICs
234 or the effect size of activity. In some cases, for tasks that required less run time, the same
235 subjects participated in more than one task. Because of the separate analysis for each
236 task, these overlaps in the subject pools are not of direct relevance to the analysis, but are
237 nonetheless reported here. Fourteen subjects performed both the theory-of-mind task and
238 the attentional reorienting task. Six subjects performed only the attentional reorienting
239 task and six subjects performed only the theory-of-mind task. Eighteen subjects
240 performed both the episodic memory retrieval task and the target detection task. One
241 subject performed only the episodic memory retrieval task and one subject performed
242 only the target detection task. For the social attribution of attention task, data from 20
243 subjects was used. In total across the five tasks, 66 subjects were tested.

244 *Magnetic Resonance Imaging*

245 MRI images covering the whole cerebral cortex were acquired with a 20-channel receiver
246 head coil on a Siemens Skyra scanner (Erlangen, Germany). Functional imaging used a
247 gradient echo, echoplanar pulse sequence with a 64×64 matrix (27 axial slices, 4 mm
248 thick, in-plane resolution 3×3 mm; TR 1.5 s, TE 28 ms, FA 64°; GRAPPA iPAT = 2).
249 Anatomical imaging used an MP2RAGE sequence (256×240 matrix; TR 5 s, TE 2.98 ms,

250 FA 4°; 1 mm² resolution; GRAPPA iPAT = 3). The reanalyzed data from the previous
251 study (Kelly et al., 2014) were acquired on the same scanner. The functional data was
252 acquired with a 64×64 matrix (35 axial slices, 3 mm thick, in-plane resolution 3×3 mm;
253 TR 2 s, TE 30 ms, FA 77°) and the anatomical data was acquired with an MPRAGE
254 sequence (256×224 matrix; TR 2.3 s, FA 9°; and with 1 mm² [TE 2.98 ms], 0.9 mm² [TE
255 3.08 ms], or 1.1 mm² [TE 2.93 ms] resolution).

256 *Pre-processing of fMRI data*

257 Preprocessing was done with AFNI (Cox, 1996) and FSL (Jenkinson et al., 2012). The
258 functional data were slice time-corrected and motion-corrected with FSL (Jenkinson et
259 al., 2002), and then detrended (linear and quadratic) with AFNI. The data were spatially
260 normalized to FSL's MNI-152 template with AFNI, and spatially smoothed with a
261 Gaussian kernel (5 mm FWHM). We used an ICA-based strategy for Automatic Removal
262 of Motion Artifacts (ICA-AROMA) (Pruim et al., 2015b). This toolbox runs single-
263 session ICA with Multivariate Exploratory Linear Decomposition into Independent
264 Components (MELODIC, FSL), and classifies motion-related ICs by assessing their
265 high-frequency content, correlation with motion parameters, edge fraction and CSF
266 fraction (Pruim et al., 2015b). ICA-AROMA removes noise ICs from the fMRI data by
267 calling the FSL command `fsl_regfilt` (Beckmann and Smith, 2004). Such ICA-based
268 denoising is effective in removing aberrant connectivity measures resulting from subject
269 motion (Power et al., 2012; Salimi-Khorshidi et al., 2014; Pruim et al., 2015a).

270 *Group level ICA*

271 For each of the five tasks, the fMRI data were subjected to probabilistic ICA applied on
272 temporally concatenated fMRI data, with all runs from all subjects concatenated into one

273 **matrix** (MELODIC toolbox in FSL; Beckmann and Smith, 2004). We performed the ICA
274 decomposition separately for each task (instead of grouping the tasks into one ICA)
275 because we did not want to assume that the ICA decomposition would be the same across
276 task conditions. **We applied the ICA to the voxels within a region of interest (ROI) mask**
277 **that included the TPJ and surrounding cortex, to ensure that all relevant ICs were**
278 **detected in their entirety.** The mask was constructed from the standard surface
279 cvs_avg35_inMNI152 in Freesurfer, using mri_label2vol to combine multiple labels from
280 the aparc.a2009s atlas into one mask (G_pariet_inf-Supramar, G_pariet_inf-Angular,
281 G_temp_sup-Plan_tempo, G_temp_sup-Lateral, G_temp_sup-G_T_transv,
282 S_interm_prim-Jensen, S_temporal_sup, S_temporal_transverse), and trimming temporal
283 cortex voxels anterior to the postcentral sulcus. This mask allowed a parcellation of the
284 whole temporoparietal region. The reason for using localized ICA is that it allows a finer
285 parcellation of the region (Sohn et al., 2012; Beissner et al., 2014; Igelström et al., 2015,
286 2016, in press), but the exact extent of the mask is not critical for the results. The fMRI
287 data was decomposed into 20 ICs, which isolates the major functional processes in the
288 region (Igelström et al., 2015). ICs were thresholded at $Z = 2.3$ for visual inspection
289 (mixture-model threshold of $P < 0.5$), and at $Z = 4$ for creation of winner-take-all maps
290 for the figures. **Time courses for the figures were derived from the ICA mixing matrix**
291 **(demeaned and variance-normalized signal; arbitrary y-axis) (Beckmann and Smith,**
292 **2004).** **Event-related averaged waveforms were first calculated for each subject, and these**
293 **were then averaged across subjects and presented as mean \pm SEM.**

294

295 Task-related ICs were identified using a mixed-effects multiple regression (Subjects as
296 random effects) in R v.3.0.3 (nlme package v. 3.1-113) (Pinheiro et al., 2013; R Core
297 Team, 2014) with the IC time courses as dependent variables and the predicted BOLD
298 responses for each condition as independent variables (two trial types per task). The
299 inclusion criteria for an IC to be accepted as task-related were 1) a significant positive
300 regression coefficient for the main condition of interest (“Belief” trials in the theory-of-
301 mind task; “Old” trials in the episodic memory retrieval task; “Hard” trials in the
302 attribution of attention task; “Invalid” trials in the attentional reorienting task; and
303 “Target” trials in the target detection task), and 2) a significant positive contrast in the
304 general linear test (Belief-Photo; Old-New; Hard-Easy; Invalid-Valid; Target-Standard).
305 Any ICs located at the border of the mask outside the region of interest were excluded
306 (anterior superior temporal lobe, intraparietal sulcus, lateral fissure, postcentral sulcus
307 and anterior dorsal inferior parietal lobule).

308 In fMRI experiments, one possible concern is that eye movement might affect the
309 measured cortical activity. The TPJ is not typically active in relation to eye movement,
310 unlike more ventral regions in the superior temporal sulcus and more dorsal regions in the
311 intraparietal sulcus. However, it is still important to ensure that the experimental design
312 minimizes the possibility of an eye movement confound. In all five experimental designs,
313 the analysis for identifying task-related ICs relied on the correlation of the IC time
314 courses to trial-specific models of the BOLD response. Because the trial types were
315 matched and counter-balanced with respect to visual features and processing demands
316 (story/word length, left vs right targets, etc.), eye movements should not have influenced
317 the identification of task-related ICs. All five tasks used a fixation point where necessary

318 to stabilize eye position, and were otherwise counterbalanced across the critical
319 comparisons.

320 *Functional connectivity analysis*

321 The CONN toolbox 15.c in SPM 12 (<http://www.nitrc.org/projects/conn>; Whitfield-
322 Gabrieli and Nieto-Castanon, 2012) was used for seed-to-voxel connectivity analysis
323 (Biswal et al., 1995) using the subject-specific IC time courses as seed time courses.
324 Conventional bivariate correlation analysis was used, with a voxel-wise threshold of $P <$
325 0.001 uncorrected and a cluster extent threshold of $P < 0.05$ FDR-corrected.

326 **Results**

327 We present the results from each of the five tasks separately and then discuss the
328 comparison among the tasks.

329 *Theory-of-mind*

330 The theory-of-mind task activated a bilateral posterior IC resembling TPJp in our
331 previous studies (red in **Fig. 2A**). It also activated two lateralized dorsal components, in
332 the region of the right and left TPJd (TPJd-R and TPJd-L; purple and blue, respectively,
333 in **Fig. 2A**). The TPJp activity was specific for the Belief trials, with a large effect for the
334 Belief (“B”) condition (red bar; **Fig. 2B**), and no significant activity related to the Photo
335 (“P”) condition (gray bar; **Fig. 2B**). The activation patterns for TPJd-R and TPJd-L was
336 distinct from that of TPJp, with lower specificity for the Belief condition. TPJd-L showed
337 some activity in Photo trials, whereas the activity of TPJd-R was negatively related to
338 Photo trials (**Fig. 2B**, gray bars).

339 We extracted Belief-related BOLD time courses from the three task-related ICs to
340 examine the temporal properties of these processes. We found a latency difference
341 between the posterior and dorsal components. While TPJp showed a typical BOLD
342 response during the story stimulus (peak at 11 s), TPJd-R and TPJd-L showed a later
343 onset and peak (peaks at 17-18 s), indicating involvement in a more delayed process
344 compared to that of TPJp (**Fig. 2C**).

345 To further characterize these zones of activation and relate them to previously reported
346 TPJ subdivisions (Mars et al., 2012; Bzdok et al., 2013; Igelström et al., 2015), we
347 performed a functional connectivity analysis using the IC time courses as seed time
348 courses. The most strongly and selectively recruited IC in the theory-of-mind task, TPJp,
349 was connected with default mode network regions, including precuneus, STS and medial
350 and lateral PFC (**Fig. 2D**). This connectivity is similar to that of TPJp reported by others
351 and us (Mars et al., 2012; Bzdok et al., 2013; Igelström et al., 2015), and similar to
352 regions activated by theory-of-mind tasks (Dodell-Feder et al., 2011). TPJd-L and TPJd-
353 R were connected with lateralized frontoparietal networks involving the inferior temporal
354 lobe, lateral and superior frontal cortex and precuneus (**Fig. 2E** and **2F**). These
355 connectivity patterns also agree with the network participation of TPJd reported
356 previously (Mars et al., 2012; Igelström et al., 2015) (named “IPL” by Mars et al.).

357 *Episodic memory retrieval*

358 The episodic memory task activated an IC in the right angular gyrus, which was also
359 located in the region of TPJd-R (**Fig. 3A**). Its activity was specific for memory retrieval
360 (**Fig. 3B**), and it showed an activity peak at 7 s after stimulus onset (**Fig. 3C**). The IC was

361 connected to the same right-lateralized frontoparietal network as the TPJd-R component
362 activated by the theory-of-mind task (**Fig. 3D** vs. **Fig. 2F**).

363 There was a left-lateralized component in a similar region that did not reach our statistical
364 criteria. This IC, in the area of the TPJd-L, did show a significant Old/New contrast, but
365 it did not pass the statistical threshold for the Old condition ($\beta = 0.50$, $P = 0.026$). We
366 therefore did not include it here as a significantly activated IC.

367 *Attribution of attention*

368 The attribution of attention task activated two spatially similar ICs in the region around
369 the TPJd-R (**Fig. 4A**, labeled TPJd-R and TPJd-R 2, in purple and black, respectively).
370 TPJd-R was more strongly activated than TPJd-R 2 (**Fig. 4B**) but both were connected to
371 the same right frontoparietal network (**Fig. 4D** and **4E**). The event-related time courses
372 showed no difference in latency or shape, suggesting that these processes reflected
373 erroneous splitting of a single process. The frontoparietal network was similar to the
374 networks connected with TPJd-R in the theory-of-mind and episodic memory retrieval
375 tasks (**Fig. 4D** vs. **Fig. 2F** and **3D**). **Figure 4C** shows the time courses of TPJd-R and
376 TPJd-R 2 (peaks at 7 s). Because of the rapid presentation of stimuli in this task, the time
377 course showed activity from the previous trial dropping, and then rising again in response
378 to the current trial.

379 *Attentional reorienting*

380 The attentional reorienting task showed two significant ICs (**Fig. 5A** and **5B**). One was
381 located in the region of the TPJd-R and the other was located anterior to TPJd-R in a
382 location close to TPJc reported previously (Igelström et al., 2015). Event-related BOLD

383 time courses for TPJd-R and TPJc again showed a long-latency response in TPJd-R (peak
384 at 7 s) compared with TPJc (peak at 4 s) (**Fig. 5C**).

385 The TPJd-R component was connected to the right frontoparietal control network (**Fig.**
386 **5D**). TPJc was connected with regions in the ventral attention network, including the
387 anterior cingulate cortex, anterior insula and the inferior frontal cortex, and showed a
388 strong bias towards the right hemisphere (**Fig. 5E**).

389 *Target detection*

390 The target detection task activated one IC matching the TPJd-R and one IC in the anterior
391 supramarginal gyrus in the region labeled TPJa in our previous study (**Fig. 6A** and **6B**).
392 The location of TPJd-R appeared to be located more posterior than in the other tasks (**Fig.**
393 **6A**); however, it was connected with the same right frontoparietal network as the TPJd-R
394 regions activated in the other tasks and in our previous study (**Fig. 6D**). TPJa was
395 connected to regions of the ventral attention network, including the right inferior frontal
396 gyrus, anterior insula and anterior cingulate cortex (**Fig. 6E**). Like in the theory-of-mind
397 and attentional reorienting tasks, the event-related BOLD time course of TPJd-R showed
398 a longer-latency response (peak at 7 s) compared to the early peak of TPJa (peak at 4 s)
399 (**Fig. 6C**).

400 *Summary*

401 The attentional reorienting and target detection tasks activated supramarginal regions
402 (TPJc and TPJa, respectively) connected with the ventral attention network, whereas the
403 theory-of-mind task uniquely activated the posterior TPJ (TPJp), which was connected
404 with the default mode network. All five tasks activated TPJd-R in the dorsal angular

405 gyrus, which showed connectivity with the right-lateralized frontoparietal control
406 network. The BOLD response of TPJd-R showed a longer latency than that of the other
407 ICs activated in the same task.

408 **Discussion**

409 The present findings show that the right dorsal TPJ is active during a range of tasks
410 including social, attentional and memory tasks, whereas other TPJ zones are active in a
411 more task-specific way (summarized in **Fig. 7**). The domain-specific TPJ processes in
412 TPJp, TPJc and TPJa showed a shorter-latency BOLD response compared to the domain-
413 general process in TPJd, further strengthening the suggestion that the computations
414 performed by these areas are distinct from each other.

415 *Separation of functions within the TPJ*

416 There was clear spatial separation of the theory-of-mind task (activating the TPJp), and
417 the attentional reorienting and target detection tasks (activating the TPJc and TPJa,
418 respectively). These TPJ regions were also connected to distinct networks. The TPJp was
419 connected with classical theory-of-mind/default mode regions, including precuneus and
420 medial prefrontal cortex. The TPJc and TPJa were both connected with the ventral
421 attention network. Thus, this study shows spatial separation of processes related to
422 theory-of-mind and attentional reorienting. The spatial relationship between theory-of-
423 mind and attentional functions has been debated in previous studies, but a general pattern
424 of a more posterior locus for theory-of-mind has emerged (Decety and Lamm, 2007;
425 Carter and Huettel, 2013; Geng and Vossel, 2013; Kubit and Jack, 2013). The clear
426 separation observed here is likely made possible by linear decomposition of overlapping

427 signals using ICA. The difference between TPJc and TPJa was more ambiguous,
428 especially given their similar connectivity patterns. Attentional reorienting tasks and
429 target detection tasks have generally been grouped together in meta-studies, but when
430 they were separated, a more anterior location of target detection activity compared to
431 activity in attentional reorienting tasks was seen (Kubit and Jack, 2013), similar to the
432 present findings.

433 The dorsal location of activity in episodic memory retrieval in the present experiment
434 was similar to the dorsal activations seen in previous studies (Konishi et al., 2000;
435 Wagner et al., 2005; Hutchinson et al., 2009). However, episodic memory retrieval
436 activity in Old/New tasks is often dominantly expressed in the left hemisphere, in
437 contrast to the right-lateralization observed here. Our result does not exclude the
438 possibility of relevant left-lateralized retrieval-related activity. First, the TPJd-R
439 component showed strong functional connectivity to the left TPJd (**Fig. 3C**), indicating
440 involvement of the opposite hemisphere. Second, we observed a TPJd-L component that
441 did not meet our strict inclusion criteria of a significant association with both the Old
442 condition and the Old/New contrast. In a conventional analysis aiming to identify activity
443 significant for the Old/New contrast regardless of significance of the Old trials, TPJd-L
444 would have been identified as active.

445 *A global role of the dorsal TPJ*

446 The TPJ has been suggested to be a hub or nexus in which multiple brain systems
447 converge and communicate (Carter and Huettel, 2013; Geng and Vossel, 2013). In the
448 current study, not the whole TPJ, but specifically the TPJd-R, the subdivision connected

449 to the right frontoparietal control network, was recruited in all five tasks. These findings
450 suggest that the TPJd may be a major site of functional convergence and interaction.

451 An influential theory about TPJ function suggests that it is involved in post-perceptual
452 processes such as the updating of internal models of the current context based on
453 incoming sensory information (Geng and Vossel, 2013). It was suggested that stimuli that
454 violate expectations in some way, such as invalidly cued targets, oddballs, or conflicting
455 social cues, activate the TPJ for this reason (Geng and Vossel, 2013). In the memory
456 domain, the TPJ has been suggested to be a buffer or convergence zone to manipulate or
457 bind episodic memories (Baddeley, 2000; Vilberg and Rugg, 2008; Shimamura, 2011).
458 An integrative function of the TPJ is also consistent with roles of the TPJ in representing
459 the subjective experience of one's own body (Tsakiris et al., 2008; Blanke et al., 2015) or
460 one's own state of awareness (Graziano and Kastner, 2011; Kelly et al., 2014), functions
461 that also rely on the integration of external stimuli with internal models. The TPJd is part
462 of the frontoparietal control system, which is spatially interposed between the dorsal
463 attention network and the default mode network (Vincent et al., 2008) and serves a
464 regulatory role in maintaining a balance between them (Spreng et al., 2013). This
465 frontoparietal system has been suggested to be a "flexible hub" that rapidly adapts its
466 brain-wide connectivity according to the current context and task demands (Addis et al.,
467 2007; Christoff et al., 2009; Summerfield et al., 2010; Gerlach et al., 2011; Ellamil et al.,
468 2012; Meyer et al., 2012; Cole et al., 2013). The TPJd is thus positioned to play a central
469 role in multiple interacting brain systems.

470 ***Limitations of findings***

471 An important limitation of this study is that it did not quantify the voxel-wise differences
472 across the five tasks in the spatial location of the TPJ ICs. Our data-driven method was
473 effective in reducing TPJ fMRI data to the main spatiotemporal processes in the region,
474 which allowed us to identify task-related activity with unprecedented power and clean
475 separation. However, the TPJ heterogeneity and random starting parameters of the ICA
476 algorithm make the method unsuitable for quantifying and comparing the exact
477 coordinates of activity. The exact spatial configuration of group-level parcellations can
478 differ for each subject cohort, as observed in our previous study (Igelström et al., 2015).
479 Therefore, it is not known whether the slight spatial variability between the tasks was
480 caused by anatomical heterogeneity, task-related activity, or variability of the ICA
481 algorithm. For example, the heterogeneity observed in the localization of TPJd-R
482 between different tasks may indicate that slightly different TPJd regions interact with the
483 frontoparietal control network in different tasks, it may reflect anatomical differences in
484 TPJ organization between subject cohorts, and it may reflect the random starting
485 parameters of the ICA.

486 *Conclusions*

487 We used localized ICA to study the TPJ during five behavioral tasks known to activate
488 the region. Localized ICA can isolate spatiotemporal processes from each other and from
489 the background noise, distilling the noisy fMRI data to a small number of processes and
490 minimizing multiple comparisons. The local ICs can then be placed into brain-wide
491 networks using functional connectivity analysis. If two ICs in different subject cohorts
492 show similar connectivity, they are likely to be, if not functionally equivalent, at least
493 very closely related. Using this method we found that the TPJ contains both domain-

494 specific and domain-general neural processes, which are separable in space and show
495 distinct temporal properties. Processes specific to attentional reorienting and target
496 detection were located in the supramarginal gyrus and were associated with the ventral
497 attention network. A posterior TPJ component specifically contained theory-of-mind
498 activity and was connected with default mode regions. A right-lateralized dorsal TPJ
499 zone within the frontoparietal control network was activated across all the tested domains
500 and showed a longer-latency BOLD response compared to the domain-specific processes.
501 These findings strongly support the concept of the TPJ as a cognitive hub that mediates
502 interactions between multiple brain networks, but also show that more functionally
503 specific processes occur adjacent to the zone of convergence.

504

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- 658

659 **Figure Legends**

660 **Figure 1.** Schematic representation of task designs. **A.** Theory-of-mind task. A story
661 requiring either attribution of belief or reasoning about a photo was shown for 10
662 seconds, followed by a True/False question for 4 seconds. There were 20 trials in total. **B.**
663 Episodic memory retrieval task. The task was divided over four runs, each consisting of
664 an encoding phase (“E”) before the run began, and a retrieval phase (“P”) (bottom panel).
665 In the encoding phase subjects were asked to memorize words presented sequentially on
666 the screen (33 words). In the retrieval run (25 old words intermixed with 50 new words
667 and 25 fixation trials), subjects indicated with a button press whether a word was old or
668 new. There were 400 trials in total. **C.** Attribution of attention task. An object with either
669 negative or positive salience was presented on the right or left for 1 second (this example
670 shows a car fire). After a 0.5 second interval, the face of a cartoon character was
671 presented centrally for 2 seconds. Its gaze was directed either toward or away from the
672 object (G+ or G-) and its emotional expression either matched or mismatched the valence
673 of the object (E+ or E-). Subjects rated the character’s level of awareness of the object on
674 a scale of 1 (not aware) to 3 (very aware). Four trial types were possible: G-E-, G+E+,
675 G+E- and G-E+. The trials in which the gaze and expression cues were inconsistent
676 (G+E- and G-E+) were labeled “Hard” trials (see Methods for more details). There were
677 384 trials in total. **D.** Attentional reorienting task. A central cue pointing right or left
678 predicted the location of a target in 75 % of trials. Subjects were asked to indicate which
679 side the target appeared on. There were 200 trials in total. **E.** Target detection task. A
680 visual standard stimulus (“OOOO”) was presented on the screen every 1.5 seconds. In 5

681 % of trials, this was replaced by the target stimulus (“XXXX”). The subjects silently
682 counted how many targets they saw. There were 480 trials in total.

683 **Figure 2.** ICs activated in the theory-of-mind task. **A.** Location of significant ICs shown
684 as a winner-take-all map, created from Z score maps thresholded at $Z > 4$. **B.** Regression
685 coefficients for the Belief (B) and Photo (P) conditions for the three significantly task-
686 related ICs. **C.** Event-related IC time courses for the Belief condition during the 14-s
687 story + question block (black bar) for TPJp (red), TPJd-L (blue) and TPJd-R (purple).
688 The y-axis is shown in arbitrary units. **D-F.** Connectivity patterns of the three task-related
689 ICs obtained in the theory-of-mind task: the TPJp (**D**), TPJd-L (**E**) and TPJd-R (**F**).

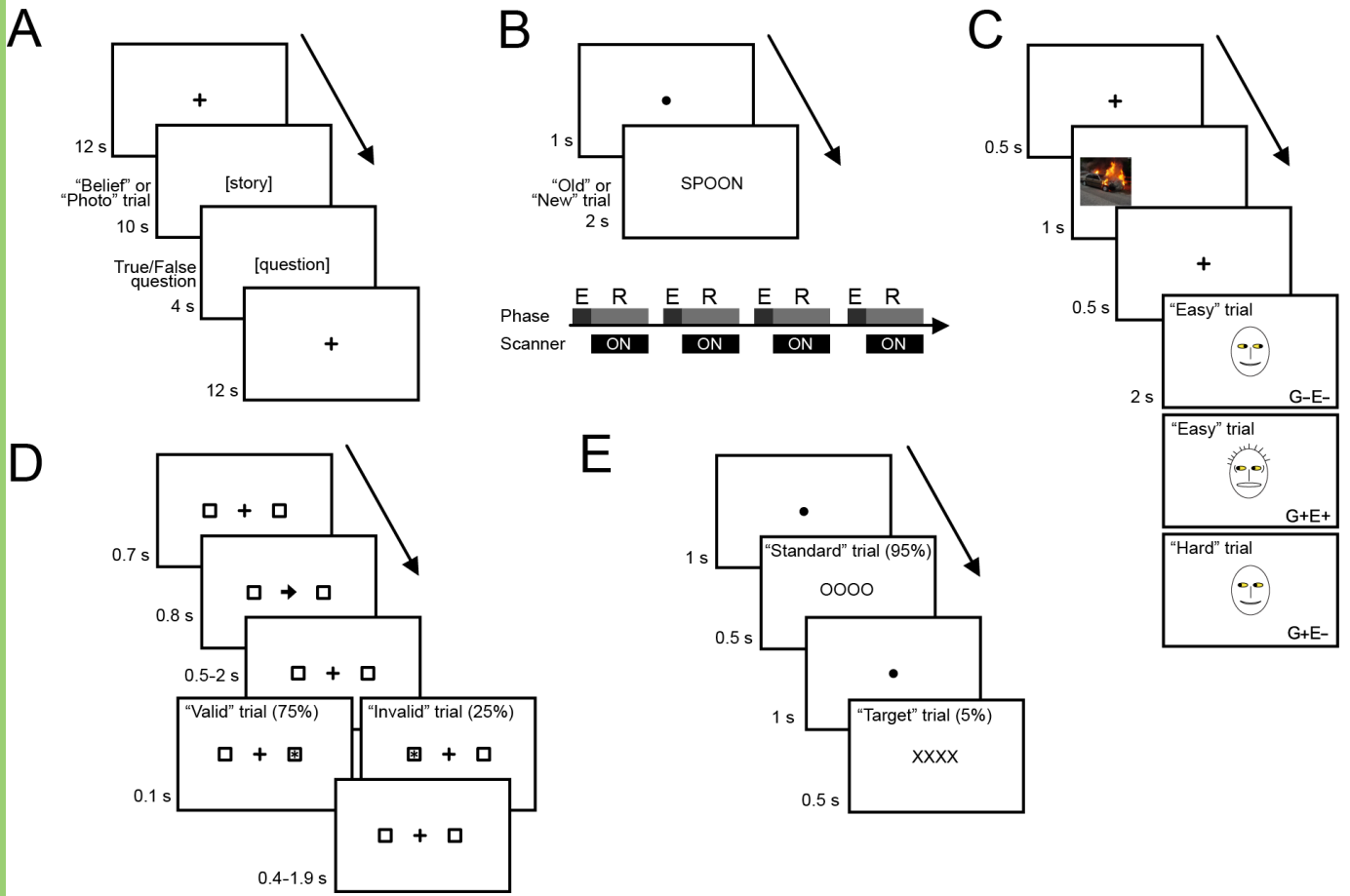
690 **Figure 3.** ICs activated during episodic memory retrieval. **A.** Location of the significant
691 IC created from a Z score map thresholded at $Z > 4$. **B.** Regression coefficients for the
692 Old (O) and New (N) conditions for the significantly task-related IC. **C.** Event-related IC
693 time courses for the Old condition for TPJd-R. The y-axis is shown in arbitrary units. **D.**
694 Connectivity of TPJd-R.

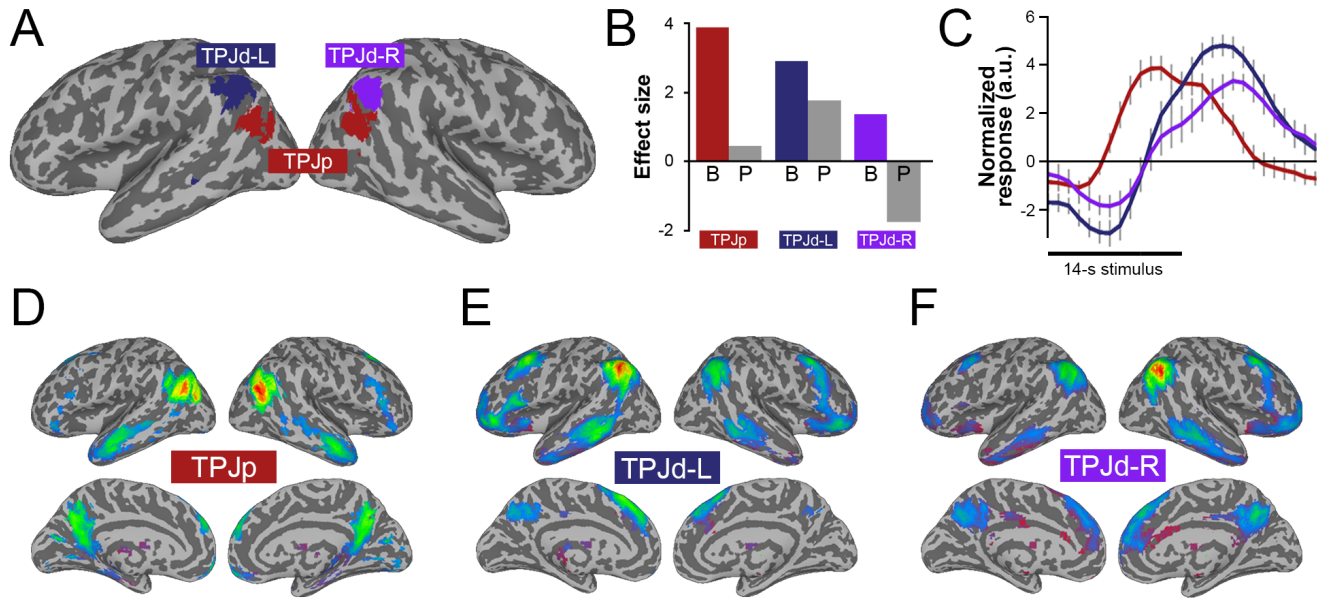
695 **Figure 4.** ICs activated during social attribution of attention. **A.** Location of significant
696 ICs shown as a winner-take-all map, created from Z score maps thresholded at $Z > 4$. **B.**
697 Regression coefficients for the Hard (H) and Easy (E) conditions for the two significantly
698 task-related ICs. **C.** Event-related IC time courses for the Hard condition for TPJd-R
699 (purple) and TPJd-R2 (black). Due to the rapid trial presentation in this task, the signal
700 was still returning to baseline at the beginning of the trial. The y-axis is shown in
701 arbitrary units. **D-E.** Connectivity of the task-related ICs: TPJd-R (**D**) and TPJd-R 2 (**E**).

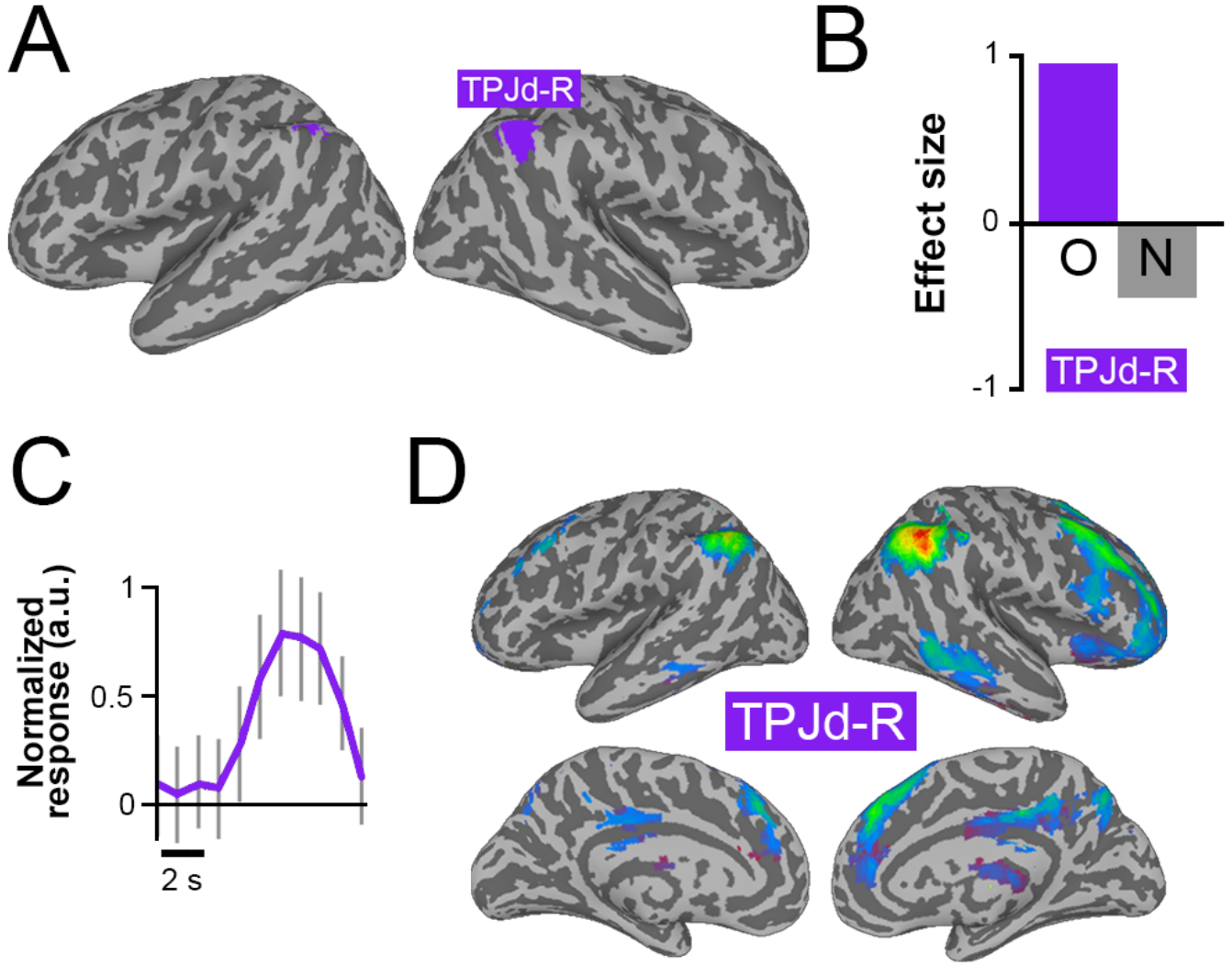
702 **Figure 5.** ICs activated during the attentional reorienting task. **A.** Location of significant
703 ICs shown as a winner-take-all map, created from Z score maps thresholded at $Z > 4$. **B.**
704 Regression coefficients for the Invalid (I) and Valid (V) conditions for the two
705 significantly task-related ICs. **C.** Event-related IC time courses for Invalid trials for the
706 TPJd-R (purple) and TPJc (orange). The y-axis is shown in arbitrary units. **D-E.**
707 Connectivity of the task-related ICs: TPJd-R (**D**) and TPJc (**E**).

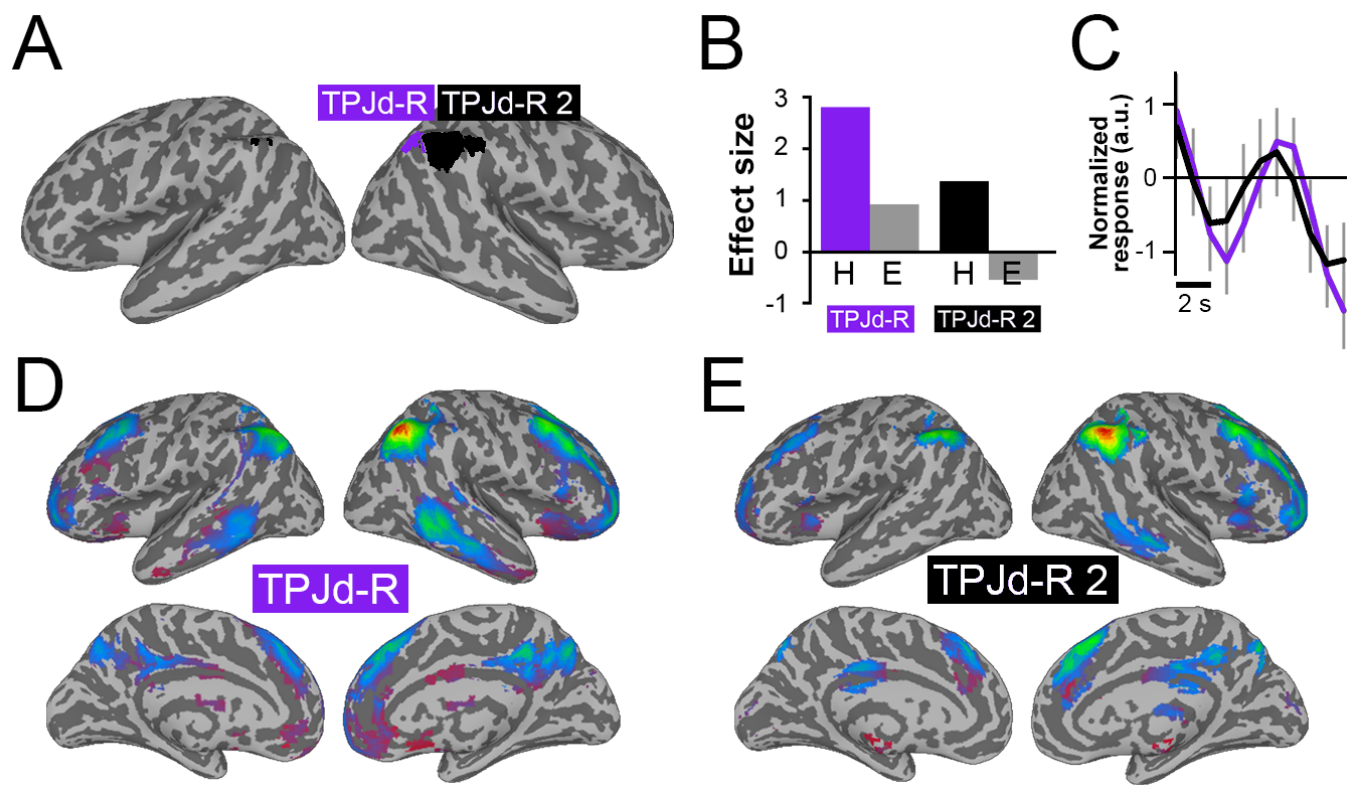
708 **Figure 6.** ICs activated in the oddball target detection task. **A.** Location of significant ICs
709 shown as a winner-take-all map, created from Z score maps thresholded at $Z > 4$. **B.**
710 Regression coefficients for the Target (T) and Standard (S) conditions for the two
711 significantly task-related ICs. **C.** Event-related IC time courses for the target condition
712 for the TPJd-R (purple) and TPJa (green). The y-axis is shown in arbitrary units. **D-E.**
713 Connectivity of the task-related ICs: TPJd-R (**D**) and TPJa (**E**).

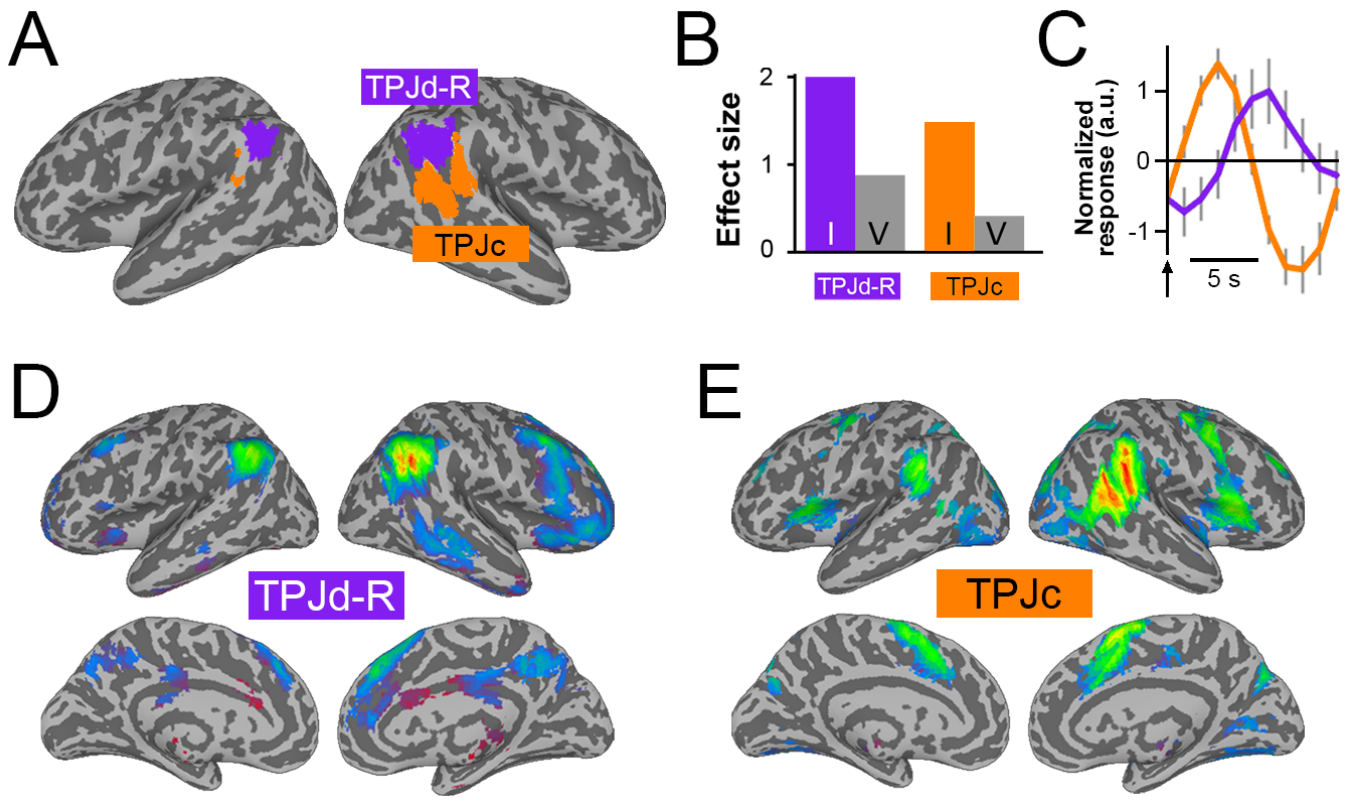
714 **Figure 7.** Simplified schematic summary of task activations. The task-related
715 temporoparietal independent components from Figures 2-6 are shown in their
716 approximate locations with black outlines, and their network connectivity is marked with
717 matching colors but no outlines (see Figures 2-6 for the exact distribution and
718 connectivity of the independent components). All tasks activated regions within the
719 TPJd-R (purple area), which was connected with the right-lateralized frontoparietal
720 network. The theory-of-mind task also activated TPJd-L (blue; connected with the left-
721 lateralized frontoparietal network) and TPJp (red; connected with the default mode
722 network). The attentional reorienting task and the target detection task activated TPJc and
723 TPJa, respectively (orange and green), which were connected with partially overlapping
724 regions of the ventral attention network.

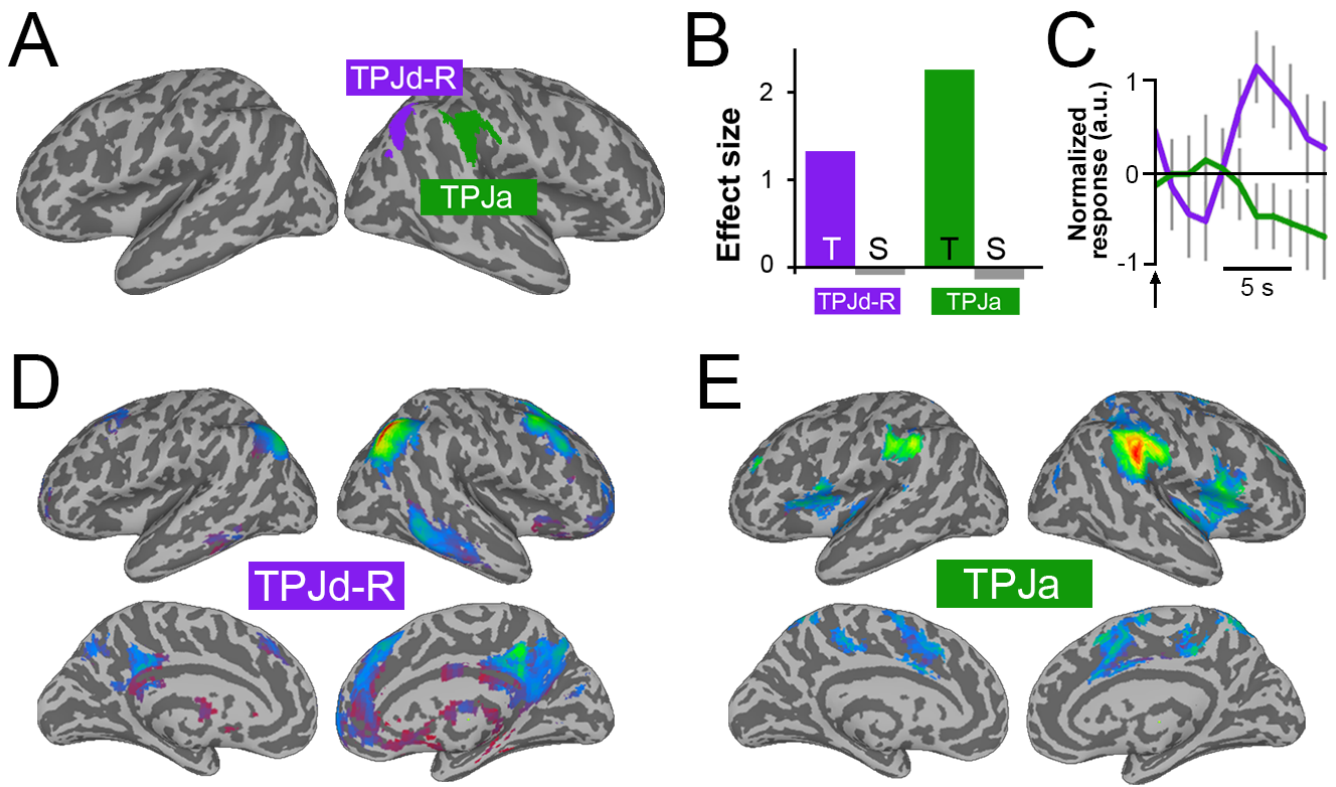


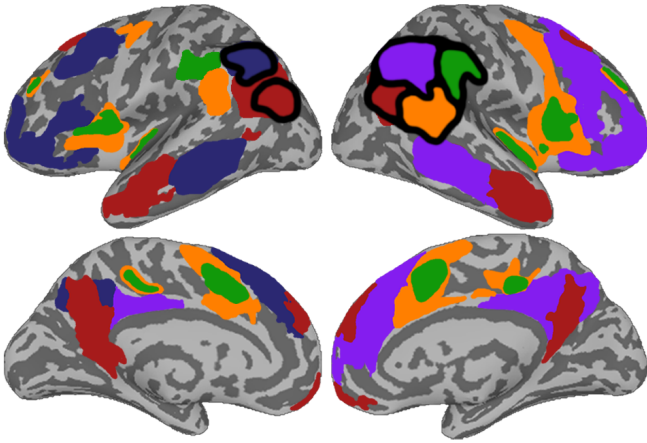












	TPJd-L	TPJd-R	TPJp	TPJc	TPJa
Theory-of-Mind (Belief vs Photo)	✓	✓	✓		
Episodic Memory Retrieval (Old vs New)		✓			
Attribution of Attention (Hard vs Easy)		✓			
Attentional Reorienting (Invalid vs Valid)		✓		✓	
Target Detection (Target vs Standard)		✓			✓