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The evolution of the temporoparietal junction and posterior superior temporal sulcus

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1 **Title:** The evolution of the temporoparietal junction and posterior superior temporal sulcus

2

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17

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21

1 **Abstract**

2
3 The scale at which humans can handle complex social situations is massively increased
4 compared to other animals. However, the neural substrates of this scaling remain poorly
5 understood. In this review, we discuss how the expansion and rearrangement of the
6 temporoparietal junction and posterior superior temporal sulcus (TPJ-pSTS) may have played
7 a key role in the growth of human social abilities. Comparing the function and anatomy of the
8 TPJ-pSTS in humans and macaques, which are thought to be separated by 25 million years of
9 evolution, we find that the expansion of this region in humans has shifted the architecture of
10 the dorsal and ventral processing streams. The TPJ-pSTS contains areas related to face-
11 emotion processing, attention, theory of mind operations, and memory; its expansion has
12 allowed for the elaboration and rearrangement of the cortical areas contained within, and
13 potentially the introduction of new cortical areas. Based on the arrangement and the function
14 of these areas in the human, we propose that the TPJ-pSTS is the basis of a third
15 frontoparietal processing stream that underlies the increased social abilities in humans. We
16 then describe a model of how the TPJ-pSTS areas interact as a hub that coordinates the
17 activities of multiple brain networks in the exploration of the complex dynamic social scenes
18 typical of the human social experience.

19 **Introduction**

20 The ability to function in dynamic and complex social situations is one of the traits that make
21 humans unique amongst other species (Buckner & Krienen, 2013). While other animals do
22 function in social groups and hierarchies, none have been able to adapt to and thrive in the
23 type of complex environments that characterize human social interactions, such as those
24 posed by walking through Times Square in New York City or attending the 30,000+ Society for
25 Neuroscience conference (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007).
26 Social cognition consists of multiple domains, both verbal and non-verbal. Non-verbally, for
27 instance, we must be able to quickly scan faces in a room to read 'the mood' of a social
28 gathering or read the body positions of people as we enter a bar (Zaki & Ochsner, 2009).
29 Verbally, we must be able to extract the hidden 'emotional' meaning of apparently neutral
30 sentence during a job interview. While the brain areas involved in processing social stimuli are
31 distributed across cortex, a region in the right temporoparietal junction-posterior superior
32 temporal sulcus (TPJp-STS) appears especially important. The TPJ-pSTS brings into proximity
33 posterior STS areas involved in processing biological motion (such as facial expressions),
34 nodes of the ToM network, and nodes of the attention networks, along with other areas that
35 may be relevant to processing social information. In this review, we will discuss how the
36 expansion and rearrangement of this region in the course of evolution in humans vs.
37 macaques supports these non-verbal social functions, and then propose a new framework for
38 the dynamic interaction of these areas during social cognition.

39

40 **Anatomy and evolution of TPJ-pSTS**

41 In this review, we use the term TPJ-pSTS to encompass a set of cortical areas and structures
42 that spans the inferior parietal lobule to the posterior STS in the dorsal-ventral axis, and the
43 angular gyrus, and posterior aspect of the supramarginal gyrus in the caudal-rostral axis (see
44 **Figure 1A**). We use this label to provide a unifying term for these regions and areas that are

45 often discussed separately in other studies and reviews. In this section, we review the
46 similarities and differences in the anatomy of the TPJ-pSTS in humans vs. macaques, the
47 model system most often used to study cognition in primates.

48
49 The human TPJp-STS is a large associative cortical region bordered by multiple sensory
50 systems. Posteriorly and inferiorly to this region are extrastriate and ventral-occipital visual
51 areas, such as the MT complex (MT/MST/FST in **Figure 1A**). Antero-ventrally to this region, in
52 the Sylvian fissure, is auditory cortex (represented by A1), and antero-dorsal is the
53 somatosensory system (represented by S1). Superior to this region are the parietal
54 oculomotor/attention areas (LIPv/d). This region is one of the last to develop in humans,
55 maturing in young adulthood at a similar time as prefrontal cortex (Hill *et al.*, 2010; Sotiras *et*
56 *al.*, 2017). It is also one of the most morphologically variable between individuals (Croxson,
57 Forkel, Cerliani, & Thiebaut de Schotten, 2017; Mueller *et al.*, 2013; van Essen & Dierker,
58 2007a), perhaps a sign of its role in high-level integrative cognitive operations (Buckner &
59 Krienen, 2013).

60
61 A number of parcellation schemes for dividing human cortex into individual areas have been
62 recently proposed (Glasser *et al.*, 2016; Gordon *et al.*, 2014; Power *et al.*, 2011; Yeo *et al.*,
63 2011), with the aim of mapping the locations and boundaries of higher-level cortical areas that
64 do not have clear macaque homologues. However, because of the individual morphological
65 variability of this region, combined with its complex functional architecture, the parcellation of
66 the TPJ-pSTS into cortical areas has been difficult. Numerous schemes have been proposed,
67 often with little consensus (see **Figure 1B**). However, certain themes appears consistent. A
68 major theme is a right-left asymmetry in the organization of the TPJ-pSTS. This is evident
69 when comparing the effect of lesions to opposite hemispheres: whereas left TPJ strokes often
70 result in language impairment (aphasia), right TPJ is one of the sites most commonly lesioned

71 in strokes that cause visuospatial neglect (Bartolomeo, 2014; Corbetta & Shulman, 2011).
72 Moreover, functional MRI studies in healthy subjects have found multiple functions to be
73 asymmetrically located in the right TPJ-pSTS, including orienting of attention, theory of mind
74 operations, and face-emotion recognition (reviewed in more detail below). Parcellation
75 schemes based on resting state-functional connectivity and task fMRI studies have also found
76 asymmetries in the organization of this region, with several studies finding large discrepancies
77 in the border locations of purportedly homologous networks between hemispheres (Gordon et
78 al., 2014; Power et al., 2011; Yeo et al., 2011).
79
80 This fits with the differences in the patterns of cortical expansion in the right versus left TPJ
81 detailed in Van Essen *et al.* (van Essen, Glasser, Dierker, Harwell, & Coalson, 2011). In
82 particular, the border of the anterior TPJ parcel (TPJa), usually located on the supramarginal
83 gyrus, is often more posterior in the right versus left hemisphere (**Figure 1B**, the black line
84 indicates the corresponding posterior border of anterior TPJ in the left hemisphere).
85 Functionally, the TPJa is involved in the orienting of attention (Corbetta, Patel, & Shulman,
86 2008; Patel et al., 2015). Ventrally, in the pSTS, this parcel is either extended (Yeo et al.,
87 2011) (**Figure 1B** top left panel), part of a series of areas running perpendicular to the STS
88 (Glasser et al., 2016; Igelström, Webb, Kelly, & Graziano, 2016) (**Figure 1B** bottom right
89 panel), or is ambiguous in areal assignment and difficult to parcellate (Power et al., 2011) (gray
90 in **Figure 1B** top right panel). The pSTS overlaps with areas involved in face-emotion
91 recognition and processing biological motion. Posterior to the TPJa on the angular gyrus is the
92 TPJp, an area whose definition is generally agreed upon by task, functional connectivity, and
93 DTI parcellation schemes, and is most often identified as a node of the default mode network
94 (Raichle et al., 2001) or as part of the theory of mind network (Mars, Sallet, et al., 2012b).
95 Superior to the TPJa/p on the lateral bank of the IPS (latIPS) is a region spanning the length of
96 the inferior parietal lobule, implicated variously as a part of the frontoparietal task-control

97 network (Dosenbach et al., 2007; Nelson et al., 2010) and additionally involved in retrieval of
98 information from long-term memory (Sestieri, Shulman, & Corbetta, 2017). Architectonic
99 parcellations may coarsely align with these subdivisions in the anterior-posterior axis, but do
100 not appear to capture the dorsal-ventral organization (Caspers et al., 2008; Igelström &
101 Graziano, 2017).

102
103 In macaques, the candidate TPJ-pSTS region shares some anatomical similarities. In addition
104 to a similar architectonic/connectivity based parcellation (Caspers et al., 2008; 2012;
105 Gregoriou, Borra, Matelli, & Luppino, 2006; Rozzi et al., 2006), the macaque TPJ-pSTS,
106 located in the macaque IPL, is also surrounded by visual, somatosensory, auditory, and
107 attention/oculomotor areas (see **Figure 2A** and **B**). In addition, signatures of purportedly
108 homologous functional areas have been observed within this region, including the lateral
109 parietal node of the default mode network (Mantini et al., 2011; Vincent et al., 2007), a theory
110 of mind area (Sliwa & Freiwald, 2017), and neurons demonstrating attention-reorienting activity
111 (Constantinidis & Steinmetz, 2001). However, major anatomical differences are apparent
112 when comparing this region between the two species. Specifically, the TPJ-pSTS is one of the
113 most expanded cortical regions in humans versus macaques (see **Figure 2C**) (Hill et al.,
114 2010). This is true regardless of whether the comparison is performed by landmark registration
115 (Hill et al., 2010) or by cortical thickness (Sotiras et al., 2017).

116
117 The cortical expansion is most obvious when considering the relative positions of MT, LIP, and
118 auditory cortex in macaques versus their purported homologues in humans (**Figure 2A** and **B**).
119 While auditory cortex lies inside of the Sylvian fissure in both species, the other two areas
120 have been pushed away from the TPJ-pSTS (Krubitzer, 2009). MT in macaques is in the
121 posterior/inferior bank of the STS in macaques, but in humans the homologous areas have
122 been pushed out of the STS ventrally to the junction of the inferior temporal and lateral

123 occipital sulci (Orban, van Essen, & Vanduffel, 2004). Similarly, area LIP in macaques is on
124 the lateral bank of the intraparietal sulcus and thus on the inferior parietal lobule, but the
125 human homologues are pushed superiorly, out of the intraparietal sulcus and onto the dorsal
126 aspect of the superior parietal lobule (Glasser et al., 2016; Patel et al., 2015). This massive
127 expansion of the TPJ-pSTS had the effect of pushing apart the dorsal and ventral stream
128 visual pathways (see arrows in **Figure 2A** and **B**), opening this region to elaboration and/or
129 rearrangement of already-present areas or allowing for the emergence of new areas with new,
130 high-level functions (Buckner & Krienen, 2013). The TPJ-pSTS is also one of the most
131 morphologically variable between individuals, another potential indicator of its late evolution
132 (Buckner & Krienen, 2013; Croxson, Forkel, Cerliani, & Thiebaut de Schotten, 2017; Mueller et
133 al., 2013; van Essen & Dierker, 2007).

134
135 Below we discuss evidence that this expansion and rearrangement has allowed for the TPJ-
136 pSTS to shift from sensory integration to the integration of the cognitive operations necessary
137 for complex social functioning. It is important to note that it is not clear whether the need for
138 increased social cognitive abilities *drove* the expansion and/or the rearrangement of the TPJ-
139 pSTS, or that the TPJ-pSTS expanded first, which then allowed for the cortical areas to be
140 expanded and rearranged to subserve social cognitive processes as social complexity
141 increased. For excellent discussions of this point, see reviews by Buckner and Krienen
142 (Buckner & Krienen, 2013), Krubitzer and Seelke (Krubitzer & Seelke, 2012), Dehaene and
143 Cohen (Dehaene & Cohen, 2007), and Dunbar (Dunbar, 2016). Cortex appears to have
144 expanded well before increased societal complexity driven by the agricultural revolution
145 (Buckner & Krienen, 2013; Harari, 2015), suggesting cortical “recycling” (Dehaene & Cohen,
146 2007) may be a potential explanation for the evolution of the function of the TPJ-pSTS. On the
147 other hand, the ability to form and maintain complex and dynamic dyadic relationships may
148 have evolved first, reflected in the expansion of the TPJ-pSTS, which then allowed for the

149 creation of the complex social structures necessary for the agricultural revolution (Dunbar,
150 2016). In any case, the discussion below does not depend on the ordering of these events in
151 evolution.

152

153 **Functional Reorganization of TPJ-pSTS**

154 *pSTS Face-Emotion Recognition Areas*

155 One system in the TPJ-pSTS that has dramatically reorganized is the face processing network,
156 and in particular the circuit responsible for face-emotion recognition. In macaques, the face
157 processing network comprises of two parallel streams of areas (see **Figure 3A**), one running
158 along the inferior temporal gyrus and the inferior bank of the STS (ML, AL, and AM, pink
159 arrow), and one running superior to this in the fundus and superior bank of the STS (MF and
160 AF, blue arrow) (Tsao, Moeller, & Freiwald, 2008). Of these two streams, the superior MF/AF
161 streams appear more involved in motion processing, with MF being adjacent to MT/MST/FST
162 complex and potentially overlapping with LST, another motion processing area (Nelissen,
163 Vanduffel, & Orban, 2006; Polosecki et al., 2013). In addition, injection of muscimol into the
164 fundus of STS in or near MF interferes with use of eye-gaze information to direct attention
165 (Roy, Shepherd, & Platt, 2014), suggesting that this stream is more involved in the processing
166 of moving facial expressions as opposed to facial identity. There also appears to be a posterior
167 to anterior hierarchy in the face processing, with anterior areas (AF, AL, and AM) integrating
168 information from posterior areas (ML and MF) (Freiwald & Tsao, 2010; Schwiedrzik, Zarco,
169 Everling, & Freiwald, 2015). The posterior areas connect to the TPJ node of the macaque
170 default-mode network, whereas the anterior areas demonstrate more frontal connectivity
171 (Schwiedrzik et al., 2015).

172

173 Like in macaques, the human pSTS appears to be involved in the processing of biological
174 motion, with a major portion devoted to processing moving facial expressions (the STS-FA)

175 (Grossman, Battelli, & Pascual-Leone, 2005; Pelphrey, Morris, Michelich, Allison, & McCarthy,
176 2005; Polosecki et al., 2013) (see **Figure 3B**). According to a recent theory, the pSTS is
177 generally involved in making predictions on a short time-scale about biological mechanics—i.e.
178 predicting the trajectory of an arm or facial feature once it has started to move (Koster-Hale &
179 Saxe, 2013). In humans, however, this system has been substantially re-arranged. Not only
180 have the inferior stream face-processing areas been moved ventrally to ventral
181 occipitotemporal cortex (**Figure 3B** pink arrow), culminating in the fusiform face areas (FFA),
182 but the superior stream has been angled to be *perpendicular* to the STS (blue arrow). Similar
183 to macaques, this stream starts adjacent to the MT/MST/FST complex with an eye-gaze
184 processing area (now on the lip of the inferior bank of the pSTS (Glasser et al., 2016;
185 Marquardt, Ramezanzpour, Dicke, & Thier, 2017), but instead of advancing along the STS, it
186 culminates in the STS-FA on the opposite bank of the pSTS (Polosecki et al., 2013; Tsao et
187 al., 2008). This puts the two ends of the streams centimeters apart in temporal cortex,
188 potentially anchoring another massive expansion of cortex along the mid to anterior STS
189 (compare white arrows in **Figure 3A** and **3B**. This also puts the STS-FA much closer to the
190 TPJ in humans than in macaques.

191

192 *TPJa in Orienting of Attention*

193 Immediately superior to the STS-FA in humans is the TPJa (Mars, Sallet, et al., 2012b),
194 originally labeled the TPJ by Corbetta and Shulman (Corbetta et al., 2008; Corbetta &
195 Shulman, 2002) (**Figure 3B** green border). This area was originally posited to be involved in
196 the stimulus-driven reorienting of attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman,
197 2000), but only to behaviorally relevant stimuli (Downar, Crawley, Mikulis, & Davis, 2000;
198 Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). This hypothesis was based on the
199 stronger response of TPJ, and other regions involved in attention/eye movements, such as the
200 parietal eye region (LIP) and FEF, to unexpected sensory stimuli that require a motor

201 response. It was proposed that this region is involved in signaling the occurrence of a
202 behaviorally relevant, yet unexpected stimuli (Downar et al., 2000; Serences et al., 2005;
203 Shulman et al., 2009), and that this signal acts a 'circuit-breaker' interrupting ongoing activity in
204 dorsal attention/eye movement regions re-directing the locus of processing to the new location
205 of interest (Corbetta et al., 2008; Corbetta & Shulman, 2002). In addition, it was found that the
206 magnitude of deactivation of this area predicts accuracy of detection on a foveal visual
207 discrimination task (Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007; Shulman et al.,
208 2003; Todd & Marois, 2004). Our interpretation was that suppression of the mechanism for
209 reorienting attention to irrelevant sensory stimuli (distracters) is active when subjects primarily
210 focus their attention to important stimuli. Recent studies have further separated TPJa into two
211 halves (Dugué, Merriam, Heeger, & Carrasco, 2017; Igelström et al., 2016), with the posterior
212 half (labeled vTPJ in (Dugué et al., 2017)) specifically involved in attentional reorienting and
213 corresponding to the original TPJ definition proposed by Corbetta and Shulman (Corbetta et
214 al., 2008; Dugué et al., 2017; Igelström et al., 2016; Patel et al., 2015; Shulman et al., 2003;
215 2009), and the anterior portion selectively involved in target detection (Igelström et al., 2016).
216

217 In the macaque, however, the TPJa has no clear homologue. Single-unit electrophysiology
218 studies initially found evidence of attention orienting signals in area 7a, the architectonic area
219 that covers much of the macaque TPJ-pSTS on the dorsolateral surface of the IPL
220 (Constantinidis & Steinmetz, 2001; Steinmetz, Connor, Constantinidis, & McLaughlin, 1994). A
221 comparative fMRI study also found a macaque homologue that was roughly anatomically
222 homologous and shared similarly movie-synchronized BOLD activity (Mantini, Corbetta,
223 Romani, Orban, & Vanduffel, 2013) (**Figure 3A** green X). However, in a study specifically
224 designed to elucidate the macaque TPJa homologue, Patel *et al.* did not find the target
225 detection or search deactivation signals that robustly define the TPJa in humans (Patel et al.,
226 2015).

227

228 Moreover, theories about the role of the TPJa in orienting of attention have continued to
229 develop. For instance, the timing of task-related neural activity in the TPJa was found to be
230 too delayed to be the source of reorienting signals. In fact, visually evoked responses by
231 targets that induce reorienting of attention peak in TPJa relatively late at/near ~300 ms, a
232 latency not compatible with latency of an eye movements and/or attention shift (~200 ms)
233 (Corbetta et al., 2008; Daitch et al., 2013; Spadone et al., 2015). Accordingly, TPJa is now
234 thought to be involved in higher-level cognitive operations than just stimulus-driven reorienting,
235 including the post-perceptual updating of internal models of environmental context (Geng &
236 Vossel, 2013). A version of this idea is that TPJa indicates the end of a task by sending a reset
237 signal that interrupts ongoing activity in task-relevant regions (a sort of cognitive offset signal
238 (Corbetta et al., 2008; Jack, Shulman, Snyder, McAvooy, & Corbetta, 2006; Shulman, Ollinger,
239 Linenweber, Petersen, & Corbetta, 2001)). This theory still fits with the involvement of TPJa in
240 attention- and detection-related processes, but additionally explains a) the late onset response
241 of TPJ; b) the overall greater response to behaviorally relevant but unexpected stimuli (not
242 necessarily indicating a mismatch in space); and c) the similarity between TPJ pattern of
243 response and the P300 evoked response, which has been also interpreted as underlying late
244 post-perceptual updating (Aston-Jones & Cohen, 2005; Corbetta et al., 2008; Geng & Vossel,
245 2013). A temporally delayed response and behaviorally relevant sensory-evoked modulation
246 also fits prediction-error models of TPJp function (see below) (Koster-Hale & Saxe, 2013).

247 Another not-incompatible theory is that the TPJa is involved in the conscious awareness of
248 novel stimuli, with the neural processes underlying awareness lagging those of the actual
249 visual processing of the stimulus (Beauchamp, Sun, Baum, Tolia, & Yeshor, 2012; Webb,
250 Igelström, Schurger, & Graziano, 2016). These newer formulations elevate the complexity of
251 the processes in TPJa from a low-level stimulus-driven reorienting mechanism to a mechanism
252 related to network coordination or prediction (see below).

253

254 *TPJp in Theory of Mind Operations*

255 Posterior to the TPJa, across the STS and on the angular gyrus, is the TPJp (Decety & Lamm,
256 2007; Geng & Vossel, 2013; Mars, Sallet, et al., 2012b) (**Figure 3B** yellow border). This area
257 is involved in the understanding of the mental states of other people, known commonly as
258 theory of mind operations (Saxe & Kanwisher, 2003; Schurz, Radua, Aichhorn, Richlan, &
259 Perner, 2014; Yang, Rosenblau, Keifer, & Pelphrey, 2015). The TPJp heavily overlaps with
260 the anteroventral portion of the default-mode network angular gyrus node. In general, the
261 default-mode network, a network originally defined in humans as an area that deactivates
262 during externally oriented attention-demanding tasks, heavily overlaps with the theory of mind
263 network (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Mars, Neubert, et al., 2012a;
264 Raichle et al., 2001; Shulman et al., 1997; Yang et al., 2015).

265

266 It has been proposed that the TPJp is involved in making model-based predictions about other
267 people's beliefs and desires as well as predictions about bio-mechanical movements on a
268 time-scale longer than immediate perception, and in further updating the model based on new
269 incoming sensory information (Geng & Vossel, 2013; Koster-Hale & Saxe, 2013). These
270 prediction-error theories are based on the observation that predicted stimuli evoke lower-
271 amplitude responses compared to unpredicted stimuli; the theory posits that the extra neural
272 activity is generated by the updating the internal model (Koster-Hale & Saxe, 2013). While the
273 terminology may differ, prediction-error theories of TPJp and circuit-breaker theories of TPJa
274 empirically make equivalent hypotheses: unpredicted or unexpected stimuli will evoke a higher
275 amplitude of activity than those that are predicted or expected. The TPJp then communicates
276 with other areas within the theory of mind or default-mode networks, including a medial
277 prefrontal area thought to be involved in making even longer time-scale model-based
278 predictions (Koster-Hale & Saxe, 2013). The default-mode network has been recently linked to

279 the generation of sensory-independent but internally constrained cognition (Andrews-Hanna,
280 Reidler, Huang, & Buckner, 2010; Christoff et al., 2016), consistent with the internal generation
281 and maintenance of internal models of the intentions of other people (Buckner & Carroll, 2007;
282 Mars, Neubert, et al., 2012a).

283
284 Multiple studies have located a putative macaque homologue of the default mode network
285 angular gyrus area with an area at the junction of the IPL and superior terminus of the STS,
286 labeled as TPOC (Mantini et al., 2011; Teichert, Grinband, Hirsch, & Ferrera, 2010; Vincent et
287 al., 2007) (**Figure 3A** yellow question marks). A recent study also found an area just superior
288 of this in area 7a to be activated by social interactions (Sliwa & Freiwald, 2017). However, the
289 overlap between the default mode network and areas activated by social interactions was an
290 area far anterior on the STG, area TPO, which is superior to MF (Schwiedrzik et al., 2015;
291 Sliwa & Freiwald, 2017). This may be similar to the “social interaction” area (SI-fROI)
292 observed in humans in (Isik, Koldewyn, Beeler, & Kanwisher, 2017) in the STS near the STS-
293 FA. Mars *et al.* found a more extreme discrepancy when searching for macaque TPJ
294 homologues using functional connectivity, with the identified area located in mid-STS cortex
295 near MT/FST, MF and ML (Mars, Sallet, Neubert, & Rushworth, 2013). These observations
296 underscore the expansion and rearrangement of the TPJ-pSTS in humans versus macaques:
297 1) human TPJp demonstrates robust activation by watching movies of conspecifics interacting
298 or acting independently, whereas the purported macaque homologue in TPOC does not, and
299 2) macaque TPO is considered to be a part of the default mode network, whereas human SI-
300 fROI is not.

301

302 *AG and latIPS in Memory Retrieval*

303 Overlapping or posterior to human TPJp (Mars, Sallet, et al., 2012b; Yang et al., 2015) lays the
304 remaining posterodorsal aspect of the DMN angular gyrus node, corresponding to

305 cytoarchitectonic areas PGa and PGp (Caspers et al., 2013; Christoff et al., 2016), here
306 labeled as the postAG (**Figure 3B** purple border). This area contains heteromodal cortex
307 associated with multiple high level functions (Humphreys & Lambon Ralph, 2015; Seghier,
308 2013). Several lines of evidence converge on the role of this region in the representation of
309 information retrieved from episodic (Rugg & King, 2017; Sestieri et al., 2017) and semantic
310 (Binder & Desai, 2011) memory, perhaps allowing the construction of multi-purposes
311 event/situation models (Cohn-Sheehy & Ranganath, 2017). This function relies on the
312 presence of functional (Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008; Vincent et
313 al., 2006) and structural (Kravitz, Saleem, Baker, & Mishkin, 2011; Mufson & Pandya, 1984)
314 connections with medial temporal structures traditionally involved in memory functions (Kravitz
315 et al., 2011; Squire, 1992).

316
317 Memory retrieval in humans is associated with activity of another parietal region (Vilberg &
318 Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005), labeled here as latIPS (Sestieri et al.,
319 2017; Vilberg & Rugg, 2008) (**Figure 3B** cyan border) and located dorsally to areas TPJa and
320 TPJp (roughly corresponding to cytoarchitectonic area hIP1 (Caspers et al., 2013)). The
321 latIPS overlaps with the so-called frontoparietal control network (Dosenbach, Fair, Cohen,
322 Schlaggar, & Petersen, 2008; Duncan, 2010), which is anatomically interposed between the
323 dorsal attention network and the default-mode network (Spreng, Sepulcre, Turner, Stevens, &
324 Schacter, 2013). The role of the latIPS in memory retrieval differs from that of the postAG in
325 several ways. First, latIPS tracks the feeling of oldness (familiarity) rather than recollection
326 (Hutchinson et al., 2012; Sestieri et al., 2014). Second, it shows sustained activity consistent
327 with a role in active maintenance and manipulation of memories according to task demands
328 (Sestieri et al., 2017; Sestieri, Corbetta, Romani, & Shulman, 2011). Third, it overlaps with the
329 parietal node of the frontoparietal control network, which is thought to regulate the balance
330 between the processing of external (perceptual) information in the dorsal attention network and

331 of internal (introspective) information in the default-mode network (Dixon et al., 2018; Sestieri,
332 Corbetta, Spadone, Romani, & Shulman, 2014a). Finally, it is functionally and anatomically
333 connected with prefrontal, rather than medial temporal, regions (Uddin et al., 2010).
334

335 While activity during memory retrieval is typically observed in the left parietal cortex (Duarte,
336 Henson, & Graham, 2011; Guerin & Miller, 2009), retrieval-related activity is also observed in
337 homologue regions of the right hemisphere (e.g. (Klostermann, Loui, & Shimamura, 2009;
338 Sestieri, Shulman, & Corbetta, 2010)), and the degree of hemispheric asymmetry has not been
339 assessed with quantitative indices (Seghier, 2008). On the basis of the importance of memory
340 information for social interactions (Buckner & Carroll, 2007; Spreng, 2013), it is possible to
341 hypothesize that retrieval-related activity in the right parietal areas serve adaptive social
342 processing implemented in adjacent regions, such as the TPJ-pSTS. In particular, while
343 memory representations in the AG might contribute to social knowledge retrieval (Y. Wang et
344 al., 2017) and memory-guided inference of other's mental states (Spreng & Mar, 2012), the
345 latIPS might help to regulate the balance between exploration of the external world (dorsal
346 attention) and accessing internally stored models of social agents and situations (TPJ-pSTS) in
347 cognition (Dixon et al., 2018).
348

349 Compared to humans, evidence for the involvement of monkey parietal lobes in memory
350 functions is scarce. Based on resting-state functional connectivity data, one study
351 hypothesized that that in macaques the area would be on the posterior STG (Vincent, Kahn,
352 van Essen, & Buckner, 2010). Evidence supporting this hypothesis was described in a recent
353 fMRI study employing a serial probe-recognition task in macaques (Miyamoto et al., 2013).
354 The functional and structural properties of two parietal regions, area PG/PGOp (**Figure 3A**
355 purple question mark) of the inferior parietal lobule and PEa/DIP located in the medial bank of
356 the intraparietal sulcus (cyan question mark) resemble that of the postAG and latIPS in

357 humans, respectively (Miyamoto *et al.*, 2014). If these homologies prove to be true, this would
358 indicate that in humans the parietal site supporting episodic recollection (the postAG) has
359 shifted posteriorly compared to macaque PG/PGOp, while the site supporting the sense of
360 familiarity (latIPS) has shifted ventrally and anteriorly compared to macaque PEa/DIP.
361 However, the homologous relationships are not straightforward: the macaque episodic recall
362 area (Miyamoto *et al.*, 2013) is clearly anterior to the macaque angular gyrus node homologue,
363 TPOC (Mantini *et al.*, 2011); and PEa/DIP is located in macaque areas typically implicated in
364 visual processing, attention, or motor planning (Patel, Kaplan, & Snyder, 2014) whose
365 homologues are in the human SPL (Patel *et al.*, 2015). A study comparing functional
366 connectivity networks in humans and macaques has also found that the fronto-parietal
367 networks that comprise areas involved in memory retrieval may be unique to humans (Mantini
368 *et al.*, 2013).

369

370 **The TPJ-pSTS: A Newly Evolved Stream of Processing**

371 Based on early macaque histology and neurophysiology studies, visual processing has
372 traditionally been divided into two streams: a dorsal spatially-oriented processing stream and a
373 ventral feature-based processing stream (Kravitz *et al.*, 2011; Mishkin, Ungerleider, & Macko,
374 1983). Both pathways originate in striate cortex (V1), share a common substrate in extrastriate
375 areas (V2-V4), and then diverge from lateral occipital cortex (V4) towards either parietal
376 (spatial/action) or temporal (feature) cortex (Baizer, Ungerleider, & Desimone, 1991;
377 Ungerleider, Galkin, Desimone, & Gattass, 2008). The dorsal pathway connects to the dorsal
378 attention/oculomotor network areas in parietal and prefrontal cortex (Goldman-Rakic, 1988),
379 and the ventral to the prefrontal cortex via a separate pathway (Kravitz, Saleem, Baker,
380 Ungerleider, & Mishkin, 2013; Webster, Bachevalier, & Ungerleider, 1994). These two
381 pathways are densely interconnected and interact with each other in visual processing
382 (Cloutman, 2013). This has the effect of having mid-level sensory processing areas from all

383 modalities in close proximity to each other around the macaque TPJ-pSTS, and the TPJ-pSTS
384 in close proximity (on opposite sides of a gyrus) to attention/oculomotor (LIP) and other motor
385 planning areas (VIP, AIP).

386
387 In humans, these two streams begin to diverge more posteriorly, making room for the
388 expanded TPJ-pSTS: the dorsal stream has moved even more dorsally onto the SPL, and the
389 ventral stream more ventrally to the ventral occipitotemporal cortex. As mentioned before, the
390 pSTS stream in humans has angled perpendicularly to the STS and bisects this expansion.
391 These pSTS areas connect to the TPJa/p (Ethofer *et al.*, 2013), introducing a novel pathway
392 for sensory information to reach the TPJ-pSTS (and filling in the visual cortex to TPJ
393 connection in the Corbetta/Shulman model (Corbetta *et al.*, 2008)). The right TPJ-pSTS is
394 also connected to prefrontal areas through the more ventro-lateral branches of the superior
395 longitudinal fasciculus (Croxson *et al.*, 2005; Thiebaut de Schotten, Dell'Acqua, Valabregue, &
396 Catani, 2012) and/or the extreme capsule (also known as the inferior fronto-occipital fascicle)
397 (Mars *et al.*, 2016; Sarubbo, De Benedictis, Maldonado, Basso, & Duffau, 2013), paralleling
398 the motif of the anatomical pathways connecting language areas in the left hemisphere
399 (Margulies & Petrides, 2013; Thiebaut de Schotten *et al.*, 2012). This anatomical pathway
400 provides a direct communication channel between visual, TPJ-pSTS, and prefrontal areas that
401 is independent of the dorsal and ventral pathways. While this TPJ-pSTS pathway is different
402 from the third visual pathway proposed by Haak and Beckmann (Haak & Beckmann, 2018);
403 they may be related: their third visual pathway extends across lateral occipital cortex towards
404 the pSTS and may serve as an entry point of visual information into the TPJ-pSTS pathway.
405 The TPJ-pSTS pathway is also distinct from the parieto-medial temporal pathway described in
406 Kravitz *et al.*, though both originate in the TPJ-pSTS (Kravitz *et al.*, 2011).

407

408 We propose that the TPJ-pSTS has emerged as a hub for social cognitive processes, bringing
409 together information gleaned from exploration of the external sensory world with internally
410 generated models of social factors (see **Figure 4**). Specifically, the TPJ-pSTS receives
411 information related to facial emotions from different cortical regions and other biological motion
412 signals (body, eye) via the posterior STS, theory of mind operations via TPJp, attention via
413 TPJa, and recollection and familiarity signals related to previous experiences via the AG and
414 latIPS (Kravitz et al., 2011). We believe that with this collection of functions, the TPJ-pSTS
415 serves as a hub in a hybrid top-down/bottom-up processing pathway that underlies the quick
416 detection and use of social cues to guide exploration of and interaction with the surrounding
417 social environment (Corbetta et al., 2008; Serences et al., 2005). This pathway operates
418 independently of the separable top-down and bottom up processes instantiated in the
419 dorsal/ventral visual pathways in the TPJ-pSTS. The “bottom-up” or stimulus-driven functions
420 of this pathway are instantiated by the bias towards the processing of salient biological motion
421 and features through the pSTS. The “top-down” or goal-directed functions of this pathway
422 originate in the TPJp, supported by access to relevant explicit memory through the
423 postAG/latIPS complex. This information is then used to guide visual scanning exploration of
424 the environment (TPJa and dorsal attention network).

425 An alternative hypothesis put forth by Genovesio *et al.* is that prefrontal-parietal
426 networks have elaborated from the dorsal processing stream in the course of evolution to
427 support the socially related relational metrics (order, number, duration, distance, etc.)
428 necessary for social “foraging” or exploration (Genovesio, Wise, & Passingham, 2014). We
429 note, however, the presence of an anatomical discrepancy between areas belonging to the
430 traditional dorsal processing stream (e.g., area LIP and its human homologue on the superior
431 parietal lobule) and areas involved in computing relational metrics (located on different portions
432 of the inferior parietal lobule in both species). Moreover, inputs into this area appear to be a
433 combination of dorsal (MT) and ventral (FFA) visual processing stream areas, while outputs

434 appear to be directly to ventrolateral prefrontal cortex and not the FEF, further differentiating
435 the TPJ-pSTS pathway from the dorsal pathway.

436
437 The sequence of processing through the TPJ-pSTS might follow one of two pathways (**Figure**
438 **5A** and **B**). Both would start with incoming biological motion sensory information, such as a
439 moving facial expression in the visual periphery. Sensory processing would involve areas
440 such as MT and FFA, culminating in the activation of the pSTS STS-FA (**5A:1**, **5B:1**). At this
441 point the possibilities diverge. One pathway may involve communication of the facial
442 expression information (still in the periphery) with the TPJp as a possible updating of the
443 internal model of the mental states of the people in the social scene (**5A:2**). If the social
444 situation is familiar, this then activates the latIPS (**5A:3**), which serves two functions: a) trigger
445 the recall of associated stored memories via the AG (**5A:4a**) to be used in the theory of mind
446 operations in TPJp and elsewhere (**5A:5**), and 2) bridge the internally and externally oriented
447 operations in the TPJp and dorsal attention network respectively (**5A:4b**). If the changes
448 warrant further exploration, the TPJp communicates with the TPJa (**5A:6**) to trigger the
449 orienting of attention to the face currently in the periphery (**5A:7**). An alternative hypothesis is
450 that the external sensory information from the pSTS (**5B:2**) and the internal model information
451 from the TPJp (**5B:7**) combine in the TPJa to trigger a model updating if the facial expressions
452 violate the expectation, which then triggers further visual exploration through the dorsal
453 attention network.

454
455 One major issue that remains to be resolved in this model of TPJ-pSTS areal interactions in
456 social cognition is the role of the TPJa. While there is evidence that TPJa activity follows
457 attention reorienting, this may just be an artifact of the sparse and static stimuli used in these
458 tasks. TPJa activity may be superfluous to these artificial tasks, with attention orienting in
459 these tasks controlled by the classic top-down/bottom-up mechanisms instantiated in the

460 dorsal and ventral visual pathways. After all, macaques are able to perform these tasks
461 without a TPJa. However, in more naturalistic tasks, where the complex integration described
462 above is necessary, activity in TPJa may actually precede attention orienting and the resulting
463 exploratory saccades, based on the decision to update the internal models maintained in TPJp
464 and elsewhere. Saccades occur about twice per second in the exploration of a naturalistic
465 scene (H. X. Wang, Freeman, Merriam, Hasson, & Heeger, 2012), which is plenty of time to
466 accommodate the TPJa signals (~300ms) and still drive a saccade through the dorsal attention
467 network.

468
469 The lack of a similarly organized TPJ-pSTS in macaques makes it difficult to resolve these
470 issues. However, the study of the macaque TPJ-pSTS may yet reveal some hints about the
471 integrative function of this hub. In macaques, the areas surrounding the TPJ-pSTS tend to be
472 more secondary sensory areas involved in basic motion detection (MT/MST), somatosensory
473 and auditory functioning, and motor planning in the IPS. Perhaps in the course of 25 million
474 years of parallel evolution, then, the TPJ-pSTS in macaques has been purposed to support
475 quick navigation of *their* environment, populated less by other macaques and more by trees
476 and other non-macaque stimuli (van Schaik, Isler, & Burkart, 2012). This may be supported by
477 the presence of neural signals in macaque area 7a related to optic flow patterns (Raffi &
478 Siegel, 2007) and maze navigation (Crowe, Chafee, Averbeck, & Georgopoulos, 2004).

479
480 However, given the disparities between the macaque and human TPJ-pSTS, future
481 investigations of the interactions posed in this anatomical framework will require direct study of
482 this region in humans using techniques with high temporal and spatial resolution, such as
483 multiband fMRI, magnetoencephalography (MEG) or electrocorticography (ECoG), combined
484 with use of stimuli that simultaneously activate these areas in naturalistic ways. These may
485 include naturalistic videos of social situations, virtual reality environments, or even

486 simultaneous fMRI scanning of two people interacting (Hasson, Ghazanfar, Galantucci,
487 Garrod, & Keysers, 2012). With these techniques we will hopefully be able to understand how
488 this cortical region gives rise to the behaviors that make us unique as humans.

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489 **Figure Captions:**

490

491 **Figure 1:** Structural and functional anatomy of the human TPJ-pSTS A) Approximate definition
492 of this region compared to major sulcal/gyral features (derived from FreeSurfer labels) and
493 functional areas (from HCP parcellation scheme (Glasser et al., 2016)). B) Different resting
494 state parcellation schemes of TPJ-pSTS showing difference in posterior border of right anterior
495 TPJ parcellation (white arrows) vs. left hemisphere homologues projected to right hemisphere
496 (black border).

497

498 **Figure 2:** Location and extension of the TPJ-pSTS (red border) in A) macaques vs. B) humans
499 compared to homologous sensory areas. Arrows schematically illustrate the dorsal (blue) and
500 ventral (orange) visual pathways. C) Cortical deformation map for registering macaque cortex
501 to human from Hill *et al.* (Hill et al., 2010).

502

503 **Figure 3:** Functional architecture of TPJ-pSTS in macaques vs. humans. A) Macaque TPJ-
504 pSTS homologues. Face patches derived from (Schwiedrzik et al., 2015). Other homologues
505 locations projected from published cortical surface data (see text for citations). B) Human TPJ-
506 pSTS functional areas. Face patches, TPJp, and TPJa derived from unpublished task fMRI
507 localizer data. PostAG and latIPS borders projected from (Sestieri et al., 2010; 2011) and
508 (Sestieri et al., 2014), respectively.

509

510 **Figure 4:** Map of human TPJ-pSTS hybrid pathway showing how visual and face processing
511 areas connect through the TPJ-pSTS to prefrontal cortex.

512

513 **Figure 5:** Potential sequence of interactions and transmission of information to prefrontal
514 cortex if A) TPJa activation is late or B) early.

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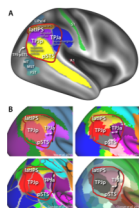
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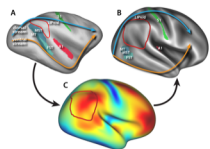
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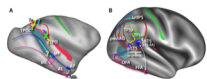
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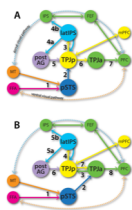
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22 **Abstract**

23

24 The scale at which humans can handle complex social situations is massively increased
25 compared to other animals. However, the neural substrates of this scaling remain poorly
26 understood. In this review, we discuss how the expansion and rearrangement of the
27 temporoparietal junction and posterior superior temporal sulcus (TPJ-pSTS) may have played
28 a key role in the growth of human social abilities. Comparing the function and anatomy of the
29 TPJ-pSTS in humans and macaques, which are thought to be separated by 25 million years of
30 evolution, we find that the expansion of this region in humans has shifted the architecture of
31 the dorsal and ventral processing streams. The TPJ-pSTS contains areas related to face-
32 emotion processing, attention, theory of mind operations, and memory; its expansion has
33 allowed for the elaboration and rearrangement of the cortical areas contained within, and
34 potentially the introduction of new cortical areas. Based on the arrangement and the function
35 of these areas in the human, we propose that the TPJ-pSTS is the basis of a third
36 frontoparietal processing stream that underlies the increased social abilities in humans. We
37 then describe a model of how the TPJ-pSTS areas interact as a hub that coordinates the
38 activities of multiple brain networks in the exploration of the complex dynamic social scenes
39 typical of the human social experience.

40 **Introduction**

41 The ability to function in dynamic and complex social situations is one of the traits that make
42 humans unique amongst other species (Buckner & Krienen, 2013). While other animals do
43 function in social groups and hierarchies, none have been able to adapt to and thrive in the
44 type of complex environments that characterize human social interactions, such as those
45 posed by walking through Times Square in New York City or attending the 30,000+ Society for
46 Neuroscience conference (Herrmann, Call, Hernández-Lloreda, Hare, & Tomasello, 2007).
47 Social cognition consists of multiple domains, both verbal and non-verbal. Non-verbally, for
48 instance, we must be able to quickly scan faces in a room to read ‘the mood’ of a social
49 gathering or read the body positions of people as we enter a bar (Zaki & Ochsner, 2009).
50 Verbally, we must be able to extract the hidden ‘emotional’ meaning of apparently neutral
51 sentence during a job interview. While the brain areas involved in processing social stimuli are
52 distributed across cortex, a region in the right temporoparietal junction-posterior superior
53 temporal sulcus (TPJp-STS) appears especially important. The TPJ-pSTS brings into proximity
54 posterior STS areas involved in processing biological motion (such as facial expressions),
55 nodes of the ToM network, and nodes of the attention networks, along with other areas that
56 may be relevant to processing social information. In this review, we will discuss how the
57 expansion and rearrangement of this region in the course of evolution in humans vs.
58 macaques supports these non-verbal social functions, and then propose a new framework for
59 the dynamic interaction of these areas during social cognition.

60

61 **Anatomy and evolution of TPJ-pSTS**

62 In this review, we use the term TPJ-pSTS to encompass a set of cortical areas and structures
63 that spans the inferior parietal lobule to the posterior STS in the dorsal-ventral axis, and the
64 angular gyrus, and posterior aspect of the supramarginal gyrus in the caudal-rostral axis (see
65 **Figure 1A**). We use this label to provide a unifying term for these regions and areas that are

66 often discussed separately in other studies and reviews. In this section, we review the
67 similarities and differences in the anatomy of the TPJ-pSTS in humans vs. macaques, the
68 model system most often used to study cognition in primates.

69
70 The human TPJp-STS is a large associative cortical region bordered by multiple sensory
71 systems. Posteriorly and inferiorly to this region are extrastriate and ventral-occipital visual
72 areas, such as the MT complex (MT/MST/FST in **Figure 1A**). Antero-ventrally to this region, in
73 the Sylvian fissure, is auditory cortex (represented by A1), and antero-dorsal is the
74 somatosensory system (represented by S1). Superior to this region are the parietal
75 oculomotor/attention areas (LIPv/d). This region is one of the last to develop in humans,
76 maturing in young adulthood at a similar time as prefrontal cortex (Hill *et al.*, 2010; Sotiras *et al.*,
77 2017). It is also one of the most morphologically variable between individuals (Croxson,
78 Forkel, Cerliani, & Thiebaut de Schotten, 2017; Mueller *et al.*, 2013; van Essen & Dierker,
79 2007a), perhaps a sign of its role in high-level integrative cognitive operations (Buckner &
80 Krienen, 2013).

81
82 A number of parcellation schemes for dividing human cortex into individual areas have been
83 recently proposed (Glasser *et al.*, 2016; Gordon *et al.*, 2014; Power *et al.*, 2011; Yeo *et al.*,
84 2011), with the aim of mapping the locations and boundaries of higher-level cortical areas that
85 do not have clear macaque homologues. However, because of the individual morphological
86 variability of this region, combined with its complex functional architecture, the parcellation of
87 the TPJ-pSTS into cortical areas has been difficult. Numerous schemes have been proposed,
88 often with little consensus (see **Figure 1B**). However, certain themes appears consistent. A
89 major theme is a right-left asymmetry in the organization of the TPJ-pSTS. This is evident
90 when comparing the effect of lesions to opposite hemispheres: whereas left TPJ strokes often
91 result in language impairment (aphasia), right TPJ is one of the sites most commonly lesioned

92 in strokes that cause visuospatial neglect (Bartolomeo, 2014; Corbetta & Shulman, 2011).
93 Moreover, functional MRI studies in healthy subjects have found multiple functions to be
94 asymmetrically located in the right TPJ-pSTS, including orienting of attention, theory of mind
95 operations, and face-emotion recognition (reviewed in more detail below). Parcellation
96 schemes based on resting state-functional connectivity and task fMRI studies have also found
97 asymmetries in the organization of this region, with several studies finding large discrepancies
98 in the border locations of purportedly homologous networks between hemispheres (Gordon et
99 al., 2014; Power et al., 2011; Yeo et al., 2011).

100
101 This fits with the differences in the patterns of cortical expansion in the right versus left TPJ
102 detailed in Van Essen *et al.* (van Essen, Glasser, Dierker, Harwell, & Coalson, 2011). In
103 particular, the border of the anterior TPJ parcel (TPJa), usually located on the supramarginal
104 gyrus, is often more posterior in the right versus left hemisphere (**Figure 1B**, the black line
105 indicates the corresponding posterior border of anterior TPJ in the left hemisphere).
106 Functionally, the TPJa is involved in the orienting of attention (Corbetta, Patel, & Shulman,
107 2008; Patel et al., 2015). Ventrally, in the pSTS, this parcel is either extended (Yeo et al.,
108 2011) (**Figure 1B** top left panel), part of a series of areas running perpendicular to the STS
109 (Glasser et al., 2016; Igelström, Webb, Kelly, & Graziano, 2016) (**Figure 1B** bottom right
110 panel), or is ambiguous in areal assignment and difficult to parcellate (Power et al., 2011) (gray
111 in **Figure 1B** top right panel). The pSTS overlaps with areas involved in face-emotion
112 recognition and processing biological motion. Posterior to the TPJa on the angular gyrus is the
113 TPJp, an area whose definition is generally agreed upon by task, functional connectivity, and
114 DTI parcellation schemes, and is most often identified as a node of the default mode network
115 (Raichle et al., 2001) or as part of the theory of mind network (Mars, Sallet, et al., 2012b).
116 Superior to the TPJa/p on the lateral bank of the IPS (latIPS) is a region spanning the length of
117 the inferior parietal lobule, implicated variously as a part of the frontoparietal task-control

118 network (Dosenbach *et al.*, 2007; Nelson *et al.*, 2010) and additionally involved in retrieval of
119 information from long-term memory (Sestieri, Shulman, & Corbetta, 2017). Architectonic
120 parcellations may coarsely align with these subdivisions in the anterior-posterior axis, but do
121 not appear to capture the dorsal-ventral organization (Caspers *et al.*, 2008; Igelström &
122 Graziano, 2017).

123
124 In macaques, the candidate TPJ-pSTS region shares some anatomical similarities. In addition
125 to a similar architectonic/connectivity based parcellation (Caspers *et al.*, 2008; 2012;
126 Gregoriou, Borra, Matelli, & Luppino, 2006; Rozzi *et al.*, 2006), the macaque TPJ-pSTS,
127 located in the macaque IPL, is also surrounded by visual, somatosensory, auditory, and
128 attention/oculomotor areas (see **Figure 2A** and **B**). In addition, signatures of purportedly
129 homologous functional areas have been observed within this region, including the lateral
130 parietal node of the default mode network (Mantini *et al.*, 2011; Vincent *et al.*, 2007), a theory
131 of mind area (Sliwa & Freiwald, 2017), and neurons demonstrating attention-reorienting activity
132 (Constantinidis & Steinmetz, 2001). However, major anatomical differences are apparent
133 when comparing this region between the two species. Specifically, the TPJ-pSTS is one of the
134 most expanded cortical regions in humans versus macaques (see **Figure 2C**) (Hill *et al.*,
135 2010). This is true regardless of whether the comparison is performed by landmark registration
136 (Hill *et al.*, 2010) or by cortical thickness (Sotiras *et al.*, 2017).

137
138 The cortical expansion is most obvious when considering the relative positions of MT, LIP, and
139 auditory cortex in macaques versus their purported homologues in humans (**Figure 2A** and **B**).
140 While auditory cortex lies inside of the Sylvian fissure in both species, the other two areas
141 have been pushed away from the TPJ-pSTS (Krubitzer, 2009). MT in macaques is in the
142 posterior/inferior bank of the STS in macaques, but in humans the homologous areas have
143 been pushed out of the STS ventrally to the junction of the inferior temporal and lateral

144 occipital sulci (Orban, van Essen, & Vanduffel, 2004). Similarly, area LIP in macaques is on
145 the lateral bank of the intraparietal sulcus and thus on the inferior parietal lobule, but the
146 human homologues are pushed superiorly, out of the intraparietal sulcus and onto the dorsal
147 aspect of the superior parietal lobule (Glasser *et al.*, 2016; Patel *et al.*, 2015). This massive
148 expansion of the TPJ-pSTS had the effect of pushing apart the dorsal and ventral stream
149 visual pathways (see arrows in **Figure 2A** and **B**), opening this region to elaboration and/or
150 rearrangement of already-present areas or allowing for the emergence of new areas with new,
151 high-level functions (Buckner & Krienen, 2013). The TPJ-pSTS is also one of the most
152 morphologically variable between individuals, another potential indicator of its late evolution
153 (Buckner & Krienen, 2013; Crosson, Forkel, Cerliani, & Thiebaut de Schotten, 2017; Mueller *et*
154 *al.*, 2013; van Essen & Dierker, 2007).

155
156 Below we discuss evidence that this expansion and rearrangement has allowed for the TPJ-
157 pSTS to shift from sensory integration to the integration of the cognitive operations necessary
158 for complex social functioning. It is important to note that it is not clear whether the need for
159 increased social cognitive abilities *drove* the expansion and/or the rearrangement of the TPJ-
160 pSTS, or that the TPJ-pSTS expanded first, which then allowed for the cortical areas to be
161 expanded and rearranged to subserve social cognitive processes as social complexity
162 increased. For excellent discussions of this point, see reviews by Buckner and Krienen
163 (Buckner & Krienen, 2013), Krubitzer and Seelke (Krubitzer & Seelke, 2012), Dehaene and
164 Cohen (Dehaene & Cohen, 2007), and Dunbar (Dunbar, 2016). Cortex appears to have
165 expanded well before increased societal complexity driven by the agricultural revolution
166 (Buckner & Krienen, 2013; Harari, 2015), suggesting cortical “recycling” (Dehaene & Cohen,
167 2007) may be a potential explanation for the evolution of the function of the TPJ-pSTS. On the
168 other hand, the ability to form and maintain complex and dynamic dyadic relationships may
169 have evolved first, reflected in the expansion of the TPJ-pSTS, which then allowed for the

170 creation of the complex social structures necessary for the agricultural revolution (Dunbar,
171 2016). In any case, the discussion below does not depend on the ordering of these events in
172 evolution.

173

174 **Functional Reorganization of TPJ-pSTS**

175 *pSTS Face-Emotion Recognition Areas*

176 One system in the TPJ-pSTS that has dramatically reorganized is the face processing network,
177 and in particular the circuit responsible for face-emotion recognition. In macaques, the face
178 processing network comprises of two parallel streams of areas (see **Figure 3A**), one running
179 along the inferior temporal gyrus and the inferior bank of the STS (ML, AL, and AM, pink
180 arrow), and one running superior to this in the fundus and superior bank of the STS (MF and
181 AF, blue arrow) (Tsao, Moeller, & Freiwald, 2008). Of these two streams, the superior MF/AF
182 streams appear more involved in motion processing, with MF being adjacent to MT/MST/FST
183 complex and potentially overlapping with LST, another motion processing area (Nelissen,
184 Vanduffel, & Orban, 2006; Polosecki et al., 2013). In addition, injection of muscimol into the
185 fundus of STS in or near MF interferes with use of eye-gaze information to direct attention
186 (Roy, Shepherd, & Platt, 2014), suggesting that this stream is more involved in the processing
187 of moving facial expressions as opposed to facial identity. There also appears to be a posterior
188 to anterior hierarchy in the face processing, with anterior areas (AF, AL, and AM) integrating
189 information from posterior areas (ML and MF) (Freiwald & Tsao, 2010; Schwiedrzik, Zarco,
190 Everling, & Freiwald, 2015). The posterior areas connect to the TPJ node of the macaque
191 default-mode network, whereas the anterior areas demonstrate more frontal connectivity
192 (Schwiedrzik et al., 2015).

193

194 Like in macaques, the human pSTS appears to be involved in the processing of biological
195 motion, with a major portion devoted to processing moving facial expressions (the STS-FA)

196 (Grossman, Battelli, & Pascual-Leone, 2005; Pelphrey, Morris, Michelich, Allison, & McCarthy,
197 2005; Polosecki et al., 2013) (see **Figure 3B**). According to a recent theory, the pSTS is
198 generally involved in making predictions on a short time-scale about biological mechanics—i.e.
199 predicting the trajectory of an arm or facial feature once it has started to move (Koster-Hale &
200 Saxe, 2013). In humans, however, this system has been substantially re-arranged. Not only
201 have the inferior stream face-processing areas been moved ventrally to ventral
202 occipitotemporal cortex (**Figure 3B** pink arrow), culminating in the fusiform face areas (FFA),
203 but the superior stream has been angled to be *perpendicular* to the STS (blue arrow). Similar
204 to macaques, this stream starts adjacent to the MT/MST/FST complex with an eye-gaze
205 processing area (now on the lip of the inferior bank of the pSTS (Glasser et al., 2016;
206 Marquardt, Ramezanpour, Dicke, & Thier, 2017), but instead of advancing along the STS, it
207 culminates in the STS-FA on the opposite bank of the pSTS (Polosecki et al., 2013; Tsao et
208 al., 2008). This puts the two ends of the streams centimeters apart in temporal cortex,
209 potentially anchoring another massive expansion of cortex along the mid to anterior STS
210 (compare white arrows in **Figure 3A** and **3B**. This also puts the STS-FA much closer to the
211 TPJ in humans than in macaques.

212

213 *TPJa in Orienting of Attention*

214 Immediately superior to the STS-FA in humans is the TPJa (Mars, Sallet, et al., 2012b),
215 originally labeled the TPJ by Corbetta and Shulman (Corbetta et al., 2008; Corbetta &
216 Shulman, 2002) (**Figure 3B** green border). This area was originally posited to be involved in
217 the stimulus-driven reorienting of attention (Corbetta, Kincade, Ollinger, McAvoy, & Shulman,
218 2000), but only to behaviorally relevant stimuli (Downar, Crawley, Mikulis, & Davis, 2000;
219 Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). This hypothesis was based on the
220 stronger response of TPJ, and other regions involved in attention/eye movements, such as the
221 parietal eye region (LIP) and FEF, to unexpected sensory stimuli that require a motor

222 response. It was proposed that this region is involved in signaling the occurrence of a
223 behaviorally relevant, yet unexpected stimuli (Downar et al., 2000; Serences et al., 2005;
224 Shulman et al., 2009), and that this signal acts a 'circuit-breaker' interrupting ongoing activity in
225 dorsal attention/eye movement regions re-directing the locus of processing to the new location
226 of interest (Corbetta et al., 2008; Corbetta & Shulman, 2002). In addition, it was found that the
227 magnitude of deactivation of this area predicts accuracy of detection on a foveal visual
228 discrimination task (Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007; Shulman et al.,
229 2003; Todd & Marois, 2004). Our interpretation was that suppression of the mechanism for
230 reorienting attention to irrelevant sensory stimuli (distracters) is active when subjects primarily
231 focus their attention to important stimuli. Recent studies have further separated TPJa into two
232 halves (Dugué, Merriam, Heeger, & Carrasco, 2017; Igelström et al., 2016), with the posterior
233 half (labeled vTPJ in (Dugué et al., 2017)) specifically involved in attentional reorienting and
234 corresponding to the original TPJ definition proposed by Corbetta and Shulman (Corbetta et
235 al., 2008; Dugué et al., 2017; Igelström et al., 2016; Patel et al., 2015; Shulman et al., 2003;
236 2009), and the anterior portion selectively involved in target detection (Igelström et al., 2016).
237
238 In the macaque, however, the TPJa has no clear homologue. Single-unit electrophysiology
239 studies initially found evidence of attention orienting signals in area 7a, the architectonic area
240 that covers much of the macaque TPJ-pSTS on the dorsolateral surface of the IPL
241 (Constantinidis & Steinmetz, 2001; Steinmetz, Connor, Constantinidis, & McLaughlin, 1994). A
242 comparative fMRI study also found a macaque homologue that was roughly anatomically
243 homologous and shared similarly movie-synchronized BOLD activity (Mantini, Corbetta,
244 Romani, Orban, & Vanduffel, 2013) (**Figure 3A** green X). However, in a study specifically
245 designed to elucidate the macaque TPJa homologue, Patel *et al.* did not find the target
246 detection or search deactivation signals that robustly define the TPJa in humans (Patel et al.,
247 2015).

248
249 Moreover, theories about the role of the TPJa in orienting of attention have continued to
250 develop. For instance, the timing of task-related neural activity in the TPJa was found to be
251 too delayed to be the source of reorienting signals. In fact, visually evoked responses by
252 targets that induce reorienting of attention peak in TPJa relatively late at/near ~300 ms, a
253 latency not compatible with latency of an eye movements and/or attention shift (~200 ms)
254 (Corbetta et al., 2008; Daitch et al., 2013; Spadone et al., 2015). Accordingly, TPJa is now
255 thought to be involved in higher-level cognitive operations than just stimulus-driven reorienting,
256 including the post-perceptual updating of internal models of environmental context (Geng &
257 Vossel, 2013). A version of this idea is that TPJa indicates the end of a task by sending a reset
258 signal that interrupts ongoing activity in task-relevant regions (a sort of cognitive offset signal
259 (Corbetta et al., 2008; Jack, Shulman, Snyder, McAvoy, & Corbetta, 2006; Shulman, Ollinger,
260 Linenweber, Petersen, & Corbetta, 2001)). This theory still fits with the involvement of TPJa in
261 attention- and detection-related processes, but additionally explains a) the late onset response
262 of TPJ; b) the overall greater response to behaviorally relevant but unexpected stimuli (not
263 necessarily indicating a mismatch in space); and c) the similarity between TPJ pattern of
264 response and the P300 evoked response, which has been also interpreted as underlying late
265 post-perceptual updating (Aston-Jones & Cohen, 2005; Corbetta et al., 2008; Geng & Vossel,
266 2013). A temporally delayed response and behaviorally relevant sensory-evoked modulation
267 also fits prediction-error models of TPJp function (see below) (Koster-Hale & Saxe, 2013).
268 Another not-incompatible theory is that the TPJa is involved in the conscious awareness of
269 novel stimuli, with the neural processes underlying awareness lagging those of the actual
270 visual processing of the stimulus (Beauchamp, Sun, Baum, Tolia, & Yeshor, 2012; Webb,
271 Igelström, Schurger, & Graziano, 2016). These newer formulations elevate the complexity of
272 the processes in TPJa from a low-level stimulus-driven reorienting mechanism to a mechanism
273 related to network coordination or prediction (see below).

274

275 *TPJp in Theory of Mind Operations*

276 Posterior to the TPJa, across the STS and on the angular gyrus, is the TPJp (Decety & Lamm,
277 2007; Geng & Vossel, 2013; Mars, Sallet, et al., 2012b) (**Figure 3B** yellow border). This area
278 is involved in the understanding of the mental states of other people, known commonly as
279 theory of mind operations (Saxe & Kanwisher, 2003; Schurz, Radua, Aichhorn, Richlan, &
280 Perner, 2014; Yang, Rosenblau, Keifer, & Pelphrey, 2015). The TPJp heavily overlaps with
281 the anteroventral portion of the default-mode network angular gyrus node. In general, the
282 default-mode network, a network originally defined in humans as an area that deactivates
283 during externally oriented attention-demanding tasks, heavily overlaps with the theory of mind
284 network (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016; Mars, Neubert, et al., 2012a;
285 Raichle et al., 2001; Shulman et al., 1997; Yang et al., 2015).

286

287 It has been proposed that the TPJp is involved in making model-based predictions about other
288 people's beliefs and desires as well as predictions about bio-mechanical movements on a
289 time-scale longer than immediate perception, and in further updating the model based on new
290 incoming sensory information (Geng & Vossel, 2013; Koster-Hale & Saxe, 2013). These
291 prediction-error theories are based on the observation that predicted stimuli evoke lower-
292 amplitude responses compared to unpredicted stimuli; the theory posits that the extra neural
293 activity is generated by the updating the internal model (Koster-Hale & Saxe, 2013). While the
294 terminology may differ, prediction-error theories of TPJp and circuit-breaker theories of TPJa
295 empirically make equivalent hypotheses: unpredicted or unexpected stimuli will evoke a higher
296 amplitude of activity than those that are predicted or expected. The TPJp then communicates
297 with other areas within the theory of mind or default-mode networks, including a medial
298 prefrontal area thought to be involved in making even longer time-scale model-based
299 predictions (Koster-Hale & Saxe, 2013). The default-mode network has been recently linked to

300 the generation of sensory-independent but internally constrained cognition (Andrews-Hanna,
301 Reidler, Huang, & Buckner, 2010; Christoff et al., 2016), consistent with the internal generation
302 and maintenance of internal models of the intentions of other people (Buckner & Carroll, 2007;
303 Mars, Neubert, et al., 2012a).

304
305 Multiple studies have located a putative macaque homologue of the default mode network
306 angular gyrus area with an area at the junction of the IPL and superior terminus of the STS,
307 labeled as TPOC (Mantini et al., 2011; Teichert, Grinband, Hirsch, & Ferrera, 2010; Vincent et
308 al., 2007) (**Figure 3A** yellow question marks). A recent study also found an area just superior
309 of this in area 7a to be activated by social interactions (Sliwa & Freiwald, 2017). However, the
310 overlap between the default mode network and areas activated by social interactions was an
311 area far anterior on the STG, area TPO, which is superior to MF (Schwiedrzik et al., 2015;
312 Sliwa & Freiwald, 2017). This may be similar to the “social interaction” area (SI-fROI)
313 observed in humans in (Isik, Koldewyn, Beeler, & Kanwisher, 2017) in the STS near the STS-
314 FA. Mars *et al.* found a more extreme discrepancy when searching for macaque TPJ
315 homologues using functional connectivity, with the identified area located in mid-STS cortex
316 near MT/FST, MF and ML (Mars, Sallet, Neubert, & Rushworth, 2013). These observations
317 underscore the expansion and rearrangement of the TPJ-pSTS in humans versus macaques:
318 1) human TPJp demonstrates robust activation by watching movies of conspecifics interacting
319 or acting independently, whereas the purported macaque homologue in TPOC does not, and
320 2) macaque TPO is considered to be a part of the default mode network, whereas human SI-
321 fROI is not.

322

323 *AG and latIPS in Memory Retrieval*

324 Overlapping or posterior to human TPJp (Mars, Sallet, et al., 2012b; Yang et al., 2015) lays the
325 remaining posterodorsal aspect of the DMN angular gyrus node, corresponding to

326 cytoarchitectonic areas PGa and PGp (Caspers *et al.*, 2013; Christoff *et al.*, 2016), here
327 labeled as the postAG (**Figure 3B** purple border). This area contains heteromodal cortex
328 associated with multiple high level functions (Humphreys & Lambon Ralph, 2015; Seghier,
329 2013). Several lines of evidence converge on the role of this region in the representation of
330 information retrieved from episodic (Rugg & King, 2017; Sestieri *et al.*, 2017) and semantic
331 (Binder & Desai, 2011) memory, perhaps allowing the construction of multi-purposes
332 event/situation models (Cohn-Sheehy & Ranganath, 2017). This function relies on the
333 presence of functional (Kahn, Andrews-Hanna, Vincent, Snyder, & Buckner, 2008; Vincent *et*
334 *al.*, 2006) and structural (Kravitz, Saleem, Baker, & Mishkin, 2011; Mufson & Pandya, 1984)
335 connections with medial temporal structures traditionally involved in memory functions (Kravitz
336 *et al.*, 2011; Squire, 1992).

337
338 Memory retrieval in humans is associated with activity of another parietal region (Vilberg &
339 Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005), labeled here as latIPS (Sestieri *et al.*,
340 2017; Vilberg & Rugg, 2008) (**Figure 3B** cyan border) and located dorsally to areas TPJa and
341 TPJp (roughly corresponding to cytoarchitectonic area hIP1 (Caspers *et al.*, 2013)). The
342 latIPS overlaps with the so-called frontoparietal control network (Dosenbach, Fair, Cohen,
343 Schlaggar, & Petersen, 2008; Duncan, 2010), which is anatomically interposed between the
344 dorsal attention network and the default-mode network (Spreng, Sepulcre, Turner, Stevens, &
345 Schacter, 2013). The role of the latIPS in memory retrieval differs from that of the postAG in
346 several ways. First, latIPS tracks the feeling of oldness (familiarity) rather than recollection
347 (Hutchinson *et al.*, 2012; Sestieri *et al.*, 2014). Second, it shows sustained activity consistent
348 with a role in active maintenance and manipulation of memories according to task demands
349 (Sestieri *et al.*, 2017; Sestieri, Corbetta, Romani, & Shulman, 2011). Third, it overlaps with the
350 parietal node of the frontoparietal control network, which is thought to regulate the balance
351 between the processing of external (perceptual) information in the dorsal attention network and

352 of internal (introspective) information in the default-mode network (Dixon et al., 2018; Sestieri,
353 Corbetta, Spadone, Romani, & Shulman, 2014a). Finally, it is functionally and anatomically
354 connected with prefrontal, rather than medial temporal, regions (Uddin et al., 2010).

355
356 While activity during memory retrieval is typically observed in the left parietal cortex (Duarte,
357 Henson, & Graham, 2011; Guerin & Miller, 2009), retrieval-related activity is also observed in
358 homologue regions of the right hemisphere (e.g. (Klostermann, Loui, & Shimamura, 2009;
359 Sestieri, Shulman, & Corbetta, 2010)), and the degree of hemispheric asymmetry has not been
360 assessed with quantitative indices (Seghier, 2008). On the basis of the importance of memory
361 information for social interactions (Buckner & Carroll, 2007; Spreng, 2013), it is possible to
362 hypothesize that retrieval-related activity in the right parietal areas serve adaptive social
363 processing implemented in adjacent regions, such as the TPJ-pSTS. In particular, while
364 memory representations in the AG might contribute to social knowledge retrieval (Y. Wang et
365 al., 2017) and memory-guided inference of other's mental states (Spreng & Mar, 2012), the
366 latIPS might help to regulate the balance between exploration of the external world (dorsal
367 attention) and accessing internally stored models of social agents and situations (TPJ-pSTS) in
368 cognition (Dixon et al., 2018).

369
370 Compared to humans, evidence for the involvement of monkey parietal lobes in memory
371 functions is scarce. Based on resting-state functional connectivity data, one study
372 hypothesized that that in macaques the area would be on the posterior STG (Vincent, Kahn,
373 van Essen, & Buckner, 2010). Evidence supporting this hypothesis was described in a recent
374 fMRI study employing a serial probe-recognition task in macaques (Miyamoto et al., 2013).
375 The functional and structural properties of two parietal regions, area PG/PGOp (**Figure 3A**
376 purple question mark) of the inferior parietal lobule and PEa/DIP located in the medial bank of
377 the intraparietal sulcus (cyan question mark) resemble that of the postAG and latIPS in

378 humans, respectively (Miyamoto *et al.*, 2014). If these homologies prove to be true, this would
379 indicate that in humans the parietal site supporting episodic recollection (the postAG) has
380 shifted posteriorly compared to macaque PG/PGOp, while the site supporting the sense of
381 familiarity (latIPS) has shifted ventrally and anteriorly compared to macaque PEa/DIP.
382 However, the homologous relationships are not straightforward: the macaque episodic recall
383 area (Miyamoto *et al.*, 2013) is clearly anterior to the macaque angular gyrus node homologue,
384 TPOC (Mantini *et al.*, 2011); and PEa/DIP is located in macaque areas typically implicated in
385 visual processing, attention, or motor planning (Patel, Kaplan, & Snyder, 2014) whose
386 homologues are in the human SPL (Patel *et al.*, 2015). A study comparing functional
387 connectivity networks in humans and macaques has also found that the fronto-parietal
388 networks that comprise areas involved in memory retrieval may be unique to humans (Mantini
389 *et al.*, 2013).

390

391 **The TPJ-pSTS: A Newly Evolved Stream of Processing**

392 Based on early macaque histology and neurophysiology studies, visual processing has
393 traditionally been divided into two streams: a dorsal spatially-oriented processing stream and a
394 ventral feature-based processing stream (Kravitz *et al.*, 2011; Mishkin, Ungerleider, & Macko,
395 1983). Both pathways originate in striate cortex (V1), share a common substrate in extrastriate
396 areas (V2-V4), and then diverge from lateral occipital cortex (V4) towards either parietal
397 (spatial/action) or temporal (feature) cortex (Baizer, Ungerleider, & Desimone, 1991;
398 Ungerleider, Galkin, Desimone, & Gattass, 2008). The dorsal pathway connects to the dorsal
399 attention/oculomotor network areas in parietal and prefrontal cortex (Goldman-Rakic, 1988),
400 and the ventral to the prefrontal cortex via a separate pathway (Kravitz, Saleem, Baker,
401 Ungerleider, & Mishkin, 2013; Webster, Bachevalier, & Ungerleider, 1994). These two
402 pathways are densely interconnected and interact with each other in visual processing
403 (Cloutman, 2013). This has the effect of having mid-level sensory processing areas from all

404 modalities in close proximity to each other around the macaque TPJ-pSTS, and the TPJ-pSTS
405 in close proximity (on opposite sides of a gyrus) to attention/oculomotor (LIP) and other motor
406 planning areas (VIP, AIP).

407

408 In humans, these two streams begin to diverge more posteriorly, making room for the
409 expanded TPJ-pSTS: the dorsal stream has moved even more dorsally onto the SPL, and the
410 ventral stream more ventrally to the ventral occipitotemporal cortex. As mentioned before, the
411 pSTS stream in humans has angled perpendicularly to the STS and bisects this expansion.
412 These pSTS areas connect to the TPJa/p (Ethofer *et al.*, 2013), introducing a novel pathway
413 for sensory information to reach the TPJ-pSTS (and filling in the visual cortex to TPJ
414 connection in the Corbetta/Shulman model (Corbetta *et al.*, 2008)). The right TPJ-pSTS is
415 also connected to prefrontal areas through the more ventro-lateral branches of the superior
416 longitudinal fasciculus (Croxson *et al.*, 2005; Thiebaut de Schotten, Dell'Acqua, Valabregue, &
417 Catani, 2012) and/or the extreme capsule (also known as the inferior fronto-occipital fascicle)
418 (Mars *et al.*, 2016; Sarubbo, De Benedictis, Maldonado, Basso, & Duffau, 2013), paralleling
419 the motif of the anatomical pathways connecting language areas in the left hemisphere
420 (Margulies & Petrides, 2013; Thiebaut de Schotten *et al.*, 2012). This anatomical pathway
421 provides a direct communication channel between visual, TPJ-pSTS, and prefrontal areas that
422 is independent of the dorsal and ventral pathways. While this TPJ-pSTS pathway is different
423 from the third visual pathway proposed by Haak and Beckmann (Haak & Beckmann, 2018);
424 they may be related: their third visual pathway extends across lateral occipital cortex towards
425 the pSTS and may serve as an entry point of visual information into the TPJ-pSTS pathway.
426 The TPJ-pSTS pathway is also distinct from the parieto-medial temporal pathway described in
427 Kravitz *et al.*, though both originate in the TPJ-pSTS (Kravitz *et al.*, 2011).

428

429 We propose that the TPJ-pSTS has emerged as a hub for social cognitive processes, bringing
430 together information gleaned from exploration of the external sensory world with internally
431 generated models of social factors (see **Figure 4**). Specifically, the TPJ-pSTS receives
432 information related to facial emotions from different cortical regions and other biological motion
433 signals (body, eye) via the posterior STS, theory of mind operations via TPJp, attention via
434 TPJa, and recollection and familiarity signals related to previous experiences via the AG and
435 latIPS (Kravitz *et al.*, 2011). We believe that with this collection of functions, the TPJ-pSTS
436 serves as a hub in a hybrid top-down/bottom-up processing pathway that underlies the quick
437 detection and use of social cues to guide exploration of and interaction with the surrounding
438 social environment (Corbetta *et al.*, 2008; Serences *et al.*, 2005). This pathway operates
439 independently of the separable top-down and bottom up processes instantiated in the
440 dorsal/ventral visual pathways in the TPJ-pSTS. The “bottom-up” or stimulus-driven functions
441 of this pathway are instantiated by the bias towards the processing of salient biological motion
442 and features through the pSTS. The “top-down” or goal-directed functions of this pathway
443 originate in the TPJp, supported by access to relevant explicit memory through the
444 postAG/latIPS complex. This information is then used to guide visual scanning exploration of
445 the environment (TPJa and dorsal attention network).

446 An alternative hypothesis put forth by Genovesio *et al.* is that prefrontal-parietal
447 networks have elaborated from the dorsal processing stream in the course of evolution to
448 support the socially related relational metrics (order, number, duration, distance, etc.)
449 necessary for social “foraging” or exploration (Genovesio, Wise, & Passingham, 2014). We
450 note, however, the presence of an anatomical discrepancy between areas belonging to the
451 traditional dorsal processing stream (e.g., area LIP and its human homologue on the superior
452 parietal lobule) and areas involved in computing relational metrics (located on different portions
453 of the inferior parietal lobule in both species). Moreover, inputs into this area appear to be a
454 combination of dorsal (MT) and ventral (FFA) visual processing stream areas, while outputs

455 appear to be directly to ventrolateral prefrontal cortex and not the FEF, further differentiating
456 the TPJ-pSTS pathway from the dorsal pathway.

457
458 The sequence of processing through the TPJ-pSTS might follow one of two pathways (**Figure**
459 **5A** and **B**). Both would start with incoming biological motion sensory information, such as a
460 moving facial expression in the visual periphery. Sensory processing would involve areas
461 such as MT and FFA, culminating in the activation of the pSTS STS-FA (**5A:1**, **5B:1**). At this
462 point the possibilities diverge. One pathway may involve communication of the facial
463 expression information (still in the periphery) with the TPJp as a possible updating of the
464 internal model of the mental states of the people in the social scene (**5A:2**). If the social
465 situation is familiar, this then activates the latIPS (**5A:3**), which serves two functions: a) trigger
466 the recall of associated stored memories via the AG (**5A:4a**) to be used in the theory of mind
467 operations in TPJp and elsewhere (**5A:5**), and 2) bridge the internally and externally oriented
468 operations in the TPJp and dorsal attention network respectively (**5A:4b**). If the changes
469 warrant further exploration, the TPJp communicates with the TPJa (**5A:6**) to trigger the
470 orienting of attention to the face currently in the periphery (**5A:7**). An alternative hypothesis is
471 that the external sensory information from the pSTS (**5B:2**) and the internal model information
472 from the TPJp (**5B:7**) combine in the TPJa to trigger a model updating if the facial expressions
473 violate the expectation, which then triggers further visual exploration through the dorsal
474 attention network.

475
476 One major issue that remains to be resolved in this model of TPJ-pSTS areal interactions in
477 social cognition is the role of the TPJa. While there is evidence that TPJa activity follows
478 attention reorienting, this may just be an artifact of the sparse and static stimuli used in these
479 tasks. TPJa activity may be superfluous to these artificial tasks, with attention orienting in
480 these tasks controlled by the classic top-down/bottom-up mechanisms instantiated in the

481 dorsal and ventral visual pathways. After all, macaques are able to perform these tasks
482 without a TPJa. However, in more naturalistic tasks, where the complex integration described
483 above is necessary, activity in TPJa may actually precede attention orienting and the resulting
484 exploratory saccades, based on the decision to update the internal models maintained in TPJp
485 and elsewhere. Saccades occur about twice per second in the exploration of a naturalistic
486 scene (H. X. Wang, Freeman, Merriam, Hasson, & Heeger, 2012), which is plenty of time to
487 accommodate the TPJa signals (~300ms) and still drive a saccade through the dorsal attention
488 network.

489
490 The lack of a similarly organized TPJ-pSTS in macaques makes it difficult to resolve these
491 issues. However, the study of the macaque TPJ-pSTS may yet reveal some hints about the
492 integrative function of this hub. In macaques, the areas surrounding the TPJ-pSTS tend to be
493 more secondary sensory areas involved in basic motion detection (MT/MST), somatosensory
494 and auditory functioning, and motor planning in the IPS. Perhaps in the course of 25 million
495 years of parallel evolution, then, the TPJ-pSTS in macaques has been purposed to support
496 quick navigation of *their* environment, populated less by other macaques and more by trees
497 and other non-macaque stimuli (van Schaik, Isler, & Burkart, 2012). This may be supported by
498 the presence of neural signals in macaque area 7a related to optic flow patterns (Raffi &
499 Siegel, 2007) and maze navigation (Crowe, Chafee, Averbeck, & Georgopoulos, 2004).

500
501 However, given the disparities between the macaque and human TPJ-pSTS, future
502 investigations of the interactions posed in this anatomical framework will require direct study of
503 this region in humans using techniques with high temporal and spatial resolution, such as
504 multiband fMRI, magnetoencephalography (MEG) or electrocorticography (ECoG), combined
505 with use of stimuli that simultaneously activate these areas in naturalistic ways. These may
506 include naturalistic videos of social situations, virtual reality environments, or even

507 simultaneous fMRI scanning of two people interacting (Hasson, Ghazanfar, Galantucci,
508 Garrod, & Keysers, 2012). With these techniques we will hopefully be able to understand how
509 this cortical region gives rise to the behaviors that make us unique as humans.

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510 **Figure Captions:**

511

512 **Figure 1:** Structural and functional anatomy of the human TPJ-pSTS A) Approximate definition
513 of this region compared to major sulcal/gyral features (derived from FreeSurfer labels) and
514 functional areas (from HCP parcellation scheme (Glasser *et al.*, 2016)). B) Different resting
515 state parcellation schemes of TPJ-pSTS showing difference in posterior border of right anterior
516 TPJ parcellation (white arrows) vs. left hemisphere homologues projected to right hemisphere
517 (black border).

518

519 **Figure 2:** Location and extension of the TPJ-pSTS (red border) in A) macaques vs. B) humans
520 compared to homologous sensory areas. Arrows schematically illustrate the dorsal (blue) and
521 ventral (orange) visual pathways. C) Cortical deformation map for registering macaque cortex
522 to human from Hill *et al.* (Hill *et al.*, 2010).

523

524 **Figure 3:** Functional architecture of TPJ-pSTS in macaques vs. humans. A) Macaque TPJ-
525 pSTS homologues. Face patches derived from (Schwiedrzik *et al.*, 2015). Other homologues
526 locations projected from published cortical surface data (see text for citations). B) Human TPJ-
527 pSTS functional areas. Face patches, TPJp, and TPJa derived from unpublished task fMRI
528 localizer data. PostAG and latIPS borders projected from (Sestieri *et al.*, 2010; 2011) and
529 (Sestieri *et al.*, 2014), respectively.

530

531 **Figure 4:** Map of human TPJ-pSTS hybrid pathway showing how visual and face processing
532 areas connect through the TPJ-pSTS to prefrontal cortex.

533

534 **Figure 5:** Potential sequence of interactions and transmission of information to prefrontal
535 cortex if A) TPJa activation is late or B) early.

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Figure 1

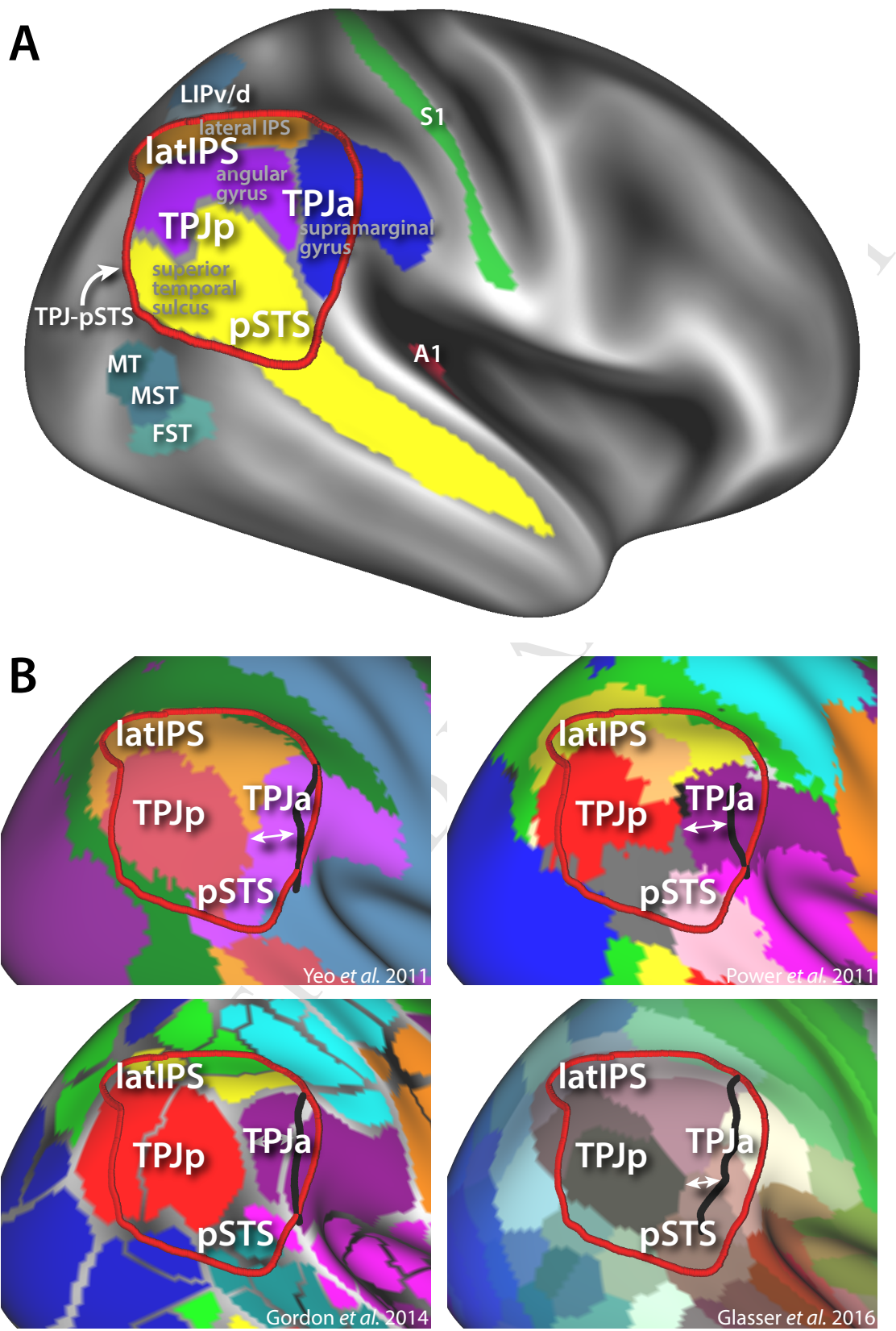


Figure 2

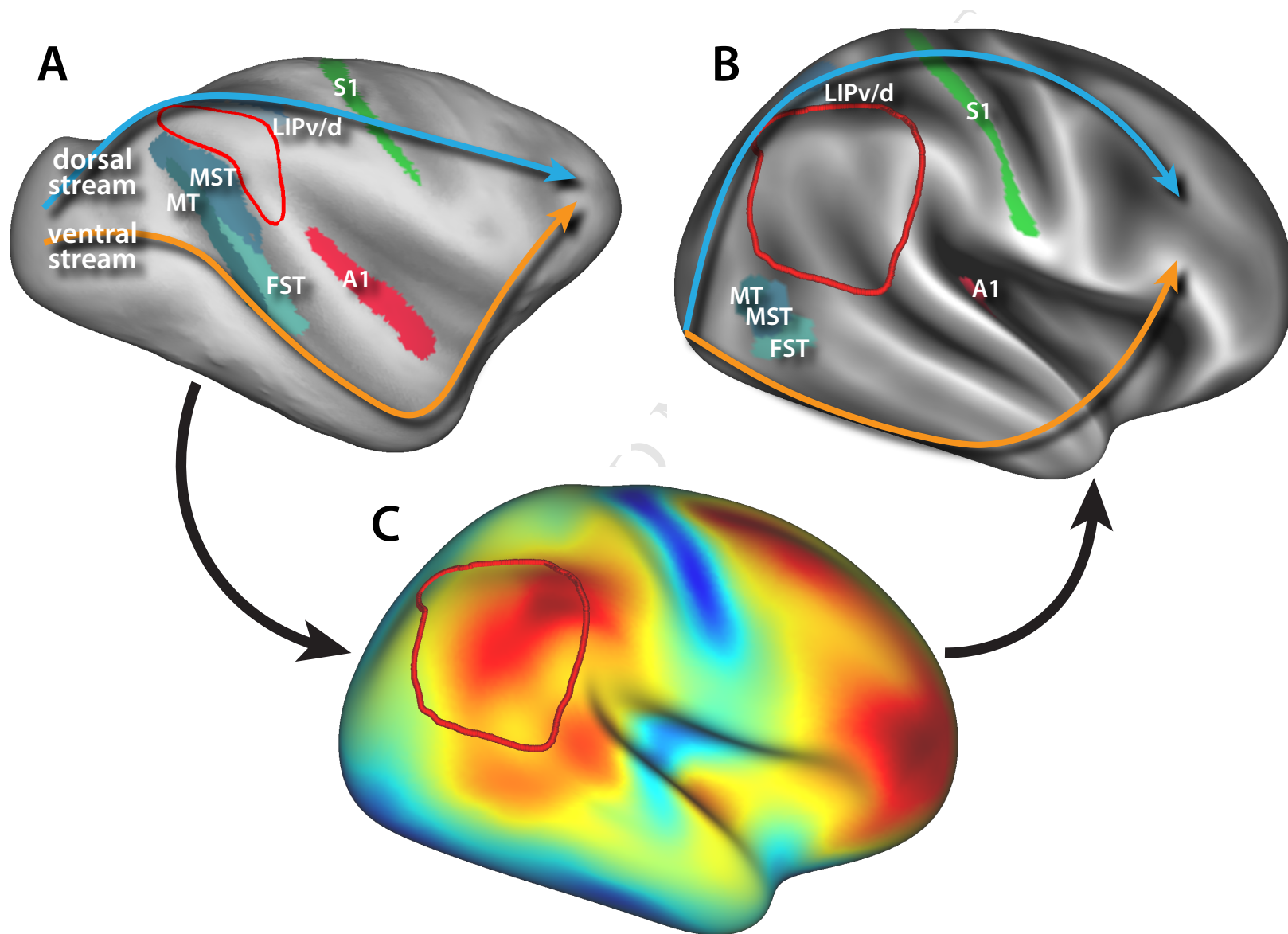


Figure 3

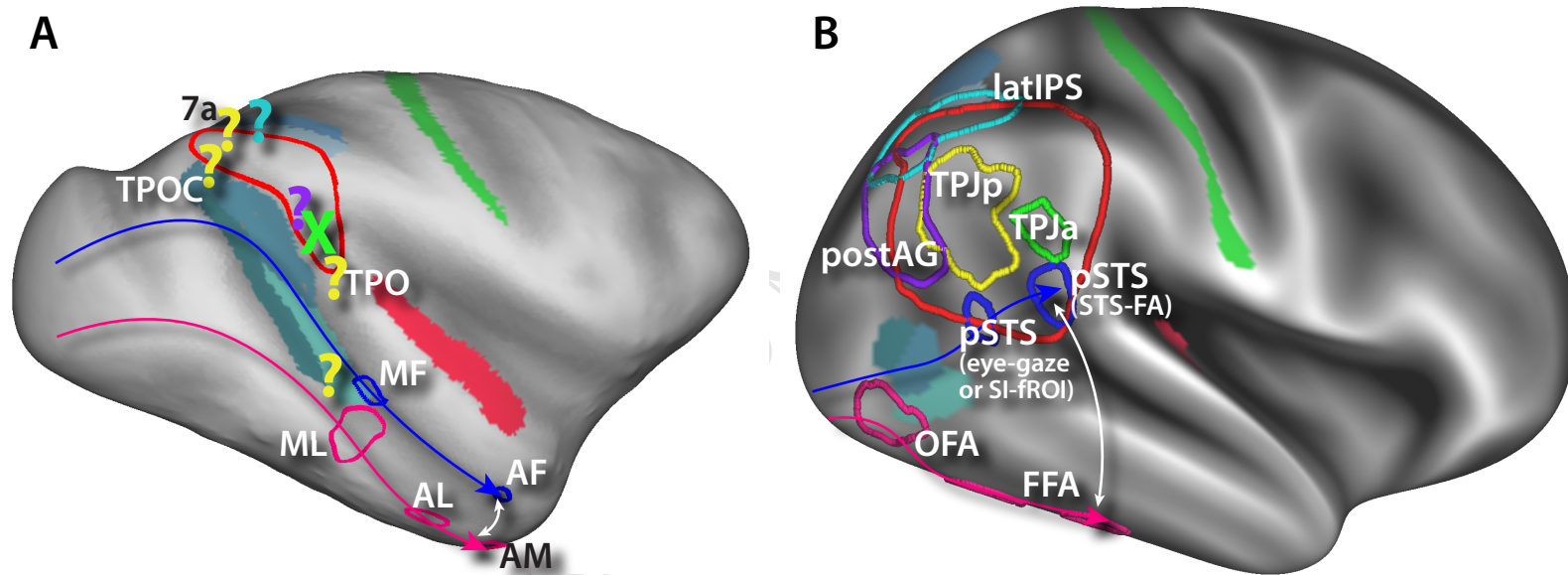


Figure 4

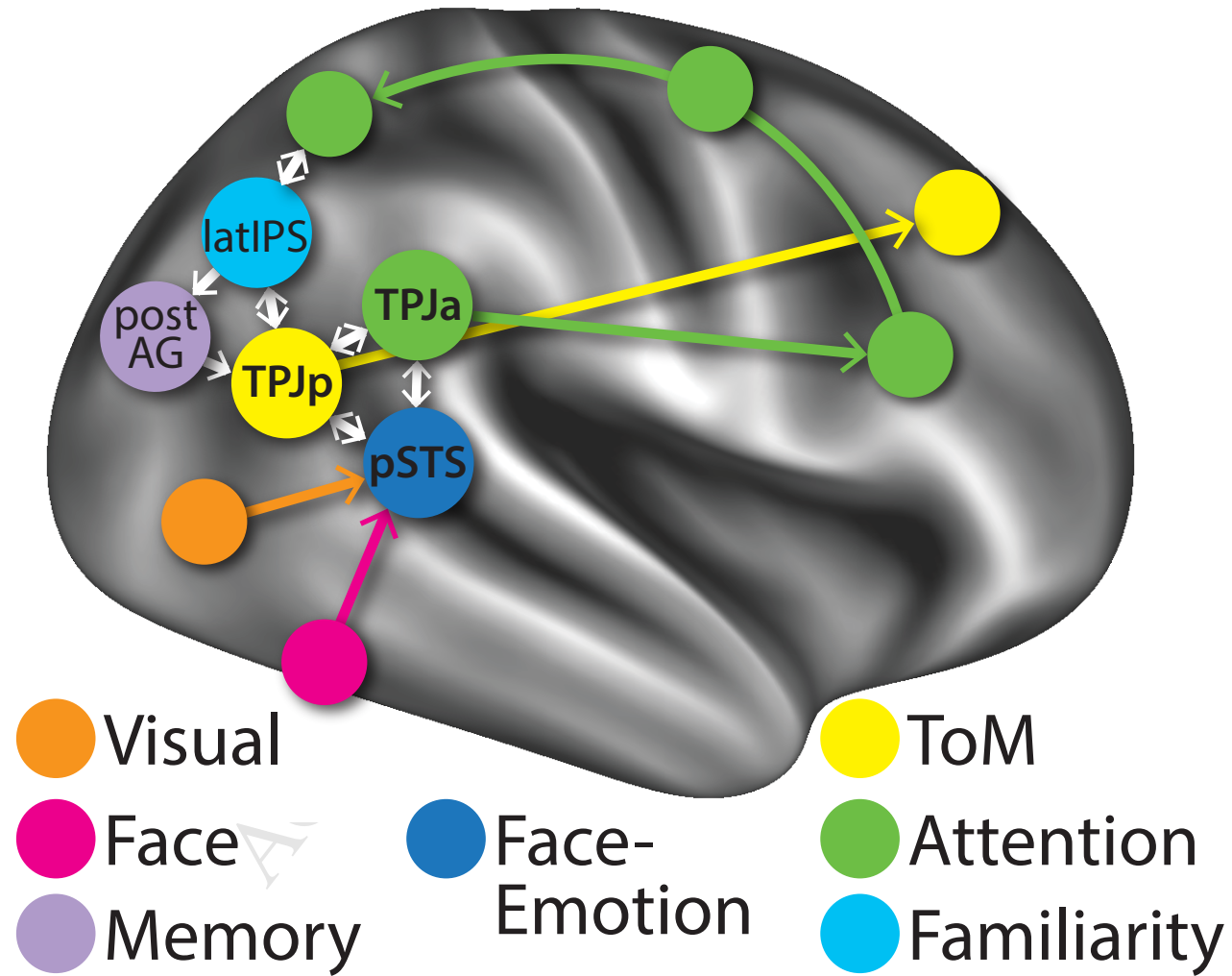
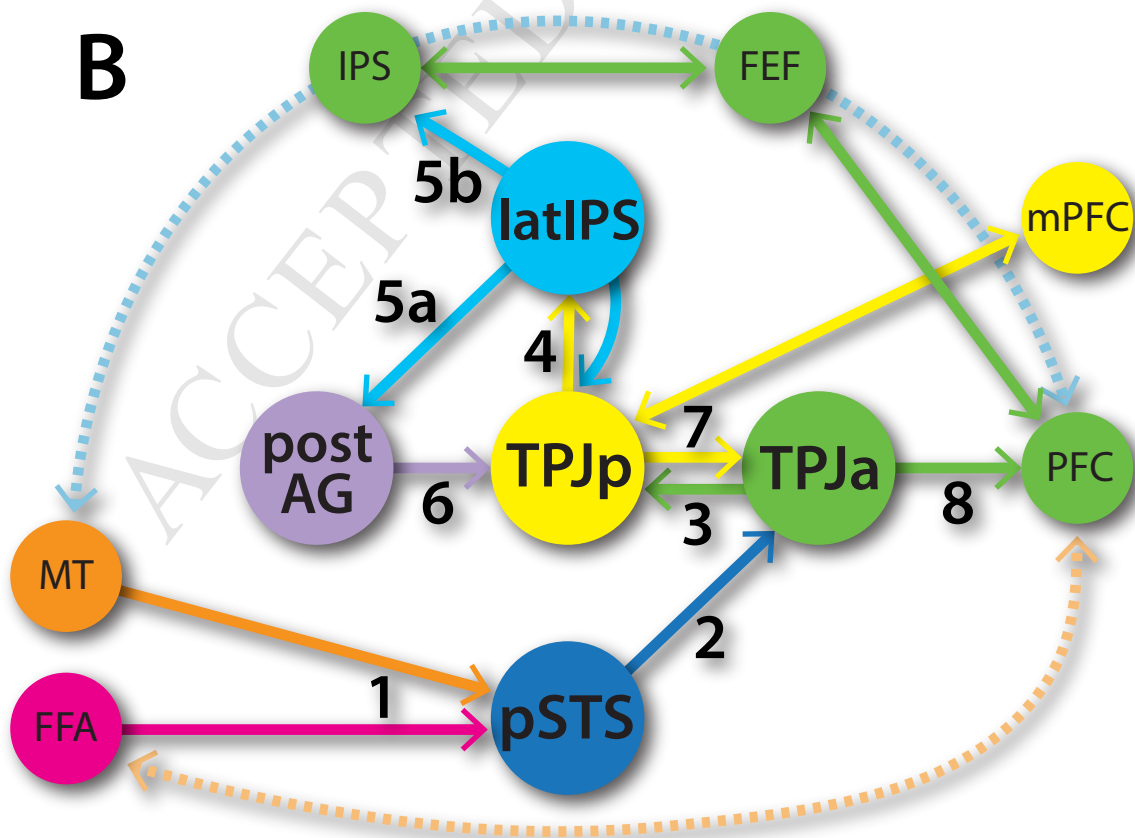
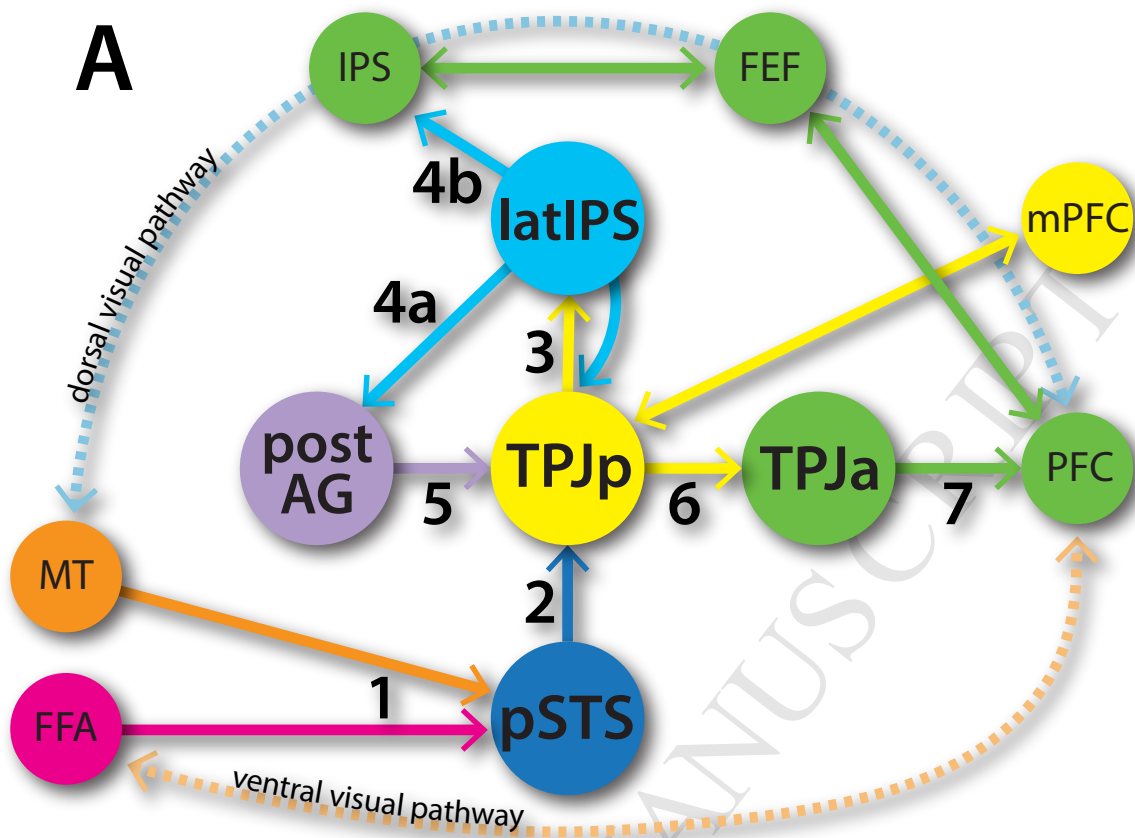


Figure 5



Author Credit Statement

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