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 x 0.45 x 4; reconstruction

286   matrix= 512 x512. 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 × 0.94 × 1.00 and reconstruction matrix = 240 ×

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 though 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/yunshiuan/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

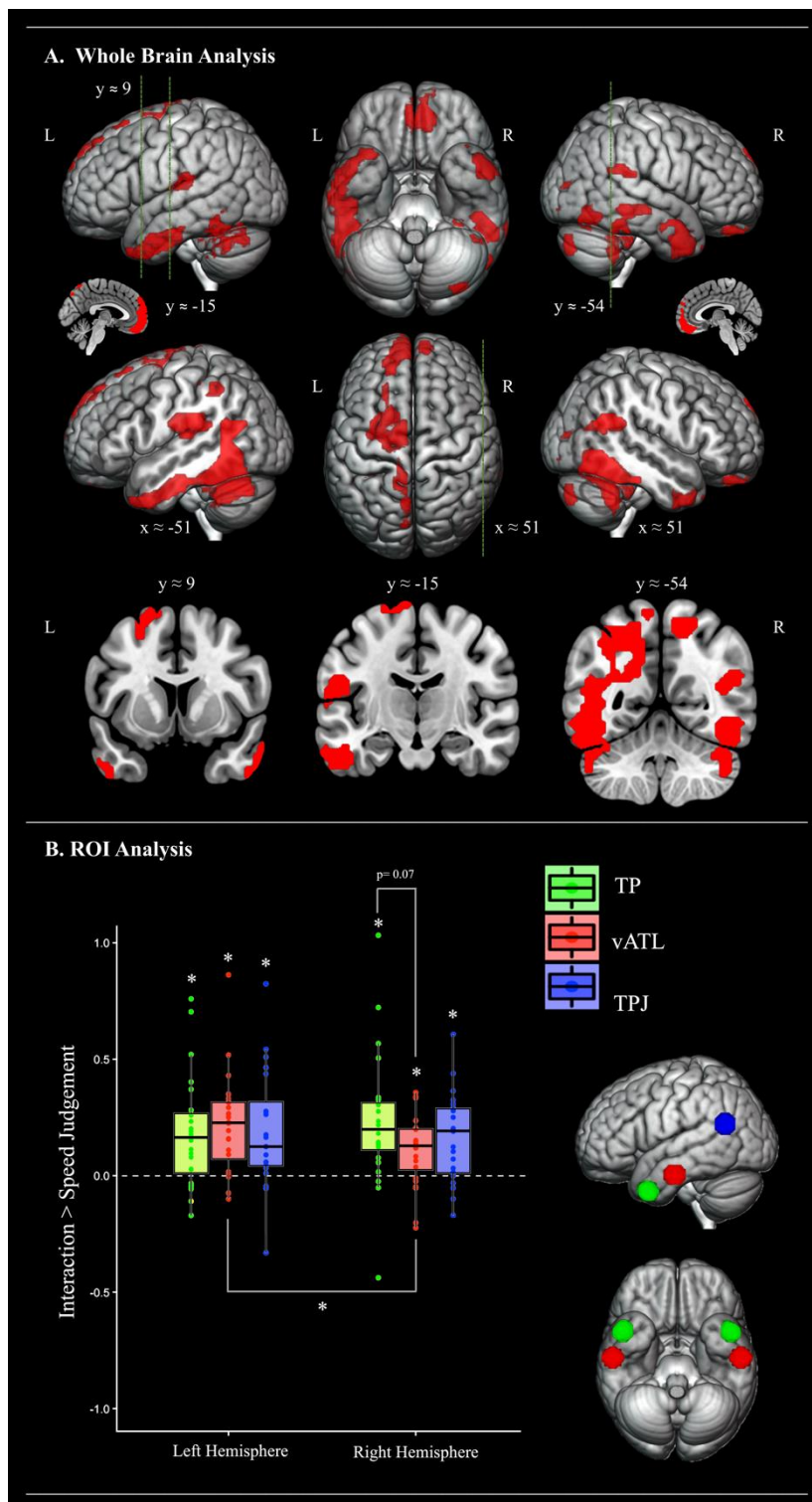418   temporal gyrus (MTG) but extended less posteriorly (to y ≈ -11) than it did in the left.

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 temporoparietal 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
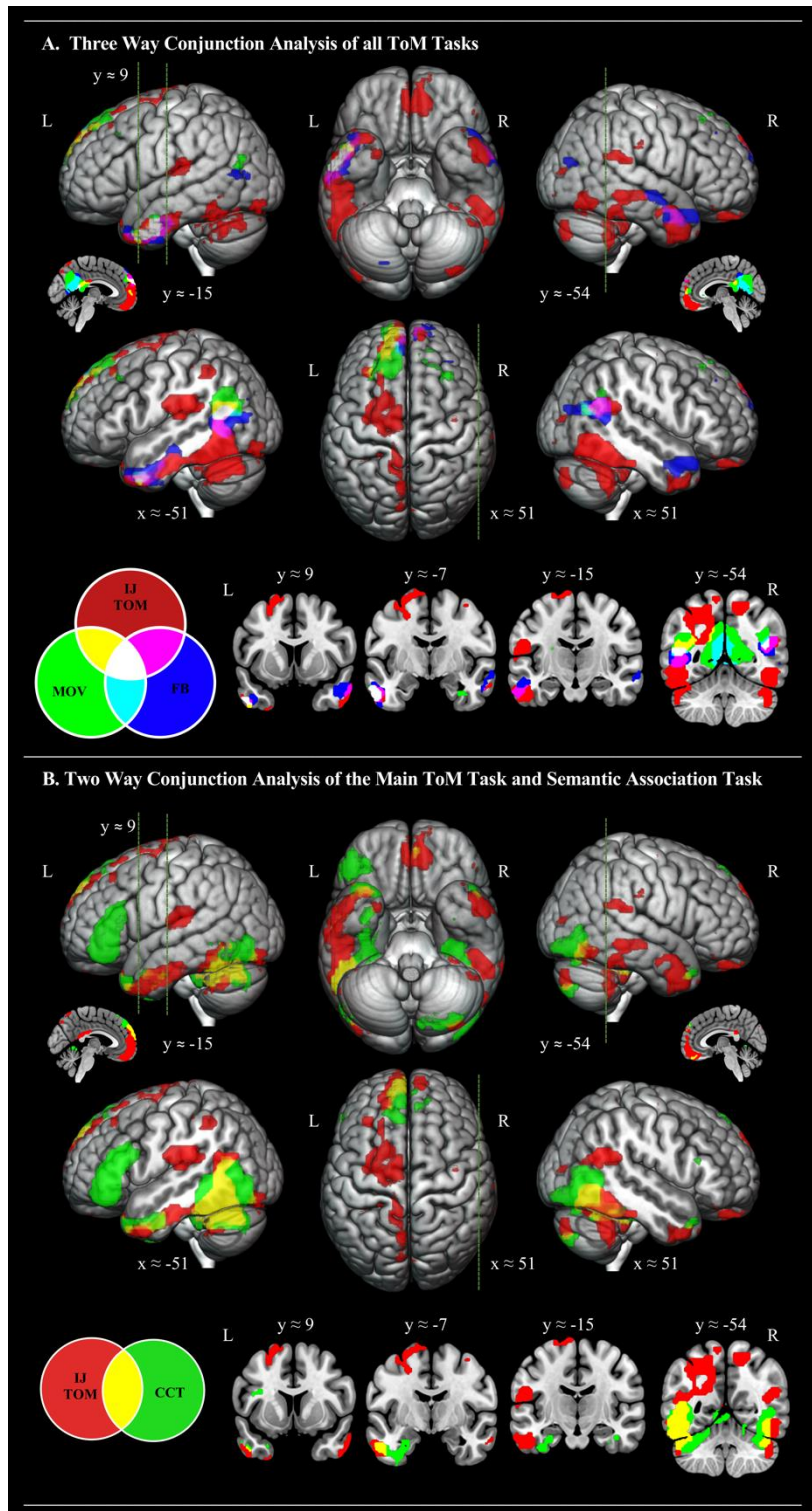
474   mPFC and bilateral TPJ.

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).

ATL Activation Common to both ToM and General Semantic Processing

Finally, we performed a conjunction analysis aimed at identifying any potential overlap 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 ≈ -15, showing the most robust overlap at y ≈ -7, and still overlapping

489   in inferior polar regions at y ≈ 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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