

The Ventrolateral Anterior Temporal Lobe is Commonly Engaged by Both Mental State Inference and Semantic Association Tasks

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Abstract

A key challenge for neurobiological models of social cognition is to elucidate whether brain regions are specialised for that domain. In recent years, discussion surrounding the role of the anterior temporal lobe (ATL) epitomises such debates; some argue it is part of a domain-specific network for social processing, while others claim it is a domain-general hub for semantic representation. In the present study, we used ATL-optimised fMRI to map the contribution of different ATL structures to a variety of paradigms frequently used to probe a crucial social ability, namely ‘theory of mind’ (ToM). Using multiple tasks enables a clearer attribution of activation to ToM as opposed to idiosyncratic features of stimuli. Further, we directly explored whether these same structures are also activated by a non-social task probing semantic representations. We revealed that common to all of the tasks was activation of a key ventrolateral ATL region that is typically invisible to standard fMRI. This constitutes novel evidence in support of the view that the ventrolateral ATL contributes to social cognition via a domain-general role in the retrieval of conceptual knowledge, and against claims of a specialised social function.

Keywords: semantic memory; social cognition; theory of mind; anterior temporal lobe; distortion-corrected fMRI

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1 **Introduction**

2 The anterior temporal lobe (ATL) plays a crucial role in support of social cognition
3 (Frith and Frith 2003, 2010; Olson et al. 2013; Binney and Ramsey 2020). Damage to this
4 region results in profound and wide-ranging socio-affective deficits in both primates and
5 humans (Klüver and Bucy 1937; Terzian and Dalle Ore 1955; Edwards-Lee et al. 1997; Kumfor
6 and Piguet 2012; Kumfor et al. 2013, 2017; Irish et al. 2014; Binney et al. 2016). Amongst
7 neurotypical samples, the findings of functional neuroimaging studies suggest an almost
8 ubiquitous involvement in the high-level processing of faces and emotions (Wong and Gallate
9 2012; Collins and Olson 2014; Collins et al. 2016), as well as in more abstracted forms of social
10 processing, such as moral cognition and mental state attribution (also known as theory of mind)
11 (Moll et al. 2005; Schurz et al. 2014; Molenberghs et al. 2016; Diveica et al. 2021).

12 Despite this, across various neurocognitive frameworks of the ‘social brain’, there is no
13 firm consensus regarding the nature of the function that the ATL performs (for a
14 comprehensive review, see Olson et al. 2007; 2013). There are likely two main drivers for this.
15 First, at a glance, it might be difficult to identify a common cognitive process that connects the
16 various social and emotional tasks that implicate the ATL (Olson et al. 2013; Binney and
17 Ramsey 2020). Second, inconsistent definitions of what anatomy it is that constitutes the ATL
18 have greatly contributed to a lack of clarity regarding the locations at which overlap, and
19 divergence of function seemingly occurs. From one perspective, the term “ATL” refers to all
20 cortex comprising the anterior half of the temporal lobe (Binney et al. 2010; Rice, et al. 2015;
21 Binney et al. 2016; Rice et al. 2018), while, at times, it has been used to specifically refer to
22 the temporal polar cortex, and the limited boundaries of Brodmann’s area 38 (Ross and Olson
23 2010; Simmons et al. 2010). Therefore, the primary aims of the present study were to provide
24 a more complete description of the ATL subregions engaged in service of social cognitive
25 tasks, and to advance understanding of the nature of their function.

26 One account of the ATL's role in social tasks is that it stores mental scripts, or schema,
27 that are formed out of prior experiences, and provide a wider context for understanding social
28 interactions (Frith and Frith 2003; Gallagher and Frith 2003). However, until more recently,
29 there has been a lack of direct evidence to support this hypothesis. Moreover, it is unclear as to
30 what extent the proposed social function of the ATL is distinct from that of more general
31 declarative memory systems. Recent proposals have more specifically associated the ATL's
32 role with the retrieval of social conceptual knowledge, which is posited as a subtype of semantic
33 memory (Zahn et al. 2007; Olson et al. 2013; Binney and Ramsey 2020). Semantic memory is
34 a term used to refer to a long-term store of general conceptual-level knowledge that is involved
35 in transforming sensory inputs into meaningful experiences, and it underpins the ability to
36 recognize and make inferences about objects, people, and events in our environment (Lambon
37 Ralph et al. 2017). Social conceptual knowledge has been defined more distinctively as person-
38 specific knowledge (Simmons et al. 2010), but also knowledge about interpersonal
39 relationships, social behaviours, and of more abstract social concepts such as *truth* and *liberty*
40 (Zahn et al. 2007; Olson et al. 2013). The claim that the ATL is engaged in retrieving this type
41 of information during social tasks is supported by a functional neuroimaging study that reveals
42 ATL activation both during a social attribution task and a task involving semantic relatedness
43 judgments about socially relevant concepts (Ross and Olson 2010).

44 Moreover, it has been suggested that social conceptual knowledge could have a special,
45 or even privileged status over other categories of semantic information (Zahn et al. 2007; Olson
46 et al. 2013). Indeed, one influential account of the ATL, the *social knowledge hypothesis*, states
47 that this region is exclusively involved in representing social categories of semantic
48 information (Simmons et al. 2010; Olson et al. 2013). Proponents of this hypothesis point to
49 the fact that a variety of socially-relevant tasks and stimuli reliably activate the region, whereas
50 the majority of functional imaging studies of general semantic processing do not (Olson et al.

51 2007, 2013; Simmons and Martin 2009; Simmons et al. 2010; Persichetti et al. 2021). Further,
52 some fMRI studies have demonstrated a greater response, specifically of the dorsolateral/polar
53 ATL subregions, when semantic judgments made on socially relevant stimuli are compared to
54 similar judgments made on non-social stimuli (Zahn et al. 2007; Ross and Olson 2010; Binney
55 et al. 2016; Rice et al. 2018).

56 However, the ATL is strongly implicated in general semantic processing on the basis
57 of decades of neuropsychological data (Patterson et al. 2007) and a growing body of brain
58 stimulation and electrophysiological studies, as well as functional neuroimaging studies that
59 take special measures to address signal dropout and distortion within this region (Binney et al.
60 2010; Visser et al. 2010; Visser et al. 2010; Lambon Ralph et al. 2017). A critical issue,
61 therefore, is how it is possible to reconcile these two sets of observations within a single unified
62 theory of ATL function.

63 When broadly defined as the anterior half of the temporal lobe, the ATL is comprised
64 of a substantial volume of cortex, amongst which there are numerous subdivisions identifiable
65 on the basis of morphology, cytoarchitecture and connectivity (Ding et al. 2009; Binney et al.
66 2012; Pascual et al. 2015), and it is highly plausible that there is either distinct or graded
67 differences in functions, including semantic function (Olson et al. 2013; Binney et al. 2016).
68 Therefore, under what might be called a '*dual ATL hub account*', social conceptual knowledge
69 could be stored within a distinct location to more general conceptual information (Zahn et al.
70 2007, 2009). Indeed, while social tasks and semantic judgements on social words activate the
71 dorsolateral/polar ATL (including the anterior middle and superior temporal gyri), the general
72 semantics literature, including data from patients and studies using ATL-optimised fMRI
73 (Binney et al. 2010; Mion et al. 2010; Visser et al. 2010; Lambon Ralph et al. 2017), converges
74 on the ventrolateral ATL (including the rostral fusiform and inferior temporal gyri) as the
75 centre-point of a domain-general conceptual hub.

76 However, two recent studies have demonstrated that using enhanced fMRI techniques
77 greatly affects the patterns of activation observed in the ATL during the processing of social-
78 relevant stimuli and leads to different conclusions (Binney et al. 2016; Rice et al. 2018). In
79 conventional approaches to acquiring fMRI, susceptibility artefacts cause signal loss and image
80 distortion around the location of the ventral ATL, which render the technique effectively blind
81 to activation in this region (Devlin et al. 2000). Spin-echo, and dual-echo echo-planar fMRI,
82 as well as post-acquisition distortion correction techniques, can be used to recover this signal,
83 in which case it becomes clear that the ventrolateral ATL activates strongly during semantic
84 judgements made on both social and non-social stimuli. Moreover, this omni-category response
85 is much greater in magnitude than that of the dorsolateral/polar ATL which nonetheless appears
86 more tuned to social stimuli (Binney et al. 2016; Rice et al. 2018). These observations support
87 a proposal in which the ATL region comprises a single semantic hub albeit with graded
88 subspecialisations towards certain types of conceptual information (Plaut 2002; Binney et al.
89 2012; Rice et al. 2015). According to this framework, the activation of the ATL in service of
90 social cognitive tasks reflects engagement of a domain-general semantic system which is
91 centred upon its ventrolateral aspects (Binney and Ramsey 2020).

92 The conclusions that can be drawn from these two studies regarding the ATL's role in
93 social cognition are limited. This is because they used tasks where the demands are primarily
94 semantic in nature and the social relevance of the stimuli may have only been a secondary
95 feature. As such, it remains an open question whether social tasks typically employed in the
96 social neuroscience literature activate the ventrolateral ATL hub. The present study tackles
97 exactly that issue, with a specific focus on mental state attribution or 'theory of mind' tasks.
98 We chose this focus because theory of mind (ToM) abilities are considered central to the
99 construct of social cognition; they are considered as fundamental to successful social
100 interactions, as they enable us to describe, explain and predict behaviour (Frith and Frith 2005;

101 Brüne and Brüne-Cohrs 2006; Apperly 2012; van Hoeck et al. 2014; Heleven and van
102 Overwalle 2018). Neuroimaging studies reliably implicate the right temporo-parietal junction,
103 medial prefrontal cortex and precuneus as part of a core network for ToM (Saxe and Kanwisher
104 2003a; Saxe and Wexler 2005; Saxe 2006; Scholz et al. 2009; Young et al. 2010; Dodell-Feder
105 et al. 2011), whereas the role of the ATL is less clear and appears to be characterised as
106 ancillary by some accounts (van Overwalle 2009; Schurz et al. 2014; Molenberghs et al. 2016).
107 It is possible that a central role of the ventrolateral ATL has gone unnoticed because fMRI
108 studies of ToM typically do not account for technical constraints around this region.

109 We set out to address two key unresolved questions. First, we aimed to determine
110 whether and to what degree different parts of the ATL are activated by established theory of
111 mind tasks. This necessitated two key design elements: (i) the use of dual-echo fMRI and
112 distortion correction to ensure full coverage of the bilateral ATL; and (ii) the use of multiple
113 theory of mind tasks. This second design feature was important because showing common
114 activation across different theory of minds tasks with a variety of stimuli means that we can
115 more confidently assess whether activation can be attributed to ToM ability itself rather than
116 being the result of task demands or idiosyncratic features of the stimuli (Ross and Olson 2010).
117 In fMRI designs, the most commonly used theory of mind tasks include social vignettes,
118 cartoons, and animations that are intended to evoke the attribution of intentions. We used
119 animations as our primary task because they do not directly involve lexical-semantic
120 processing, and because they lend themselves to the creation of a comparable non-social (and
121 non-semantic) control or baseline activation task. We also acquired data during a False Belief
122 task (Dodell-Feder et al. 2011) and a free-viewing animated film (Jacoby et al. 2016) as these
123 are established paradigms for localising the ‘mentalising’ or theory of mind network.

124 Second, we set out to directly assess overlap of ToM related activation with activation
125 evoked by semantic decisions made upon nonverbal, non-social stimuli. Overlap, and

126 particularly overlap in the ventrolateral aspect, would support the hypothesis that activation of
127 the ATL during social tasks reflects the retrieval of semantic knowledge representations (Zahn
128 et al. 2007; Olson et al. 2013; Binney and Ramsey 2020). Specifically, we chose the picture
129 version of the Camel and Cactus task (CCT), which is an established means to engage and
130 measure semantic processing, and has been previously used in neuropsychological, functional
131 imaging and brain stimulation studies (Bozeat et al. 2000; Jefferies and Lambon Ralph 2006;
132 Hoffman et al. 2012; Visser et al. 2012). Further, via these means we were also able to directly
133 test three different accounts of the ATL, amongst a single cohort of participants, as follows:

134 1. The *Social Knowledge Hypothesis*: if this hypothesis, in which the ATL only represents
135 socially-relevant conceptual knowledge and not more general semantic information
136 (Simmons et al. 2010; Olson et al. 2013), is correct, then the ATL would activate for ToM
137 tasks but not during the CCT. Moreover, this activation might be specific to the
138 dorsolateral/polar ATL (the anterior superior and middle temporal gyri).

139 2. The *Dual ATL Hub account*: if a dual hub account is correct then the ToM tasks would
140 exclusively activate the dorsolateral/polar ATL and not the ventrolateral aspect, and the
141 CCT would only activate the ventrolateral ATL.

142 3. The *Graded ATL Semantic Hub Hypothesis*: if the third account, in which the ventral
143 ATL is the centre point of a domain-general hub for both social and non-social semantic
144 processes (Binney et al. 2016), is correct, then the greatest degree of overlap between the
145 ToM tasks and the CCT will be within the ventrolateral portion. We might also observe
146 dorsolateral activation that is more selective to social stimuli.

147

148 **Methods**

149 *Data Availability statement.* Following open science initiatives (Munafò et al. 2017),
150 behavioural and neuroimaging data are openly available on the Open Science Framework
151 project page (<https://osf.io/v2gt5/>).

152

153 *Design Considerations*

154 To ensure that the imaging protocol was sensitive to changes in activation across all
155 parts of the ATL, we used a dual-echo gradient-echo echo-planar imaging (EPI) fMRI sequence
156 that is optimised to detect blood oxygen level-dependent (BOLD) signal in areas of the brain
157 that are usually prone to magnetic susceptibility-induced signal loss (Halai et al. 2015). Further,
158 to alleviate the impact of geometric distortions and mislocalisations of fMRI signal also caused
159 by magnetic susceptibility artefacts, the dual-echo sequence was combined with a post-
160 acquisition k-space spatial correction (Embleton et al. 2010).

161 Secondly, we adapted stimuli created by Walbrin et al. (2018) to fashion a two
162 alternative force choice (AFC) task involving explicit social interaction judgements and that is
163 inspired by the widely used classical Heider and Simmel (1944) animations. Walbrin and
164 colleagues' stimuli were chosen because they offer a higher number of unique trials (impacting
165 sensitivity/power) than other similar stimuli, and they are visually well-controlled to minimize
166 the contribution of low-level visual information to brain responses (i.e., they are comprised of
167 visually diverse interactive scenarios that are well-matched for overall motion energy). In order
168 to control for attentional and executive demands involved in the main task, we reconfigured
169 these stimuli to further create a well-matched perceptual judgment task (see below).

170

171 *Participants*

172 Thirty-one healthy native English speakers took part in the experiment. All participants
173 had normal or corrected-to-normal vision, no history of neurological and psychiatric conditions

174 and were right-handed as established by the Edinburgh Handedness Inventory (Oldfield 1971).
175 Participants provided written informed consent, and the study was approved by the local
176 research ethics review committee. Seven participants were excluded because of inadequate task
177 performance (under 70% accuracy) on any one of the social interaction tasks (N=3), or because
178 of failed distortion correction and therefore insufficient data quality (N=4). The final analysed
179 sample comprised of twenty-four participants (12 females, $M_{age}= 22.21$, $SD_{age}= 2.13$).

180

181 *Experimental Stimuli and Tasks*

182 *Theory of Mind (ToM)*

183 A total of 126 unique video stimuli designed by Walbrin et al. (2018) were used for the
184 main interaction judgement theory of mind (IJ-ToM) task and its corresponding control task.
185 The IJ-ToM stimuli (N = 63) featured two self-propelled circles representing animate agents
186 that were intentionally interacting and doing so in a co-operative manner in half the trials and
187 a competitive manner in the other half (see **Supplementary Figure M1**). In Walbrin and
188 colleagues' original stimulus pool (N=256) half of the scenarios concluded with successful
189 goal outcome (e.g., successfully opening a closed door) and half with unsuccessful goal
190 outcomes. Here we only used a subset of the former. In the IJ-ToM task, participants were
191 instructed to make explicit inferential judgements, via a key press, as to whether the agents'
192 actions towards one another were friendly or unfriendly (unlike the original study that sought
193 to minimize the contribution of ToM judgements, by employing a perceptual response task).
194 The associated control task used 'scrambled' versions of the interaction stimuli (N = 63) that
195 preserved many of the visual properties but featured altered motion paths such that the shapes
196 did not appear to be intentionally interacting with each other or their environment (see Walbrin
197 et al. 2018). For the present study, these control stimuli were adjusted such that in fifty per cent
198 of trials the speed of motion of one of the two shapes was slower than that of the other. This

199 was done by slowing the frame rate of one of the animation elements (i.e., one of the circles)
200 from 24 to 18 frames per second and removing frames from either the beginning (50%) or end
201 of the sequence to maintain the original duration (6 secs). Moreover, we ensured that the more
202 slowly moving object appeared an equal number of times at each relative position on the screen
203 (e.g., left versus right). Participants responded to these stimuli via key press and indicated
204 whether they believed the circles were moving at same or different speeds. Following some
205 initial pilot behavioural testing, the duration of all 126 videos was shortened from 6 to 3 sec to
206 increase task difficulty/eliminate idle time.

207 We also acquired data with two widely used functional localisers for the putative ToM
208 network, namely the False Belief (FB) paradigm (Dodell-Feder et al. 2011) and a more recently
209 validated free-viewing movie paradigm (MOV) (Jacoby et al. 2016). The former is a verbal
210 paradigm which is comprised of two sets of 10 text-based vignettes each of which are presented
211 on screen and followed by true / false questions. One of these sets requires the participant to
212 make inferences about a character's internal beliefs, and this is contrasted against descriptions
213 of facts about physical events. The MOV paradigm involves passive viewing of a commercial
214 animated film and contrasts BOLD responses to events in which characters are involved in
215 ToM against those in which characters experience physical pain (see Jacoby et al. (2016) for
216 more detail).

217

218 *Non-Verbal Semantic Association*

219 Participants also completed a non-verbal version of an established neuropsychological
220 assessment of semantic associative knowledge known as the Camel and Cactus task (CCT;
221 (Bozeat et al. 2000)). This task has been used to engage the semantic network in prior fMRI
222 studies (Visser et al. 2012; Rice et al. 2018). The version used in the present study consisted of
223 36 trials that contained pictorial stimuli and required participants to make semantic associations

224 between a probe object (e.g., a camel) and a target object (e.g., a cactus) that was presented
225 alongside a foil from the same semantic category (e.g., a rose). The CCT was contrasted against
226 a perceptual control task (36 trials) that consisted of scrambled versions of the CCT pictures
227 and required participants to identify which of two choice pictures was visually identical to a
228 probe (see more detail in Visser et al. (2012)).

229

230 *Experimental Procedure*

231 Participants underwent all testing within a single session lasting approximately one
232 hour. Each individual completed three runs of the IJ-ToM procedure reported below, followed
233 by one run of the CCT procedure, two runs of the FB localiser and one run of the MOV
234 localiser. The IJ-ToM task, the CCT and the corresponding control tasks were presented via E-
235 prime (Psychology Software Tools, 2017) and all other tasks were implemented via
236 Psychtoolbox (Brainard 1997; Pelli 1997) software. Behavioural responses were recorded
237 using an MRI compatible response box.

238

239 *Interaction Judgement ToM Task*

240 The IJ-ToM task and the speed judgement task were paired within a run using an A-
241 rest-B-rest box car block design. Each run contained six blocks per task and three trials per
242 block (18 trials per run per task). There were an equal number of trial types (e.g., *cooperative*
243 versus *competitive*) randomly distributed across blocks within a given run. Both types of active
244 blocks were 17.25 secs long and they were separated by blocks of passive fixation lasting 12
245 secs each. Each trial began with a fixation cross (duration = 500ms) which was followed by
246 the target animation (3000ms) and finished with a response cue (three question marks;
247 2000ms). A blank screen occupied an inter stimulus interval of 250ms. Each run lasted 5
248 minutes and 51 secs and consisted of unique sets of animations. The order in which these runs

249 were completed was counterbalanced across participants. Participants also completed three
250 practice blocks for each of the two tasks before the main runs began.

251

252 *Camel and Cactus Task*

253 The CCT and the corresponding perceptual identity matching control task were
254 alternated within a single run using a blocked design. There were 9 blocks per task, each
255 consisting of four trials (totalling 36 trials per task) and lasting 20 secs. A trial began with a
256 fixation cross (500ms) followed by a stimulus triad (4500ms). Participants responded via key
257 press while the probe and choice items were on screen. Active blocks were separated by brief
258 rest blocks lasting 4000ms and, overall, the run lasted for 7 mins and 12 secs.

259

260 *False Belief and animated movie localisers*

261 Each run of the false belief localiser lasted 4 minutes and 32 seconds and consisted of
262 10 trials of belief vignettes and 10 trials of the fact vignettes. Finally, the passive MOV
263 scanning run lasted 5 mins and 59 seconds including a fixation period of 10 secs prior to the
264 beginning of the movie. Further details regarding these paradigms are reported by Jacoby et al.
265 (2016).

266

267 *Imaging Acquisition*

268 All imaging was performed on a 3T Phillips Achieva MRI scanner with a 32-element
269 SENSE head coil using a 2.5 sense factor for image acquisition. The parameters of the dual-
270 echo gradient-echo EPI fMRI sequence were the following: 31 axial slices covering the whole
271 brain and obtained in an ascending sequential order with a first echo time (TE) = 12ms and
272 second TE = 35ms, repetition time (TR) = 2000ms, flip angle = 85°, FOV (mm) = 240 × 240
273 × 124, slice thickness = 4 mm, no interslice gap, reconstructed voxel size (mm) = 2.5 × 2.5 and

274 reconstruction matrix = 96×96 . Prior to image acquisition for each run, we acquired five
275 dummy scans to allow the initial magnetisation to stabilise. This was followed by acquiring
276 177 volumes for each IJ-ToM task run, 218 volumes for the CCT task run, 136 volumes for
277 each FB task run and 180 volumes for the MOV task run. Adhering to the distortion-correction
278 method, we acquired these functional runs with a single direction k space traversal in the left-
279 right phase-encoding direction. We also acquired a short EPI “pre-scan” with the participants
280 at rest. The parameters of the pre-scan matched the functional scans except that it included
281 interleaved dual direction k space traversals. This gave 10 pairs of images with opposing direction
282 distortions (10 left-right and 10 right-left) which were to be used in the distortion correction
283 procedure described below. To check the quality of the distortion corrected images, we
284 obtained a high resolution T2-weighted scan consisting of 36 slices covering the whole brain,
285 with TR= 17ms, TE= 89ms; reconstructed voxel size (mm) = $0.45 \times 0.45 \times 4$; reconstruction
286 matrix= 512×512 . Additionally, we used a T1-weighted 3D imaging sequence to acquire an
287 anatomical scan, consisting of 175 slices covering the whole brain, for use in spatial
288 normalisation procedures. The parameters of this scan were as follows: P reduction (RL)
289 SENSE factor of 2 and S reduction (FH) SENSE factor of 1, TR = 18ms, TE = 3.4ms, 8° flip
290 angle, reconstructed voxel size (mm) = $0.94 \times 0.94 \times 1.00$ and reconstruction matrix = $240 \times$
291 240.

292

293 *Data Analysis*

294 *Behavioural Data*

295 Incorrectly answered trials, missed trials and trials with response latencies that were
296 two standard deviations above or below the participant’s task mean were excluded from
297 analyses of behavioural data. Task performance was assessed in terms of both accuracy and
298 decision times and compared using paired-sample T-tests. Average decision times per block of

299 each task were also calculated so that they could be used as regressors of no interest in fMRI
300 analyses.

301

302 *Distortion Correction and fMRI pre-processing*

303 A spatial remapping correction was computed separately for images acquired at the
304 long and the short echo time, and using a method reported elsewhere (Embleton et al. 2010).
305 This was implemented via in-house MATLAB script (available upon request) as well as
306 SPM12's (Statistical Parametric Mapping software; Wellcome Trust Centre for Neuroimaging,
307 London, UK) 6-parameter rigid body registration algorithm. Briefly, in the first step, each
308 functional volume was registered to the mean of the 10 pre-scan volumes acquired at the same
309 echo time. Although this initial step was taken primarily as part of the distortion correction
310 procedure, it also functioned to correct the time-series for differences in subject positioning in
311 between sessions and for minor motion artefacts within a session. Next, one spatial
312 transformation matrix per echo time was calculated from opposingly-distorted pre-scan
313 images. These transformations consisted of the remapping necessary to correct geometric
314 distortion and were applied to each of the main functional volumes. This resulted in two
315 motion- and distortion-corrected time-series per run (one per echo) which were subsequently
316 combined at each timepoint using a simple linear average of image pairs.

317 All of the remaining pre-processing steps and analyses were carried out using SPM12.
318 Slice-timing correction referenced to the middle slice was performed on the distortion- and
319 motion-corrected images. The T1-weighted anatomical scan was co-registered to a mean of the
320 functional images using a 6-parameter rigid-body transform, and then SPM12's unified
321 segmentation and normalisation procedure and the DARTEL (diffeomorphic anatomical
322 registration through an exponentiated lie algebra; (Ashburner 2007)) toolbox were used to
323 estimate a spatial transform to register the structural image to Montreal Neurological Institute

324 (MNI) standard stereotaxic space. This transform was subsequently applied to the co-registered
325 functional volumes which were resampled to a 3 x 3x 3 mm voxel size and smoothed with an
326 8 mm full-width half-maximum Gaussian filter.

327

328 *fMRI Statistical Analysis*

329 Data were analyzed using the general linear model approach (GLM). At the within-subject
330 level, a fixed effect analysis was carried out upon each task pair (e.g., the interaction judgement
331 task and the perceptual control task), incorporating all functional runs within a single GLM.
332 Block onsets and durations were modelled with a boxcar function and convolved with the
333 canonical hemodynamic response function. A high pass filter with a cut off of 128s was also
334 applied. The extracted motion parameters were entered into the model as regressors of no
335 interest. Decision time data were also modelled to account for differences in task difficulty.
336 Due to the block design employed, there was a single value for each epoch of a task which was
337 the average of response times across the trials. These average decision times for each block
338 were mean centred. To avoid false positive activations in the surrounding CSF due to
339 physiological noise, we used an explicit mask restricted to cerebral tissue that was created from
340 tissue segments generated by DARTEL in MNI space and binarised with a 0.4 threshold.

341 At the level of multi-subject analyses, we first examined activation during the IJ-ToM
342 task at the whole brain level. Then, to quantify the degree to which different ATL subregions
343 are activated, we performed an a priori region of interest (ROI) analysis using the SPM
344 MarsBar toolbox (Brett et al. 2002). A key aim of this study was also to assess whether parts
345 of the ATL are commonly activated by different types of behavioural paradigm used to localise
346 the putative ToM network. To do this we performed a formal conjunction analysis (Price and
347 Friston 1997; Nichols et al. 2005a). In addition to our interacting geometric shapes paradigm,
348 this included a version of False Belief task (Dodell-Feder et al. 2011) which is comprised of

349 verbal vignettes, and a free-viewing movie paradigm (Jacoby et al. 2016). This analysis was an
350 important step because it would enable us to home in on those regional activations that are a
351 feature of ToM abilities irrespective of the manner in which they are probed. Moreover, if one
352 is to compare ToM tasks that are qualitatively very different from one another, it is possible to
353 attribute the common activations much more convincingly to the particular cognitive process
354 of interest, as opposed to similarities in physical stimulus properties or peripheral elements of
355 the task demands (Friston et al. 1999). Using a further conjunction analysis we also explored
356 overlap between the IJ-ToM task and a nonverbal semantic association task. This enabled us
357 to test the hypothesis that activation of the ATL during social tasks reflects the retrieval of
358 semantic knowledge representations (Zahn et al. 2007; Olson et al. 2013; Binney and Ramsey
359 2020).

360 Whole-brain multi-subject random effects analyses were conducted on each of the
361 following contrasts of interest: IJ-TOM task: interaction > speed judgements, interaction
362 judgements > rest, speed judgements > interaction judgements; CCT task: semantic >
363 perceptual judgements; FB task: false belief > false fact judgements; MOV task: mentalizing
364 > pain. One-sample t-tests were performed on all sets of contrast images following application
365 of the same explicit mask as used in the single subject analyses. The resulting statistical maps
366 were assessed for cluster-wise significance using a cluster-defining voxel-height threshold of
367 $p < .001$ uncorrected, and family-wise error (FWE) corrected cluster extent threshold at $p < .05$
368 (calculated per SPM12 under the random field theory framework; see details regarding
369 smoothness of data, the search volumes and RESELS in **Supplementary Table M1**).
370 Thresholded maps were overlaid on a MNI152 template brain using MRICroGL
371 (<https://www.nitrc.org/projects/mricrogl>). We used an AAL atlas implemented in R label4MRI
372 package (<https://github.com/yunshiuian/label4MRI>) to guide the labelling of peak co-ordinates
373 in the output tables.

374 Within the ROI analysis, (Brett et al. 2002) two ATL subregions were explored in each
375 hemisphere. A ventrolateral ATL ROI was defined by peak coordinates of activation reported
376 by an independent study of non-verbal semantic processing (Visser et al. 2012) [MNI: +/- 57,
377 -15, -24]. We also examined a polar ATL ROI which was defined on the basis of activation
378 tuned towards socially-relevant semantic stimuli as reported by Binney et al. (2016) [MNI: +/-
379 48, 9, -39]. Furthermore, so that we could compare the degree of ATL activation to that of a
380 more established ToM region, we defined a third ROI on the basis of ToM-related TPJ
381 activation reported by Saxe and Kanwisher (2003b) [+/- 54, -60, 21]. These sets of coordinates
382 defined a centre of mass for spheres with a radius of 10mm (See **Figure 1 panel B** for an
383 illustration of ROI locations). Per subject, a single summary statistic was calculated to represent
384 activation across all the voxels in an ROI (the mean of the parameter estimates) for the IJ-ToM
385 task relative to the speed judgment control task. One-sample t-tests were then performed to
386 assess group-level significance. To control for multiple comparisons, *p*-values were Bonferroni
387 corrected on the basis of the number of ROIs (multiplied by 6) as implemented in MarsBar.
388 We also conducted planned comparisons between ROIs in each hemisphere, and between
389 hemispheric homologue regions, using paired t-tests. For the conjunction analyses, we used a
390 $p < .001$ uncorrected voxel height threshold to be achieved by each contrast independently prior
391 to conjunction (Price and Friston 1997; Nichols et al. 2005a).

392

393 **Results**

394 ***Behavioural Data***

395 Mean accuracy and decision times for all tasks are displayed in **Table 1**. Performance
396 on the animated interaction friendliness judgement (IJ ToM task) was more accurate than on
397 the speed judgement control task ($t(23) = 7.50, p < .001$, Cohen's $d = 1.53$), and decision times
398 were also faster ($t(23) = -3.08, p = .005, d = 0.63$). Performance during semantic association

399 judgements (CCT task) was less accurate than performance in the perceptual identity matching
400 control task ($t(23) = -8.83, p < .005, d = -1.80$), although there was no significant difference in
401 the latency of decision times ($t(23) = -0.65, p = .522, d = -0.13$). Accuracy across the false belief
402 and false facts judgments (FB task) was comparable ($t(23) = 0.77, p = .450, d = 0.16$) although
403 decision times were faster in the false fact task ($t(23) = 2.73, p = .012, d = 0.56$).

Table 1. Behavioural data

Task	Accuracy (%)	Decision time (ms)
Interaction Friendliness Judgement	96.37 (04.35)	468.38 (125.44)
Perceptual Speed Judgement	84.88 (07.62)	524.25 (159.84)
Semantic Association Judgement	79.75 (17.84)	1491.92 (382.65)
Perceptual Identity Matching	92.59 (19.96)	1529.76 (460.57)
False Belief Judgement	70.42 (19.67)	2779.56(385.47)
False Fact Judgement	67.92 (15.87)	2560.31(354.64)

Standard deviations stated in parentheses

404 **Activation During a Social Attribution Task Given Full Temporal Lobe Coverage**

405 A whole brain univariate analysis contrasting social interaction friendliness judgments
406 with the matched speed judgement task revealed robust bilateral ATL activation that was
407 centred over the ventrolateral aspects in both hemispheres (see **Figure 1, panel A and Table**
408 **2**). In the left hemisphere, this extended from the ventrolateral temporopolar cortex (BA38),
409 along the inferior middle temporal gyrus and inferior temporal gyrus (ITG), to approximately
410 halfway along the temporal lobe ($y \approx -17$). This included a maxima that is notably similar in
411 location (MNI coordinates $x = -54, y = 6, z = -39$) to that identified in association with
412 processing of abstract social concepts (relative to matched abstract non-social concepts; $x = -$
413 $54, y = 9, z = -33$ and animal function concepts; $x = -48, y = 9, z = -39$) by Binney et al. (2016).
414 The same cluster also extended more posteriorly upon the basal surface and along the

415 fusiform/lingual and posterior inferior temporal gyri. It also traversed up into the parietal lobe
 416 and the intraparietal sulcus. In the right hemisphere, ATL activation also covered much of the
 417 ventrolateral surface (particularly the polar cortex and the anterior-most portion of the middle
 418 temporal gyrus (MTG) but extended less posteriorly (to $y \approx -11$) than it did in the left.

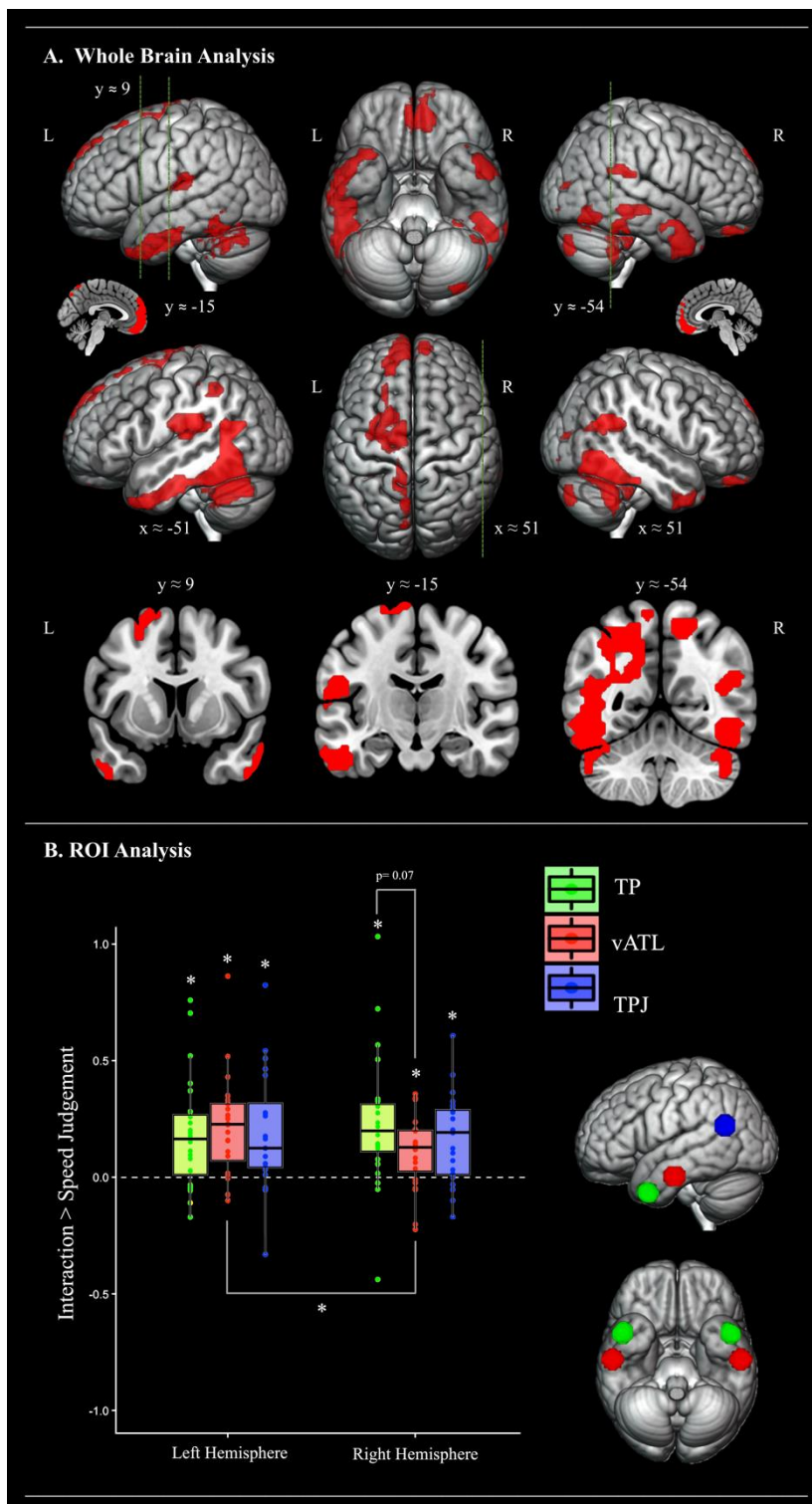


Figure 1. Panel A. Cortical regions activated during the main experimental ToM task (the interaction judgement), relative to the speed judgement control task. The statistical map was thresholded with an uncorrected voxel height threshold of $p < .001$ and a family wise error corrected minimum cluster extent threshold ($k = 152$) at $p < .05$. Cross-sections were chosen to display the location of activation found in key studies investigating ToM processing (Saxe & Kanwisher, 2003; right TPJ [51, -54, 27]), semantic processing of social concepts (Binney, Hoffman & Lambon Ralph, 2016; left TP [-48, 9, -39]) and general semantic processing (Visser, Jefferies, Embleton & Lambon Ralph, 2012; left inferior ATL [-57, -15, -24]). Panel B. Summary of the ROI analyses comparing the magnitude of activation for the interaction judgement ToM task (relative to that during speed judgments control task). An asterisk denotes a significant effect at $p < .05$ after Bonferroni correction. Numerical p -values are displayed where comparisons yielded a p -value greater than .05 but less than .1. TP = temporal pole, vATL = ventrolateral anterior temporal lobe, TPJ = temporo-parietal junction, L = left, R = right.

419 Outside of the ATL, and as expected, this contrast also revealed activation amongst key
420 nodes of the putative ToM network, including the temporoparietal junction (TPJ), the medial
421 prefrontal cortex (mPFC) and the precuneus (Frith and Frith 2003, 2006; Saxe and Kanwisher
422 2003b; van Overwalle 2009; Jacoby et al. 2016). TPJ activation was observed in both
423 hemispheres at the position of the posterior superior temporal sulcus/gyrus (STS/STG) and, in
424 the right hemisphere, it extended to more posterior regions (at $y \approx -54$) that are frequently
425 emphasized in landmark studies (Saxe and Kanwisher 2003b; Saxe and Powell 2006) and large
426 scale meta-analyses (Schurz et al. 2014; Molenberghs et al. 2016) of the theory of mind
427 network. Further activation was revealed in the left posterior MTG, the left insula, and bilateral
428 temporooccipital and cerebellar regions.

429 Activation during the social interaction friendliness judgments was also contrasted with
430 passive fixation/rest. There was notably little activation in the ATLs, except for a small cluster
431 in the left superior temporal pole (see **Supplementary Figure 1** and **Supplementary Table**
432 **R1**). This is consistent with the idea that there is automatic semantic activation (e.g., mind-
433 wandering) during periods of passive fixation, and it demonstrates the importance of using
434 active baseline tasks for detecting ATL activation which has been highlighted in prior meta-
435 analyses and empirical investigations (Binder et al. 1999, 2009; Visser, Jefferies, et al. 2010).
436 Outside of this region there was robust bilateral fronto-parietal activation including of the
437 bilateral TPJ and the ventrolateral prefrontal cortex, and activation of the mPFC, the precuneus,
438 and temporooccipital and cerebellar regions. The contrast revealing greater activation for the
439 speed judgment relative to the social attribution task is reported in **Supplementary Figure 2**
440 and **Supplementary Table R2** and revealed the right middle frontal gyrus and a number of
441 midline structures.

442

Table 2 Significant activation clusters in the social interaction judgement > speed judgement contrast ($p < .05$, FWE-corrected, corresponding to an extent threshold of $k = 152$ following a cluster-defining threshold of $p < .001$, uncorrected)

Cluster Name and Location of Maxima	Cluster Extent (voxels)	Peak (Z)	MNI Coordinates (mm)		
			x	y	z
L temporal – parietal – occipital	2242				
anterior ITG / sulcus		5.72	-57	-6	-30
anterior ITG		5.26	-54	6	-39
posterior ITG		5.07	-51	-51	-24
precuneus		4.78	-12	-60	42
posterior ITG		4.76	-45	-60	-9
inferior parietal lobule		4.68	-39	-51	45
precuneus		4.49	-9	-75	48
middle/anterior ITG		4.42	-48	-21	-27
posterior MTG		4.23	-48	-54	3
cerebellum		4.21	-51	-51	-36
posterior MTG		4.10	-39	-60	15
anterior MTG/TP		4.04	-42	18	-42
R temporal – parietal – occipital	1708				
inferior occipital gyrus		5.52	48	-63	-12
occipital pole		5.01	30	-90	-6
middle occipital gyrus		4.74	33	-75	3
posterior MTG		4.39	63	-36	-9
cerebellum		4.35	36	-42	-33
cerebellum		4.29	27	-78	-42
cerebellum		4.28	36	-84	-39
posterior STG/TPJ		4.26	57	-39	21
cerebellum		4.24	42	-48	-30
posterior STS/TPJ		4.22	42	-60	18
cerebellum		4.21	45	-51	-42
middle occipital gyrus		4.05	39	-81	12
Bilateral frontal	1017				
L anterior SFG		5.46	-3	63	21
R anterior orbital gyrus		5.30	9	45	-24
R anterior gyrus rectus		5.21	6	51	-18
L middle SFG		5.08	-12	60	27
L middle SFG		4.93	-12	57	36
R middle SFG		4.81	3	60	30
R anterior mPFC		4.77	9	63	-9
R anterior mPFC		4.77	3	57	-6
R anterior mPFC		3.45	3	60	6
L temporal-parietal	362				
superior parietal lobule		4.65	-54	-27	18
middle STG		3.60	-63	-15	9
R anterior temporal	160				
anterior MTG		4.57	60	6	-33

anterior ITG		4.54	51	12	-45
anterior MTG/TP		3.97	51	18	-39
anterior MTG/TP		3.54	45	24	-39
anterior MTG		3.37	60	-9	-24
L dorsal frontal	410				
middle superior frontal sulcus		4.38	-24	3	60
posterior superior frontal sulcus		4.29	-24	0	48
posterior SFG		4.15	-12	-12	78
posterior superior frontal sulcus		4.01	-30	-6	63
posterior SFG		3.30	-21	27	60
R parietal	152				
superior postcentral gyrus		4.29	24	-42	57
superior parietal lobule		4.09	18	-57	60
precuneus		3.32	9	-63	54

The table shows up to 12 local maxima per cluster more than 8.0 mm apart. L= left; R= right; ITG = inferior temporal gyrus; TP= temporal pole; MTG= middle temporal gyrus; TPJ= temporo-parietal junction; AG= angular gyrus; SFG = superior frontal gyrus; mPFC= medial frontal cortex; STS= superior temporal sulcus;

443 We used an a priori ROI-based approach to compare the magnitude of regional
 444 responses to the social attribution task both within each hemisphere and between hemispheric
 445 homologues. We focused upon two key ATL subregions, the temporopolar cortex and the
 446 posteriorly adjacent ventrolateral surface, as well as temporo-parietal cortex (i.e., the TPJ)
 447 frequently implicated in theory of mind. The positions of these ROIs and the results are
 448 displayed in **Figure 1, panel B**. Bonferroni-corrected one-sample T-tests revealed significant
 449 activation during social interaction judgements in the left vATL ($t(24) = 5.09$, Cohen's $d =$
 450 1.04), temporal pole ($t(24) = 3.77$, Cohen's $d = .77$) and TPJ ($t(24) = .20$, Cohen's $d = .04$)
 451 and also the right vATL ($t(24) = 3.57$, Cohen's $d = .73$), temporal pole ($t(24) = 4.03$, Cohen's
 452 $d = .82$) and TPJ ($t(24) = .17$, Cohen's $d = .04$) (all $p < .005$). Numerically speaking, across all
 453 the ROIs, the left vATL revealed the largest effect size, and the TPJ showed the weakest effects.
 454 Planned statistical comparisons (see **Supplementary Table R3**) confirmed greater activation
 455 in the left as compared to the right vATL ($t(24) = 2.45$, $p = .02$, Cohen's $d = .50$). There were
 456 no other significant pairwise differences.

457 ***Common Activation of the ATL Across Three Different ToM Paradigms***

458 In the subsequent analysis, we aimed to map out subregions of the bilateral ATL in
459 which there is overlapping activation between some of the different types of behavioural
460 paradigm used to localise the putative ToM network (Dodell-Feder et al. 2011; Jacoby et al.
461 2016). The results of independent whole-brain analyses contrasting two further ToM tasks (the
462 False Belief task and the free-viewing movie paradigm) with their respective control tasks are
463 reported in **Supplementary Figures 3 and 4 and Supplementary Tables R4 and R5**. We
464 formally assessed activation overlap between the three ToM tasks using a conjunction analysis
465 performed across the whole brain (Nichols et al. 2005b). For complete visualisation of the
466 results and to capture the full extent of both the overlap and divergence in the topography of
467 activation, the three whole brain activation maps are overlaid on each other in **Figure 2 panel**
468 **A**, whereas a map limited to the formal statistical conjunction can be found in **Supplementary**
469 **Figure 5 and Supplementary Table R6**. Regarding ATL activation, the conjunction analysis
470 revealed three-way overlap between the ToM tasks exclusively within the left ventrolateral
471 ATL. This extended over the anterior ITG and MTG from about $y \approx -7$ to $y \approx 9$ and is also
472 strikingly similar to ATL regions reported as activated by social concepts by (Binney, et al.
473 2016). As would be expected from prior literature, 3-way overlap was also observed in the
474 mPFC and bilateral TPJ.

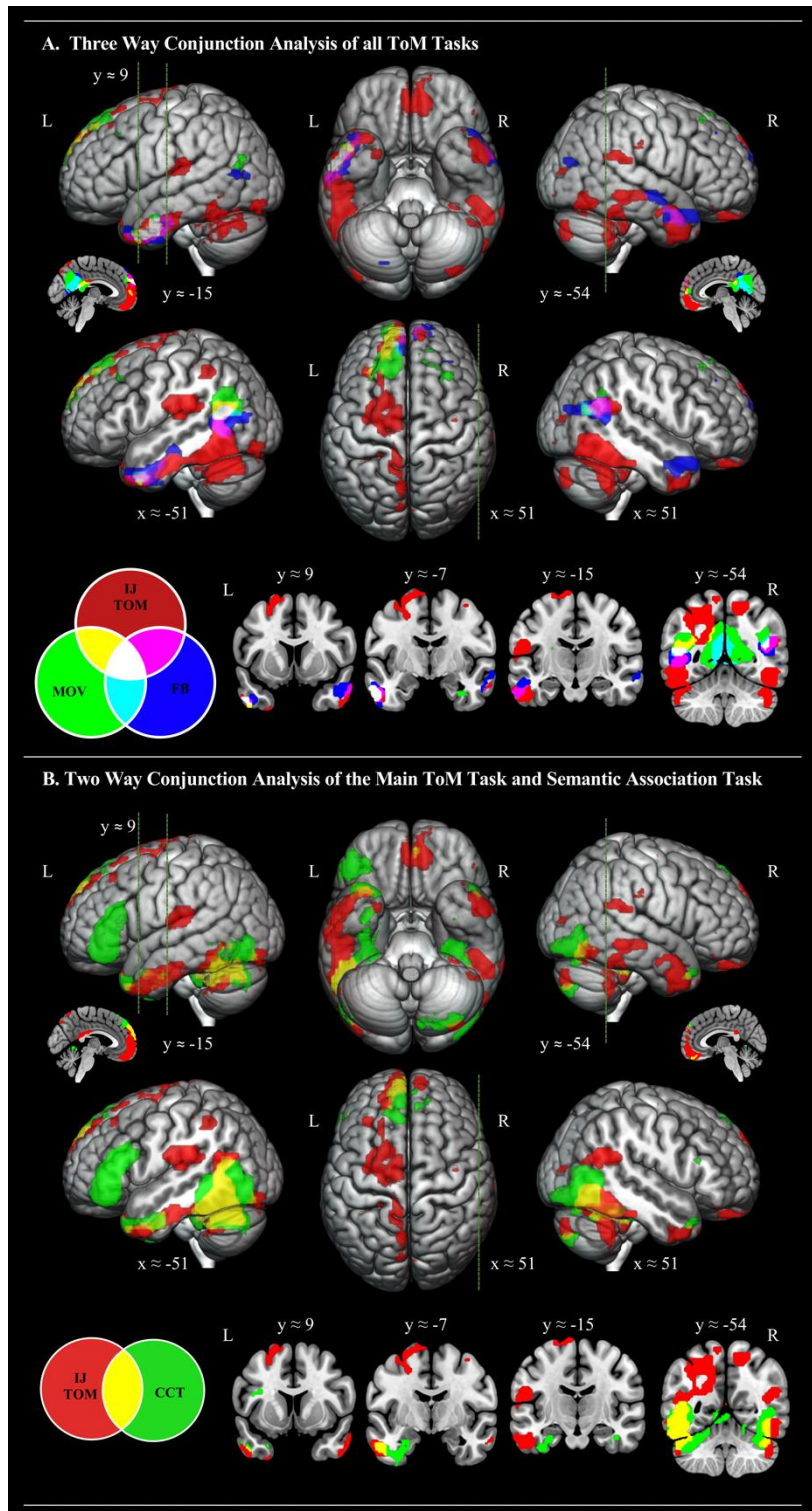


Figure 2. Panel A. Topological overlap of cortical regions activated by the interaction judgement > speed judgement contrast, the false belief story > photograph contrast, and the mentalising > pain contrast from the free-viewing movie localiser. Each of the three statistical maps were independently thresholded with an uncorrected voxel height threshold of $p < .001$ and then overlaid within MRICron using additive colour blending. White patches indicate three-way overlap between all three ToM contrasts. **Panel B.** Topological overlap of cortical regions activated by the interaction judgement > speed judgement contrast (red), and the nonverbal semantic association (Camel and Cactus task) > perceptual judgement contrast (green). The two statistical maps were independently thresholded with an uncorrected voxel height threshold of $p < .001$ and then overlaid within MRICron using additive colour blending. Yellow patches indicate overlap between theory of mind and general semantic processing. Cross-sections were chosen to display the location of activation found in key studies investigating ToM processing (Saxe & Kanwisher, 2003; right TPJ [51, -54, 27]), semantic processing of social concepts (Binney, Hoffman & Lambon Ralph, 2016; left TP [-48, 9, -39]) and general semantic processing (Visser, Jefferies, Embleton & Lambon Ralph, 2012; left inferior ATL [-57, -15, -24]), as well one further key area of 3-way overlap ($y = -7$).

475 **ATL Activation Common to both ToM and General Semantic Processing**

476 Finally, we performed a conjunction analysis aimed at identifying any potential overlap

477 between ATL regions engaged by theory of mind tasks and those engaged by general semantic

478 processing. The same sample of participants and the same ATL-optimised dual-echo imaging
479 sequence were used to acquire fMRI data while individuals completed a nonverbal semantic
480 association task. The result of an independent whole-brain analysis contrasting this task with
481 a matched control task is reported in **Supplementary Figure 6** and **Supplementary Tables**
482 **R7**. This contrast was entered into a whole brain conjunction analysis along with the interacting
483 geometric shapes paradigm. The full extent of overlap and divergence between ToM activation
484 and general semantic activation is displayed in **Figure 2 panel B**, while the results of the formal
485 statistical conjunction are found in **Supplementary Figure 7** and **Supplementary Table R8**.
486 Both theory of mind and general semantics activated the left ventrolateral ATL. Specifically,
487 there was a cluster of 114 commonly activated voxels in the left ventral ATL with the activation
488 starting to converge at $y \approx -15$, showing the most robust overlap at $y \approx -7$, and still overlapping
489 in inferior polar regions at $y \approx 9$. There was a further common ATL activation (extent = 32
490 voxels) within the left medial temporal pole. On the basis of this analysis, the right ATL
491 appeared only to be activated by the IJ-ToM task. Outside of the ATL region, there was also
492 overlap in the left pMTG and TPJ region, as well as the left mPFC and bilateral inferior
493 temporo-occipital regions.

494

495 **Discussion**

496 The present study was aimed at evaluating alternative accounts of the role of the anterior
497 temporal lobes (ATL) in social cognition. One account, the *social knowledge hypothesis*,
498 proposes that this region serves a domain-specific mnemonic role exclusively representing
499 socially-relevant semantic information (Simmons et al. 2010; Olson et al. 2013). Further, this
500 proposal particularly emphasises the dorsolateral and polar subregions of this relatively large
501 and structurally heterogenous area (Zahn et al. 2007; Ross and Olson 2010). Another
502 hypothesis, which we refer to as the ‘*dual hub*’ account, distinguishes between two separate

503 ATL hubs, one for social semantic and one for general semantic processing. Alternatively, the
504 *graded semantic hub* hypothesis, holds that the ATL is a unified domain-general conceptual
505 hub involved in the representation of all manner of conceptual-level knowledge (Binney, et al.
506 2016; Lambon Ralph et al. 2017). According to this account, the ventrolateral ATL is a critical
507 centre-point for general semantic knowledge representation. Other ATL sub-regions, including
508 the dorsolateral surface and the poles, are characterised as having connectivity-driven graded
509 variations in semantic function, including a ‘sensitivity’ to information that is perceived
510 primarily within certain sensorimotor modalities and/or has a particular behavioural (e.g.,
511 social) relevance (Plaut 2002; Visser and Lambon Ralph 2011; Binney et al. 2012; Binney et
512 al. 2016). The key findings of the present study were as follows:

- 513 1. By using distortion-corrected dual-echo fMRI, we were able to confirm, within a
514 whole-brain analysis, that the bilateral ventrolateral ATL is engaged by a nonverbal
515 task of the kind that has frequently been employed to localise the putative theory of
516 mind network. A region of interest analysis revealed that the left ventrolateral ATL was
517 more activated than the right homologue, and both these regions were as robustly
518 activated as the TPJ which is another key node in the theory of mind network.
- 519 2. Moreover, the left ventrolateral ATL activation was confirmed as a key feature of
520 theory of mind by the fact that it was activated robustly across three different paradigms
521 employing a range of verbal and nonverbal stimuli.
- 522 3. Finally, the left ATL activation associated with theory of mind greatly overlapped with
523 that evoked by semantic association judgements performed on non-social picture
524 stimuli.

525 Overall, these findings support the hypothesis that the ATL is a domain-general conceptual
526 hub and suggest that its contribution to social cognition is specifically related to the retrieval

527 of a broad class of semantic knowledge representations (Binney and Ramsey 2020). These
528 findings are not compatible with the social knowledge hypothesis nor the dual hub hypothesis.
529

530 *The Functional Contribution of ATL Subregions to Social and Semantic Cognition*

531 A link between certain parts of the ATL (e.g., temporopolar cortex; for a review see
532 Olson et al. 2013) and social cognition has been recognised for well over a century, owed in
533 part to the acclaimed work of Brown and Schafer (1888) and, later, Klüver and Bucy (1937)
534 who performed bilateral ATL resection in non-human primates. These investigations are best
535 known for the profound post-operative changes in social behaviour, including emotional
536 blunting and hypersexuality. However, Klüver and Bucy's primary aims were to establish
537 whether these bilateral lesions led to high-level perceptual deficits, namely visual and auditory
538 associative agnosias or, as referred to by these authors, 'psychic blindness'. Indeed, this set of
539 studies detail a broad symptom complex that was chiefly characterised by a failure to generate
540 the meaning of visual and auditory stimuli. Therefore, it appears that their subjects were
541 exhibiting multimodal semantic deficits that might explain, and not just co-present with, the
542 social-affective disturbances.

543 In more recent years, the social neurosciences have seen another rise in interest
544 regarding the specific role played by the ATL (for a review see Olson et al. 2013). In particular,
545 there emerged the *social knowledge hypothesis*, which states that this region supports a domain-
546 specific class of semantic knowledge: social concepts (Zahn et al. 2007; Ross and Olson 2010;
547 Simmons et al. 2010). Although this account acknowledges supporting evidence from within
548 comparative and behavioural neurology, it is primarily based on functional neuroimaging data
549 which specifically points to the dorsolateral and polar ATL (also see Zahn et al., 2007).

550 Another long-standing series of studies have implicated the ATL in more general forms
551 of semantic processing (Lambon Ralph et al. 2017). These include detailed neuropsychological

552 investigations of a disorder known as semantic dementia (SD). The SD syndrome falls within
553 the spectrum of frontotemporal dementia and exhibits relatively focal atrophy and
554 hypometabolism centred on the bilateral anterior temporal lobes (Mummery et al. 2000; Nestor
555 et al. 2006). This is coupled with a progressive, central impairment of semantic memory that
556 is evident in both expressive and receptive semantic tasks, and across all modalities including
557 spoken and written language, object use, picture-based tasks, environmental sound tasks, and
558 in olfaction and taste (Hodges and Patterson 2007; Luzzi et al. 2007; Patterson et al. 2007;
559 Piwnica Worms et al. 2010). Moreover, this human disorder displays striking parallels to the
560 observations of Klüver and Bucy, in that the multimodal semantic deficit is accompanied by a
561 range of socio-affective deficits, which include impaired emotion recognition and empathy,
562 impaired capacity for ToM, and a loss of person-specific knowledge (Edwards-Lee et al. 1997;
563 Binney et al. 2016; Snowden et al. 2018; Ding et al. 2020). This patient evidence is bolstered
564 by a now extensive set of multi-method studies that used electrophysiological recordings,
565 neurostimulation techniques (TMS/tDCS) and/or functional neuroimaging in neurotypical
566 samples (Marinkovic et al. 2003; Pobric et al. 2008; Binney et al. 2010; Chan et al. 2011;
567 Binney and Lambon Ralph 2015; Shimotake et al. 2015) all of which point to a role of the ATL
568 in general semantic processing. However, as compared to the social knowledge hypothesis, this
569 literature has converged upon a different subregion, the ventrolateral ATL, as the critical
570 substrate for semantic knowledge representation. This includes the findings of ATL-optimised
571 fMRI studies and the data from SD which reveals that the ventrolateral ATL is, alongside the
572 temporopolar regions, the most atrophied ATL subregion in this disorder (Galton et al. 2001;
573 Binney et al. 2010; Mion et al. 2010). Moreover, it is noteworthy that Klüver and Bucy (1939)
574 also remarked that the symptoms they observed in non-human primate's failed to appear after
575 resections limited to the dorsolateral convolutions of the temporal lobe. Nor did they present
576 after severing connections of the temporal lobe to the frontal or to the occipital lobes.

577 The findings of the present study are most compatible with this second set of
578 observations and implicate the ventrolateral ATL in both social and general semantic
579 processing. To our knowledge, they represent the first firm demonstration using fMRI of
580 ventrolateral ATL activation during the types of social (and more specifically, theory of mind)
581 paradigms that are typically employed in the social neuroscience literature. This ATL
582 subregion is frequently missing from fMRI studies probing theory of mind because of
583 methodological considerations we were able to overcome (see below). The fact that three very
584 different theory of mind paradigms evoked ventrolateral ATL activation suggest that it is a
585 feature of ToM irrespective of the paradigm with which it is probed and therefore that it reflects
586 a core cognitive component of theory of mind. Moreover, the fact that this activation
587 overlapped directly with that evoked by a set of non-social semantic judgements is consistent
588 with the claim that engagement of the ATL by social tasks reflects access to a broad class of
589 domain-general conceptual representations (Binney and Ramsey 2020).

590 Our results complement recent studies that found evidence of a role of the left
591 ventrolateral ATL in accessing abstract social concepts (Binney et al. 2016; Rice et al. 2018)
592 as well as other forms of social conceptual knowledge such as person semantics (Rice et al.
593 2018). The fact that we were able to demonstrate ventrolateral ATL activation in response to
594 both nonverbal (the interacting shapes task) and verbal (the false belief vignettes) theory of
595 mind tasks is consistent with the notion that the ventrolateral ATL is a supramodal hub engaged
596 in semantic retrieval irrespective of the sensory, motor or linguistic modality through which
597 concepts are probed (Lambon Ralph et al. 2017).

598 The dorsal ATL subregion previously implicated in domain-specific representation of
599 social conceptual knowledge (e.g. Zahn et al. 2007) was notably absent within our main set of
600 contrasts. One possible explanation for this is the fact that we did not compare the interacting
601 shapes task to a matched non-social but nonetheless semantic task, which would be the required

602 contrast to reveal activation associated with category-specific social semantic representations.
603 We did contrast semantic judgments made on social and non-social stimuli in two prior studies,
604 and these revealed a sensitivity of activation to social stimuli in the polar ATL (Binney et al.
605 2016; Rice et al. 2018). However, these findings do not support a dual hub account of the ATL
606 in which there are functional subdivisions and discrete activations for difference classes of
607 concept. Instead, they were in alignment with a ‘graded hub’ account in which the whole ATL
608 comprises a single semantic hub but it has graded subspecialisations towards certain types of
609 conceptual information (Plaut 2002; Binney et al. 2012; Rice et al. 2015). This is because the
610 adjacent ventrolateral ATL responded equally to both the social and non-social stimuli, and to
611 a much greater extent than the dorsolateral subregion. According to graded hub hypothesis, the
612 ventrolateral ATL region is the centre-point of the hub and has a modality/domain/category-
613 general semantic function. The sensitivity of the dorsolateral/polar ATL to social stimuli may
614 follow from this subregion’s close proximity to and strong connectivity with the limbic system
615 (via the uncinate fasciculus; Binney et al. 2012; Papinutto et al. 2016; Bajada et al. 2017), and
616 could reflect a specialisation in the assimilation of, for example, emotion-related or
617 interoceptive information into coherent semantic representations (Olson et al. 2007; Vigliocco
618 et al. 2014; Rice et al. 2015).

619 A clear difference the way in which the ATL was engaged by the semantic judgements
620 and the theory of mind tasks is that the latter was far more bilateral. Moreover, ToM elicited
621 bilateral ATL activation regardless of the verbal/non-verbal nature of the stimuli. The role of
622 the ATL in semantic cognition is proposed to be bilateral although, again, perhaps with graded
623 specialisations towards processing verbal semantic information in the left hemisphere (Lambon
624 Ralph et al. 2001; Rice et al. 2015). The role of the ATL in social cognition has been ascribed
625 with a right lateralisation within some accounts (see Gainotti 2015) although the fMRI studies
626 reviewed above (Ross and Olson 2010; Binney et al. 2016; Rice et al. 2018) most strongly

627 implicate the left ATL (also see Rice et al. 2015; Pobric et al. 2016). An interesting aim for
628 future neuroimaging studies is to explore factors (e.g., stimulus modality) that could potentially
629 drive differences in the activation of bilateral ATL subregions both in the context of social and
630 general semantic tasks.

631

632 *The status of the ATL in neurobiological accounts of social cognition*

633 Animal ablation studies (Brown and Schafer 1888; Klüver and Bucy 1937) and case
634 descriptions of the profound consequences for humans of focal ATL lesions (Terzian and Dalle
635 Ore 1955) and degeneration (e.g. Edwards-Lee et al. 1997) provided some relatively early clues
636 as to the importance of the anterior temporal cortex for socio-affective competences.
637 Nonetheless, the ATL often does not feature prominently within contemporary neurobiological
638 frameworks for understanding social behaviour (Decety and Lamm 2007; Lieberman 2007;
639 Adolphs 2009; van Overwalle 2009; Spunt and Adolphs 2017). It is overshadowed by
640 prefrontal, medial and lateral temporoparietal regions, and seemingly attributed with an
641 ancillary status. This could be due, at least in part, to the predominance of fMRI in the social
642 neurosciences and the fact that this technique is typically blind to activation in a significant
643 proportion of this region (Devlin 2002). Inconsistencies in the presence and location of ATL
644 activation across various social domains, relative to the TPJ for example, could explain a
645 modest appetite for further exploring the region's contribution.

646 Here, and in two prior ATL-optimised fMRI studies (Binney et al. 2016; Rice et al.
647 2018), we have shown that when steps are taken to alleviate the technical limitations of the
648 fMRI technique, robust ATL activations are observed across a variety of social stimuli and
649 social tasks. Activation also occurs in a ventrolateral ATL region that is one of the most
650 affected in patients with both striking semantic and social impairments (Binney et al. 2010;
651 Binney et al. 2016; Kumfor et al. 2016). Moreover, in the present study, we have demonstrated

652 that left ventrolateral ATL activation is at least as robust, in extent and magnitude, as that of
653 another key social region (the TPJ), and at least as consistent across different tasks and stimuli.
654 Overall, we interpret this as initial evidence from neurotypical samples to complement that
655 obtained from patient studies, that the ventrolateral ATL is of equal functional import to social
656 cognition as other key nodes of the ‘social brain’ (such as the TPJ, the mPFC and the
657 precuneus).

658 Several authors have argued that progress in social neuroscience theory will rapidly
659 accelerate if it embraces established and detailed models from within other more general
660 domains of cognition (Spunt and Adolphs 2017; Amodio 2019; Ramsey and Ward 2020).
661 Taking a similar perspective, we have recently proposed that a unifying feature amongst many
662 forms of social cognitive processing is the retrieval of conceptual knowledge, and that it could
663 be productive to understand social cognition to essentially be an example of semantic cognition
664 (Binney and Ramsey 2020). This would appear a reasonable viewpoint given that social
665 interaction is, at its core, a process of *meaningful* exchange between persons. The main
666 practical implication of this proposal, at least for the present discussion, is that social and
667 semantic cognition rely on the same cognitive and brain mechanisms, and this positions the
668 ventrolateral ATL at the heart of social cognition. According to this framework, other key
669 nodes of the ‘social brain’, including the mPFC and the TPJ, could also serve a domain-general
670 role rather than one that is specialised towards processing social information (van Overwalle
671 2009; Seghier et al. 2010; Cabeza et al. 2012; Bzdok et al. 2016; Humphreys et al. 2020;
672 Diveica et al. 2021). In summary, we argue that there is a growing need to re-evaluate the
673 relative contribution of all these regions, as well as develop a better understanding of the way
674 they interact in service of social cognition.

675

676 ***Conclusions and Future Directions***

677 In conclusion, our findings support the claim that the ventrolateral ATL is an important
678 contributor to social cognition and point to a specific role as a domain-general hub for
679 conceptual knowledge representations that help inform our understanding of others and guide
680 our own meaning-driven social behaviours. A key methodological determinant underpinning
681 these findings was the use of a neuroimaging technique that maximises the signal obtained
682 from across the entire ATL region. However, the present study is also limited by its
683 methodology. To a large extent, fMRI remains the predominant mode of investigation in the
684 social neurosciences. However, it cannot be escaped that the inferences it allows are merely
685 correlational and not at all causal. For this reason, the field needs to increasingly turn to patient
686 models such as stroke, temporal lobe epilepsy, and frontotemporal dementia (Kumfor et al.
687 2017; Rankin 2020, 2021), as well as non-invasive techniques, such as transcranial magnetic
688 stimulation, that can be used to more directly probe the neural architecture of cognition in
689 neurological healthy samples. This will enable us to get a firmer grasp on key questions
690 including those regarding the laterality of function within the ATL and the TPJ, as well as the
691 functional necessity of distinct subregions.

692

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