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Overlapping Neural Correlates Underpin Theory of Mind and Semantic Cognition
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Overlapping Neural Correlates Underpin Theory of Mind and Semantic Cognition:

Evidence from a Meta-Analysis of 344 Functional Neuroimaging Studies

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Abstract

Key unanswered questions for cognitive neuroscience include whether social cognition is underpinned by specialised brain regions, and to what extent it simultaneously depends on more domain-general systems. Until we glean a better understanding of the contribution made by domain-general cognitive systems, theories of social cognition will remain fundamentally limited. In the present study, we evaluate a recent and novel proposal that the semantic cognition network plays a crucial role in supporting social processes. We specifically focus on theory of mind (ToM) abilities and adopt a meta-analytic activation likelihood estimation approach to synthesise the results of a large set of functional neuroimaging studies. Our primary aim was to establish the degree of topological overlap between the cortical networks involved in ToM and semantic tasks. Moreover, we sought to account for key methodological differences across the two sets of tasks, including the fact that ToM studies tend to use nonverbal stimuli while the semantics literature is dominated by language-based tasks. We observed extensive overlap between the two networks in regions strongly implicated in semantic cognition, including the anterior temporal lobes and the left temporoparietal junction (TPJ). Activation specific to ToM was identified in the right TPJ, bilateral anterior mPFC, and right precuneus. These findings persisted even after controlling for discrepancies in the types of experimental stimuli used in each domain. Overall, the findings support the claim that ToM draws upon more general semantic retrieval processes and are against the view that ToM is underpinned solely by a domain-specific social neurocognitive system.

Keywords: semantic cognition, social cognition, theory of mind, mentalizing, meta-analysis

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1 ***1.   Introduction***

2   The capacity to understand and respond appropriately to the thoughts and actions of others is

3 of vital importance to our daily lives. When this ability breaks down, there are profound consequences

4 for an individual's ability to thrive in society (Frith, 2007; Frith & Frith, 2007). Therefore, a key

5 challenge for neuroscience is to develop a full account of the cognitive and brain basis of social

6 interaction.

7   The dominant mode within social neuroscience has been to seek out specialised neural

8 subsystems dedicated to processing social (as opposed to more general kinds of) information (Apperly

9 et al., 2005; Happé et al., 2017; Saxe & Powell, 2006; Spunt & Adolphs, 2017). This approach has

10 uncovered evidence for the existence of category-selective cortex; regions that preferentially activate

11 during the perception of certain social stimuli, such as faces (Kanwisher & Yovel, 2006), bodies

12 (Downing & Kanwisher, 2010), and dyadic social interactions (Landsiedel et al., 2022). It has been

13 argued that more complex inferential processes such as mental state attribution, or Theory of Mind,

14 also engage highly specialised social brain areas (Apperly et al., 2005; Brüne & Brüne-Cohrs, 2006;

15 Dodell-Feder et al., 2011; Gweon et al., 2012; Jacoby et al., 2016; Jenkins et al., 2014; Koster-Hale

16 & Saxe, 2013; Ross & Olson, 2010; Saxe & Baron-Cohen, 2006; Saxe & Kanwisher, 2003; Saxe &

17 Wexler, 2005; Scholz et al., 2009; Simmons et al., 2010). However, the extent to which 'higher-order'

18 systems (e.g., declarative memory; cognitive control) exhibit domain-specificity of this kind is hotly

19 debated (e.g., Apperly et al., 2005; Binney & Ramsey, 2020; Ramsey & Ward, 2020). One factor

20 keeping this debate from being resolved is that, to date, the role of domain-general systems in social

21 cognition has received comparatively little attention and is not well understood. Consequently,

22 neurobiological accounts of human social behaviour fall short of being comprehensive.

23   Recently, however, there has been increased interest in the involvement of a set of distributed

24 domain-general networks in social processing. This includes the 'multiple-demand network' (MDN)

25 and the 'default mode network' (DMN; Darda & Ramsey, 2019; Diveica et al., 2021; Zaki et al.,

26   2010; Duncan, 2010; Fedorenko, 2014; Fedorenko et al., 2013; Hughes et al., 2019; Jackson et al.,

27   2022; Mars et al., 2012; Schilbach et al., 2006; Spreng & Grady, 2010), both of which include regions

28   previously linked to social processing. These lines of enquiry have not only broadened the scope of

29   the cortical regions believed to contribute to social cognition, but they also provide support for

30   theories that recast social cognition as fundamentally built upon a set of more generalisable systems

31   and processes (for more on this debate, see Amodio, 2019; Binney & Ramsey, 2020; Lockwood et

32   al., 2020). More recently, it has been argued that a third network, known as the semantic cognition

33   network (SCN; Humphreys et al., 2015; Jackson et al., 2019), has a crucial role in supporting social

34   cognition (Balgova et al., 2022; Binney & Ramsey, 2020; Diveica et al., 2021).

35   Semantic cognition (supported by the SCN) refers to the acquisition and flexible retrieval of

36   conceptual-level knowledge that transforms sensory inputs into meaningful, multimodal experiences.

37   Conceptual knowledge critically underpins our capacity to use our sensory information to recognise

38   and interact with objects, words, people, and events in our environment (Patterson et al., 2007;

39   Lambon Ralph et al., 2017). The SCN is comprised of the IFG and posterolateral temporal cortex

40   (inclusive of the pMTG and pITG), which play a particular role in control-related processes, and the

41   ATL which underpins semantic representation processes (Jackson, 2021; Jefferies, 2013; Noonan et

42   al., 2013; Lambon Ralph et al., 2017). Research has only recently begun to explore the SCN's

43   relationship to social cognition. However, Binney and Ramsey (2020) suggest it could prove to be

44   productive to understand social cognition as, essentially, an example of semantic cognition. This is

45   because social interaction is, at its core, a process of *meaningful* exchange between persons; for

46   example, it involves understanding the communicative intent of a speaker, and/or understanding how

47   an actor's interaction with their environment reflects their thoughts, beliefs, or intentions. This

48   'primary systems' view of social cognition is supported by the high degree of overlap in anterior

49   temporal lobe (ATL), frontal, temporoparietal and midline cortical structures in the networks recruited

50   by social and semantic tasks in both functional neuroimaging reviews (Binney & Ramsey, 2020; also

51   see Diveica et al., 2021 and Hodgson et al., 2022) and direct fMRI comparisons of social and non-

52   social stimuli (Balgova et al., 2022; Binney, Hoffman et al., 2016; Paunov et al., 2019; Rice et al.,

53   2018 see also Deen et al., 2015; Paunov et al., 2019). Moreover, there is preliminary evidence for a

54   relationship between social and semantic cognition within the neuropsychological and comparative

55   neuroscience literature; in the context of ATL damage, there appears to be a tight coupling of general

56   semantic deficits and social impairments (Bertoux et al., 2020; Irish et al., 2014; Klüver & Bucy,

57   1937; Miller et al., 2012; Souter et al., 2021; for a review see Olson et al., 2013 and Rouse et al.,

58   2023).

59   The present study is the first attempt to use a meta-analytic approach to simultaneously

60   investigate the whole brain networks associated with social and semantic cognition and explore the

61   extent to which they are overlapping. Meta-analyses of functional imaging data allow the extraction

62   of reliable findings from across large numbers of studies, thereby circumventing the limitations of

63   individual studies (Cumming, 2014; Eickhoff et al., 2012) which include low statistical power (Button

64   et al., 2013) and vulnerability to idiosyncratic design/analysis choices (Botvinik-Nezer et al., 2020;

65   Carp, 2012). We chose to focus on one key aspect of social cognition, namely mental state attribution

66   or 'theory of mind' (ToM). This is a logical starting place for three reasons. First, ToM is considered

67   central to social cognition as it is fundamental to successful social interactions (Apperly, 2012; Brüne

68   & Brüne-Cohrs, 2006; Frith & Frith, 2005; Heleven & van Overwalle, 2018; van Hoeck et al., 2014).

69   Second, it is a well-established area of research with a large body of literature, as is requisite for meta-

70   analytic investigation. Third, ToM abilities enable one to describe, explain, predict, and infer the

71   intentions, beliefs, and affective states of others (Adolphs, 2009; Brüne & Brüne-Cohrs, 2006; Frith

72   & Frith, 2007, 2012; Frith & Frith, 2010; Happé et al., 2017; Premack & Woodruff, 1978). As such,

73   ToM includes inferential processes that allow one to go beyond what is directly observable through

74   the senses, thus appearing to be comparable to, and perhaps explained by, more domain-general

75   semantic processes that are specialized for the extraction of meaning from sensory inputs (Binney &

76   Ramsey, 2020).

77   In the present study, we explored the relationship between the regions consistently engaged

78   in ToM and the SCN. Most neural accounts of ToM implicate the temporoparietal junction (TPJ)

79   alongside medial prefrontal cortex (mPFC) and the precuneus. Some accounts also include the

80   posterior superior temporal sulcus (pSTS) and the ATL (Amodio & Frith, 2006; Mar, 2011;

81   Molenberghs et al., 2016; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005; Saxe, 2006; Saxe &

82   Powell, 2006; Schurz et al., 2014, 2017). It is key to note that the term 'TPJ' is less frequently used

83   in the semantic cognition literature than in social neuroscience, and the corresponding definition can

84   be vague and heterogeneous. For present purposes, we interpret the label TPJ to refer to a large area

85   that includes the posterolateral temporal cortex and the inferior parietal lobe, including the angular

86   gyrus (AG) (Hodgson et al., 2022; Seghier, 2013, 2022; Seghier et al., 2010). Some accounts of

87   semantic cognition include the AG and argue it is involved in the integration and storage of conceptual

88   knowledge (Kuhnke et al., 2020). However, the AG has also been attributed to other domain-general

89   processes that extend beyond semantic processing (Cabeza et al., 2012; Geng & Vossel, 2013;

90   Humphreys, Lambon Ralph, et al., 2021; Humphreys & Tibon, 2022)). In the present study, we

91   specifically anticipated overlap in the ATL and the TPJ as both regions are frequently implicated in

92   putatively domain-specific social processes as well as semantic cognition (Balgova et al., 2022;

93   Diveica et al., 2021; Humphreys, Lambon Ralph et al., 2021; Olson et al., 2013; Seghier et al., 2010).

94   We further aimed to investigate a potential hemispheric dissociation between social and

95   semantic cognition at these sites. In semantic cognition, the role of the ATL is viewed as bilateral

96   (albeit with a leftwards asymmetry when probed with verbal semantic information; Lambon Ralph et

97   al., 2001; Rice, Hoffman, et al., 2015), whereas the role of the ATL in social cognition has been

98   ascribed right lateralisation (Younes et al., 2022; Zahn et al., 2009). Evidence for this distinction is

99   limited, however, because claims that the right, but not the left ATL, is key for social processing are

100   based chiefly upon patient studies (Borghesani et al., 2019; Gainotti, 2015; Gorno-tempini et al.,

101   2003; Irish et al., 2014). Individual fMRI studies, on the other hand, typically indicate bilateral

102   involvement or possibly a leftward asymmetry (Balgova et al., 2022; Binney, Hoffman, et al., 2016;

103   Rice et al., 2018; Ross & Olson, 2010 but see Zahn et al., 2002; also see Arioli et al., 2021; Catricalà

104   et al., 2020; Lin, Yang, et al., 2018; Pobric et al., 2016; Rice, Lambon Ralph, et al., 2015). The

105   laterality of TPJ involvement in social cognition is unclear. In neuroimaging studies, it is often

106   observed bilaterally (Molenberghs et al., 2016; Schurz et al., 2014), but selectivity of this region for

107   ToM is argued to be limited to the right hemisphere by some authors (Perner et al., 2006; Saxe &

108   Wexler, 2005) while others have reported greater selectivity in the left (Aichhorn et al., 2006, 2009).

109   In semantic cognition, activation of regions within the TPJ tends to be left lateralised (Handjaras et

110   al., 2017; Kuhnke et al., 2022; Seghier, 2013; Seghier et al., 2010). Collectively, these findings paint

111   a complex picture regarding how the ToM and semantic networks converge and diverge at these ATL

112   and TPJ sites.

113   These laterality differences may be of critical importance to differentiating semantic and

114   social cognition networks. Alternatively, they could reflect a methodological confound which is that

115   their typical neuroimaging assessments tend to use different types of stimuli. A key aim of this study,

116   therefore, was to investigate whether methodological factors give rise to a skewed pattern of activity

117   in each domain. Most fMRI studies probing semantic cognition have used verbal stimuli (e.g.,

118   words/sentences) (Rice, Lambon Ralph, et al., 2015; Visser, Jefferies, et al., 2010). In contrast,

119   nonverbal stimuli such as animations, vignettes, or free-viewing movie paradigms are popular in the

120   ToM literature (Diveica et al., 2021; Molenberghs et al., 2016). Although both semantic cognition

121   and ToM are typically viewed as modality-independent processes (Gallagher et al., 2000), these

122   prevalent methodological differences could mar between-domain comparisons because activation

123   patterns within each domain shift according to the stimulus presentation format. For example, a meta-

124   analysis of fMRI studies found that non-verbal compared to verbal ToM tasks, evoke greater

125   activation in the left precentral gyrus and left and right IFG, and lower activation in the mPFC,

126   precuneus, and bilateral TPJ (Molenberghs et al., 2016). Similarly, Visser et al.'s (2010) meta-analysis

127   of semantic cognition found that the laterality of ATL activation depends on whether stimuli were

128   presented in the auditory versus visual modality (also see Krieger-Redwood et al., 2015; Rice,

129   Lambon Ralph, et al., 2015). Thus, left unaccounted for, these kinds of systematic methodological

130   differences could create the appearance of divergence between the two task-associated networks when

131   there is, in fact, a common system with meaningful covariation driven by properties of the stimuli. In

132   the present study, we controlled for stimulus format (verbal, non-verbal) and input modality (visual,

133   auditory) to disentangle pervasive from context dependent network differences. In the same vein, we

134   controlled for inter-domain differences in the types of baseline/control tasks used (e.g., active versus

135   passive) and screened for the presence of social stimuli in the studies of semantics.

136   In summary, to determine the degree to which ToM and semantic cognition share an

137   underlying neural basis, we performed a systematic comparison between an update of Molenberghs

138   et al.'s (2016) large-scale neuroimaging meta-analysis of ToM (previously reported in Diveica et al.,

139   2021) and a comprehensive meta-analysis of semantic cognition and the SCN (Jackson, 2021) with a

140   primary focus on the ATL and TPJ. Moreover, we assessed the effect of stimulus format and sensory

141   input modality on network overlap. To our knowledge, this is the first direct comparison of these two

142   large-scale networks via these means (see Hodgson et al., 2022 for a region-specific analysis).

143

144   *2. Materials and Methods*

145   *Data Availability statement.* Following open science initiatives (e.g., Munafò et al., 2017), the raw

146   data sets, including study characteristics and the input and output files of all analyses, are openly

147   available on the Open Science Framework (OSF) project page (https://osf.io/ydnxh/).

148

149   *2. 1. Literature selection and inclusion criteria*

150   We leveraged a Theory of Mind (ToM) dataset curated by (Diveica et al., 2021), and a Semantic

151   Cognition (SCN) dataset compiled by (Jackson, 2021). Both these studies performed a comprehensive

152   and up-to-date literature review and followed best practice guidance for conducting meta-analyses

153   (Müller et al., 2018). Below, we provide a brief description of each of these original datasets.

154   The general semantics analysis (257 studies, 415 contrasts, 3606 peaks) reported by Jackson (2021)

155   was designed to capture all aspects of semantic cognition, including activation of conceptual level

156   knowledge, as well as engagement of control processes that guide context- or task-appropriate

157   retrieval of concepts. Studies were included if they compared a (more) semantic with a non- (or less-

158   ) semantic task or meaningful (or known) with meaningless (or unknown) stimuli. It included studies

159   published between 2008 and 2019. The ToM analysis (136 experiments, 2158 peaks, 3452

160   participants) reported by Diveica et al. (2021) included studies published between 2014 and 2020 that

161   employed a primary task involving inferences about the mental states of others, including their

162   beliefs, intentions, and desires (but not sensory or emotional states). These studies were also required

163   to compare the ToM task to a non-ToM task. Studies that looked at the passive observation of actions,

164   social understanding, mimicry or imitation were not included unless the primary task included a clear

165   ToM component. Studies investigating irony comprehension, those that employed trait inference

166   tasks, and those that employed interactive games were also excluded. Both Jackson and Diveica et al.

167   excluded contrasts that made comparisons between sub-components of the process of interest (but

168   see the final paragraph in this Section). For example, Diveica et al. excluded affective ToM >

169   cognitive ToM contrasts and from the semantic cognition studies, and Jackson excluded abstract

170   semantics > concrete semantics contrasts. This was critical for the present study because we were

171   interested in common, core semantic/ToM processes that are subtracted out by these contrasts.

172   For these two datasets to be compared, it was essential to ensure that a similar, if not identical set

173   of general exclusion criteria (i.e., those pertaining to the sample demographics, the imaging method,

174   etc.) were applied. To this end, we initially planned to use the general inclusion/exclusion criteria

175   described by Diveica et al. (2021) and reapply them to both the ToM and SCN datasets. In practice,

176   we needed to implement a few minor modifications to these criteria. Below we summarise the final

177   set of general criteria that we applied in the present study and highlight discrepancies from the

178   approaches of Diveica et al. (2021) and Jackson (2021):

179   1. We included only peer-reviewed articles in English, and studies that employed task-based

180   fMRI or PET, and only those that report whole-brain activation coordinates localised in one of

181   two standardised stereotactic spaces (Talairach (TAL) or Montreal Neurological Institute

182   (MNI)). Coordinates reported in TAL space were converted into MNI space using the

183   Lancaster transform (tal2icbm transform (Lancaster et al., 2007) embedded within the

184   GingerALE software version 3.0.2; http://brainmap.org/ale). Results from region-of-interest or

185   small-volume correction analyses were excluded.

186   2. We included only studies that tested healthy adults to control for age-related changes in neural

187   networks supporting cognition (e.g., see Hoffman & Morcom, 2018). A deviation from Diveica

188   et al. (2021) was that we only considered studies reporting data from participants aged 18-40

189   years. If the age range of participants in a given study was not stated, we included the results

190   in our datasets as long as the mean age of the participants was less than 40 years (if stated) and

191   there was no clear indication that adults outside the range of 18-40 were included in the sample.

192   This was a similar criterion to that used by Jackson (2021).

193   3. Diveica et al. (2021) included contrasts between the experimental task (i.e., ToM processing)

194   and either an active control condition or rest/passive fixation. Jackson (2020) only included

195   contrasts against active baselines. Therefore, we added additional contrasts involving

196   rest/passive fixation into the SCN dataset. In the present study, active control conditions were

197   characterised as either a high-level or low-level baseline; thus, over and above Diveica et al.

198   (2021) and Jackson (2020), the present study differentiated low-level active baselines (e.g.,

199   visual stimulation with a string of hashmarks as a control for sentence reading) from

200   rest/passive fixation. With these extra steps, we aimed to better account for methodological

201   differences across domains (see more detail in **Section 2.3.1**).

202   4. Where present, multiple contrasts from the same group of participants were included if they

203   met all the other inclusion criteria. We controlled for within-group effects by pooling contrasts

204   into a single experiment (Müller et al., 2018; Turkeltaub et al., 2012) like Diveica et al. (2021)

205   and Jackson (2020). This means that, when we refer to the numbers of experiments that

206   constituted the units of input, we have counted contrasts from a single participant sample as

207   one single experiment. In follow-up contrast analyses that compared different conditions (e.g.,

208   stimulus format or input modality), initially pooled contrasts related to these different

209   conditions were separated (see more detail in **Section 2.2**). While Diveica and colleagues

210   excluded the contrast with a smaller number of peaks after separating, we retained both of these

211   contrasts to maximise the use of all available data.

212   Two further adjustments were made to the SCN dataset to make it optimally comparable to the

213   ToM dataset. As discussed above, both Jackson and Diveica et al. excluded contrasts that made

214   comparisons between sub-components of the process of interest and thus could subtract away core

215   processes associated with ToM and semantic cognition. In the case of ToM, this left only those

216   contrasts comparing ToM tasks with non-ToM tasks. Jackson, however, also included a small number

217   of contrasts that compared more semantic tasks with less semantic tasks (e.g., an identity

218   classification task using faces with varying degrees of familiarity used by Rotshtein et al., (2005) or

219   a task contrasting personal familiar and famous familiar faces used by Sugiura et al., (2006)). In the

220   present study, we excluded these because they could subtract out some core processes or common

221   regions. While this was likely of little consequence in Jackson's (2021) study, the inclusion of these

222   contrasts could, in principle, weaken the comparison of SCN data with the ToM data. An exception

223   was applied to contrasts that pitted intelligible sentences against scrambled sentences because they

224   were an important source of data in the verbal and auditory domain, and we reasoned that, while there

225   is meaning present in both stimuli types at the single word level, the critical difference was

226   meaningfulness at the sentence level. Finally, we identified and excluded a small number of

227   experiments in Jackson's SCN dataset (n=4) that used contrasts that could be viewed as probing ToM-

228   related processing.

229   The final ToM dataset used in the present study comprised 114 experiments from 2800 participants,

230   159 contrasts, and 1893 peaks. The final SCN dataset used in the present study comprised 214

231   experiments, including data from 3934 participants, 410 contrasts, and 3803 peaks.

232

2.2. Categorising Contrasts by Stimulus Format and Sensory Input Modality

234   In line with our secondary aim of accounting for the effects of stimulus format and sensory input

235   modality on network overlap, individual contrasts from both the ToM and SCN datasets were further

236   categorised as being chiefly within the verbal domain or the non-verbal domain. Verbal paradigms

237   used spoken or written language stimuli. Examples of non-verbal paradigms include those using

238   pictures (e.g., of objects or actions), animations, videos, or environmental sounds (see Rice et al.,

239   2015 for a similar approach). Moreover, contrasts were independently categorised according to

240   whether stimuli were presented in the visual or auditory modality (see Molenberghs et al., 2016;

241   Visser et al., 2010 for similar approaches). In cases where both types of stimuli (e.g., verbal and non-

242   verbal) were used in the same task, the contrast was excluded (e.g. Sommer et al., (2010)).The reader

243   is referred to **Table 1** and the **Supplementary Information** for the number of studies and a list of

244   excluded contrasts in each of these categories.

245

2.3. Further Methodological Considerations

247   Following the application of general inclusion/exclusion criteria and the categorization

248   described in **Section 2.2**, we took additional steps to further characterize the two revised datasets and

249   evaluate the potential for other confounds to influence their comparison. As we shall describe below,

250   this led to further refinement which improved the suitability of the datasets for addressing our key

251   research questions.

252   ***2.3.1. Controlling for type of baseline***

253   In semantic cognition research, it is widely accepted that the results of neuroimaging studies

254   are affected, in important ways, by the choice of baseline task; a failure to perform adequate matching

255   of baselines to experimental conditions in terms of perceptual input, response and

256   attentional/executive demands, decreases sensitivity of subtractive designs to activation in brain areas

257   associated with cross-modal integration, semantic processing and response selection (Price et al.,

258   2005). Indeed, the use of passive rest or simple fixation as a baseline results in failure to reveal task-

259   positive activation in anterior temporal areas (Binder et al., 2009; Price et al., 2005; Visser, Jefferies,

260   et al., 2010), because minimal baseline task demands increase the opportunity for spontaneous

261   semantic processing (associated with daydreaming and inner speech) to occur at an equal or greater

262   depth/magnitude than that associated with more focused task-related semantic processing (Andrews-

263   Hanna et al., 2014; Binder et al., 2009, 2016; Chiou et al., 2020; Humphreys et al., 2015; Visser,

264   Jefferies, et al., 2010). While it is not typically discussed in the literature, this is also an important

265   consideration for neuroimaging studies of social cognition because various forms of social inference

266   are likely to occur during a state of mind-wandering (see, e.g., Diaz et al., 2013).

267   We observed that our SCN and ToM datasets differed considerably in the types of baselines used

268   and that there was a higher degree of variability among semantic cognition studies (see **Table 1** and

269   the **Supplementary Information**). This could have led to a confound in the inter-domain

270   comparisons, namely a difference in the sensitivity to activation associated with cross-modal

271   processing. To explore these issues, we (a) quantified these differences using three categories of

272   baseline and (b) mapped the effect of including/excluding contrasts that used these baselines on the

273   outcomes of ALE analysis within each domain. The results of this preliminary analysis informed our

274   final approach to defining the datasets used for the inter-domain comparisons (see below). Previous

275   attempts to deal with this issue have only distinguished between two types of baselines (e.g., Visser

276   et al., 2010), but with a view to capturing greater specificity in these effects, we operationalized three,

277   as follows:

1. High-level baselines were defined as those including an active task designed to approximate the demands of the main/experimental task without engaging the process of interest (ToM or semantic processing). This includes being generally well-matched to the experimental task in terms of perceptual (visual, auditory) properties, and means of behavioural output (overt/covert).

2. Low-level baselines were defined as having a task that required active engagement but one that differed from the main task in numerous ways, including perceptual properties, means of behavioural output, or difficulty.

3. Finally, the third category of baselines were those which required only passively watching a blank screen or maintaining visual fixation.

Our chief motivation for this finer differentiation of baseline types was to arrive at an optimal scenario in which we could remove cross-domain confounds while retaining as many data points, and therefore as much power, as possible. We decided on a stepwise approach in which we would compute the ALE map for each domain (i) with all contrasts included, then (ii) without contrasts involving rest/fixation, and finally, (iii) with neither the rest/fixation nor low-level baseline contrasts included. We visually compared the ALE maps generated at each step, as well as the associated output tables, paying attention to the gain or loss of suprathreshold clusters. We decided a priori that if inclusion/exclusion resulted in minimal change to the activation maps, then we would opt to retain contrasts in the sample.

We found that, in the case of the SCN data set, excluding passive/resting baselines resulted in additional activation in the left inferior temporal lobe and in right medial temporal areas (see **Supplementary Figure R2b and Supplementary Table R2**). The exclusion of contrasts utilising low-level baselines did not lead to any appreciable differences in the distribution of activations, but the size of clusters was reduced owing to the reduced sample and power. In the case of the ToM data, the impact of these exclusions was negligible due to a very low number of experiments with low-

303   level and passive baselines (**Supplementary Figure R2a and Supplementary Table R1**). Overall,

304   these outcomes are consistent with an expectation that the inclusion of passive baselines would

305   occlude activation within parts of the SCN (Binder et al., 2009, 2016; Humphreys et al., 2015; Visser,

306   Jefferies, et al., 2010). Exclusion of lower-level baselines, on the other hand, might be an overly

307   conservative approach that prohibits the detection of activation that is common across domains. We,

308   therefore, opted to exclude only contrasts involving rest/passive baselines from the cross-domain

309   comparisons reported in the Results section.

310

311   ### 2.3.2. *Controlling for the 'socialness' of semantic stimuli*

312   20 studies (48 contrasts) in Jackson's (2021) original SCN data set, having otherwise met our

313   revised exclusion/inclusion criteria, involved a task or stimuli that were, to some degree, social in

314   nature. For example, some studies used social or emotion concepts, and others probed person

315   knowledge through famous faces (e.g., Elfgren et al., 2006; Grabowski et al., 2001; Leveroni et al.,

316   2000). These studies required further consideration, particularly because of an ongoing debate

317   concerning whether social semantics and general semantics depend upon independent or overlapping

318   representational systems (Arioli et al., 2020; Binney et al., 2016; Binney & Ramsey, 2020; Olson et

319   al., 2013; Pexman et al., 2023). It is possible that ToM tasks engage social concepts and therefore the

320   same regions engaged by social semantic processing (e.g., the dorsal ATL; Binney & Ramsey, 2020;

321   Ross & Olson, 2010; Zahn et al., 2007) without relying on general semantic areas. In this case, if we

322   were to pool social semantic contrasts and general semantic contrasts, then we might obtain an

323   exaggerated picture of the extent to which the ToM network overlaps with the general processing

324   semantic network. However, there was also a pragmatic reason for including these studies: they are a

325   key source of data related to non-verbal semantic processing (see **Table 1**) and excluding them could

326   compromise our ability to remove the confounding effect of stimuli type. To account for this, we

327   examined the effect of including/excluding these studies in our general semantic dataset. These results

328   are fully reported in the **Supplementary Information No 2.** Briefly, the overall pattern remained

329   almost the same when the social contrasts were excluded, apart from losing a small cluster in the right

330   IFG and slightly less extensive left temporopolar activation. These differences are likely to be due to

331   the reduction in the number of studies included and concern brain regions that were not the focus of

332   the present study, and thus are not central to the conclusions made. Therefore, we decided to retain

333   the social contrasts as part of our SCN dataset and include them in the cross-domain comparisons

334   reported in the **Results** section.

335   *Table 1.* *The number of experiments, contrasts, and peaks split according to the stimulus format, input*

336   *modality, type of baseline, and presence of social content.*

Experiment Type	Theory of Mind				Semantic Cognition			
	Peaks	Sample Size	Experiments	Contrasts (%)	Peaks	Sample Size	Experiments	Contrasts (%)
Total	**3803**	**2800**	**114**	**159 (100%)**	**1893**	**3934**	**214**	**410 (100%)**
Baseline								
High	2387	2749	111	151 (95%)	1800	3064	170	283 (69%)
Low	1026	33	2	2 (1%)	19	880	47	88 (21%)
Rest	387	98	5	6 (4%)	74	388	24	38 (9%)
Both	3	NA	NA	NA	NA	12	1	1 (0.2%)
Social Content*								
Yes	NA	NA	NA	NA	2881	3610	193	323 (79%)
No	NA	NA	NA	NA	527	323	20	48 (12%)
Mixed	NA	NA	NA	NA	8	10	1	1 (0.2%)
Stimulus* Content-Type								
Verbal	2684	988	46	59 (37%)	542	3261	175	296 (72%)
Non-Verbal	525	1858	71	89 (56%)	1244	701	37	57 (14%)
Both/None	207	53	4	5 (3.1%)	33	341	15	19 (5%)
Input Modality*								
Visual	2707	2664	106	142 (89%)	1715	2864	152	285 (70%)
Auditory	592	91	6	7 (4%)	64	1023	60	76 (19%)
Both/None	117	45	2	4 (3 %)	40	180	8	11 (3%)

*The experiment counts exclude experiments using rest as the baseline conditions. See text for further details. Contrast % rounded up to the nearest 0.1%.

337

2.3. Data Analysis

We performed coordinate-based meta-analyses, using the revised activation likelihood estimation (ALE) algorithm as implemented in the GingerALE 3.02 software (http://brainmap.org/ale) (Eickhoff et al., 2009, 2012, 2017; Laird et al., 2005). To ensure sufficient statistical power, analyses were only performed on samples comprising a minimum of 17 experiments (Eickhoff et al., 2016). Each analysis was comprised of two stages. The first stage consisted of independent analyses of the ToM and SCN datasets, which were used to identify areas of consistent activation within each domain. Here, the ALE meta-analytic method treats the activation coordinates reported by each experiment as the center points of three-dimensional Gaussian probability distributions which differ in width to account for the reliability of the peak estimate based on the size of the participant sample (Eickhoff et al., 2009). These spatial probability distributions are aggregated, creating a voxel-wise modelled activation (MA) map for each experiment in the sample. Then, the voxel-wise union across the MA maps of all experiments is computed, resulting in an ALE map that quantifies the convergence of results across experiments (Turkeltaub et al., 2012). GingerALE tests for above-chance convergence (Eickhoff et al., 2012), thus permitting random-effects inferences. Following the recommendations of Müller et al. (2018), these ALE maps were thresholded using cluster-level family-wise error (FWE) correction of $p < .05$ with a prior cluster-forming threshold of $p < .001$ (uncorrected), which was estimated via 5000 permutations. Cluster-level FWE correction has been shown to offer the best compromise between sensitivity to detect true convergence and spatial specificity (Eickhoff et al., 2016).

The ALE maps generated in this first stage were used as inputs for the second stage of analysis, comprised of conjunction and contrast analyses. These analyses were aimed at identifying similarities and differences, respectively, in neural activation between the SCN and ToM sets of studies. Conjunction images were generated using the voxel-wise minimum value of the ALE maps

362 (Nichols et al., 2005). Contrast images were created by directly subtracting one ALE map from the

363 other (Eickhoff et al., 2011). Differences in ALE scores were compared to a null distribution that was

364 estimated via a permutation approach with 5000 repetitions. The contrast maps were thresholded

365 using an uncorrected cluster-forming threshold of p <.001, and a minimum cluster size of 100 mm^3.

366 Thresholded ALE maps were plotted on a MNI152 template brain using MRICroGL

367 (https://www.nitrc.org/projects/mricrogl). We used FSL maths commands and FSL VIEW

368 (https://www.nitrc.org/projects/fsl) to binarise the ALE maps for better visual clarity when displaying

369 the conjunction.

370   In a final step, we conducted post hoc cluster analyses that afforded a complementary

371 approach to evaluating whether clusters of activation identified in the two independent ALE analyses

372 of the SCN and ToM data were driven by certain methodological characteristics (i.e., input modality

373 and stimulus format). We examined the list of experiments that contributed to each cluster by at least

374 one peak and computed the likelihood of contribution of a given experiment type. For these purposes,

375 we used Fisher's exact tests of independence and post-hoc pairwise comparisons in R studio Version

376 1.4.1106 (https://www.rstudio.com).

377   In summary, our analysis pipeline proceeded as follows. To address our primary question

378 about similarities in the brain networks underpinning semantic and social cognition, we conducted

379 independent ALE analyses on the ToM and SCN datasets which generated whole-brain activation

380 maps. These maps were then used to create conjunction and contrast analyses aimed at identifying

381 overlap and differences in the topology of activation between the two domains. We repeated these

382 analyses having divided the SCN and ToM datasets into subsets containing experiments that used

383 VERBAL stimuli on one hand, and NON-VERBAL stimuli on the other. This allowed examination

384 of the effect of stimulus format. Then we split the datasets into subsets containing experiments that

385 used VISUAL and AUDITORY stimuli and repeated the analyses to investigate the impact of sensory

386 input modality. Finally, we performed cluster analyses to check whether the likelihood of finding

387   activation within each cluster identified in the primary ALE analyses of the ToM and GS data depends

388   on experiment type (VERBAL, NON-VERBAL, VISUAL, AUDITORY).

389

390   ***3. Results***

391   ***3.1. General Overlap Between Networks Subserving Theory of Mind and Semantic Cognition***

392   Our principal analyses explored the extent to which neural networks engaged by ToM and semantic

393   cognition tasks overlap (and diverge). Overall, the results reveal extensive areas of overlap including

394   at key areas of interest (see **Figure 1** and **Table 2;** also see the independent ALE analysis results for

395   each separate domain in **Supplementary Information No. 2: Supplementary Figure R1** and

396   **Supplementary Table R1**). Specifically, there was a conjunction of ToM and SCN activity within

397   the bilateral ATL that covered the temporal pole (TP) and the banks of the anterior STS, the MTG

398   and STG in both hemispheres. In the left but not the right hemisphere, the area of overlap extended

399   along the whole length of the MTG/STG towards the lateral temporoparietal junction (including the

400   AG) as well as medial portions of the IPL. There was also a conjunction of activation in the left

401   posterior ventral temporal lobe (ITG/FG), and in the lateral frontal cortex including pars orbitalis,

402   triangularis and opercularis of the left IFG and the ventral precentral gyrus. There were smaller

403   clusters on the bank of the right inferior frontal sulcus (pars triangularis), the left dorsomedial frontal

404   cortex and left inferior precuneus.

405   In the context of this large overlap, the contrast analyses revealed key differences between ToM

406   and SCN (**Figure 1**). On the lateral surface of the bilateral ATL the activation for ToM included an

407   area of anterior MTG that the SCN did not. Moreover, in the right IPL/AG (within the TPJ), activation

408   was only consistently identified for ToM. While both ToM and semantic cognition elicit reliable

409   activation in the left TP, as well as the IPL/AG (TPJ), the contrast analyses revealed that voxels in

410   this same areas had significantly higher ALE values for ToM compared to the SCN. Beyond our key

411   areas of interest, compared to the semantic studies, ToM studies also showed higher convergence of

412   activation in the right IFG, right precentral gyrus, bilateral anterior mPFC, left precuneus and left

413   cerebellum. On the other hand, SCN experiments also showed increased convergence of activation in

414   the ventral portion of the left pMTG stretching to the posterior ITG and FG, in the left MFG/IFG

415   spreading towards the insula, and in the left inferior precuneus and right dorsal mPFC.
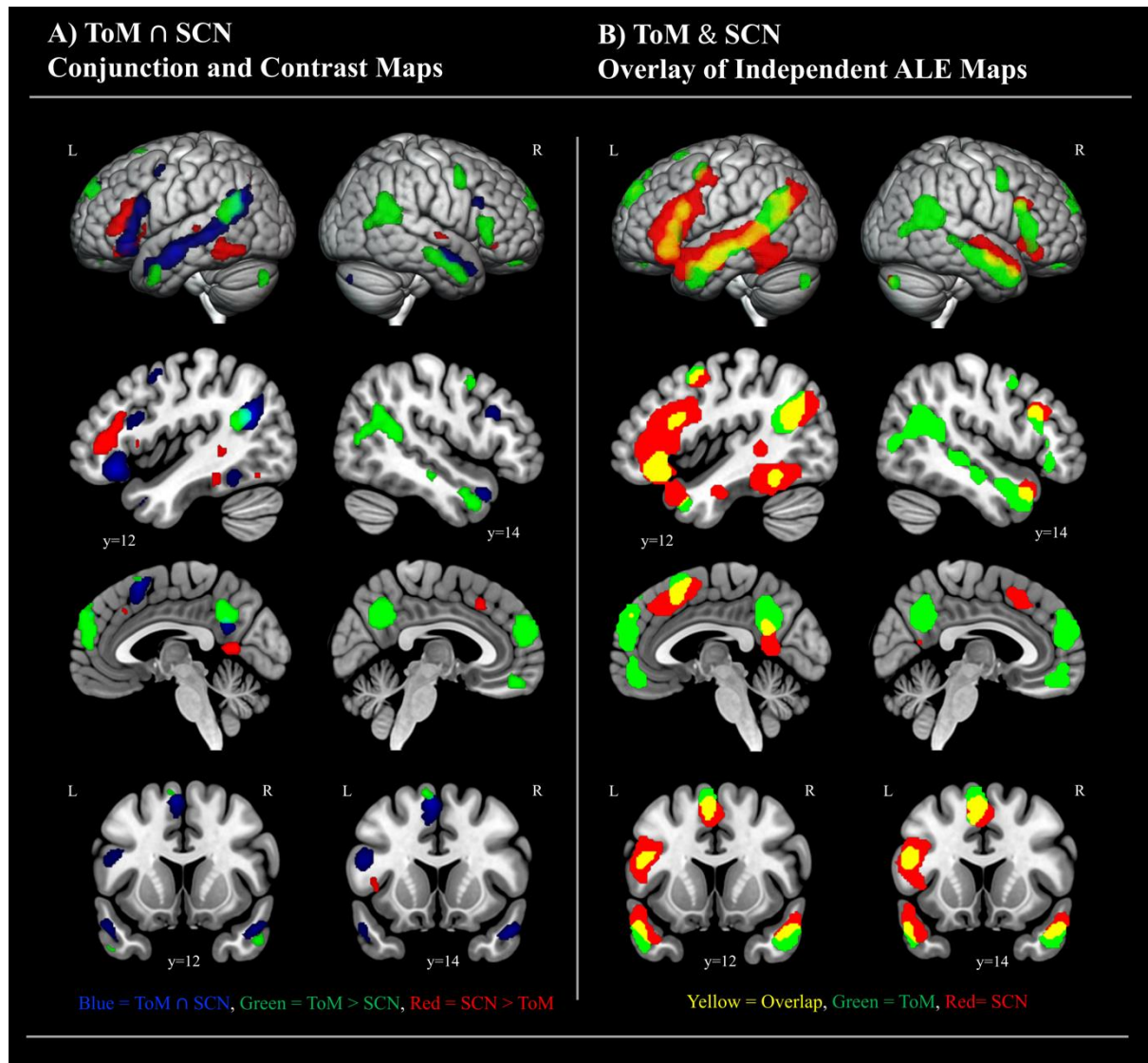
416 **Figure 1** *Common and differential activation for ToM (N=113) and SCN (N= 211).* **Panel A** *displays*

417 *the conjunction alongside statistically significant differences revealed by the contrast analyses. The*

418 *contrast maps in* **Panel A** *were thresholded with a cluster forming threshold at p<.001 and a minimum*

419 *cluster size of 100mm³. In* **Panel B,** *we have overlaid the binarised versions of the complete ALE*

420 *maps resulting from independent analysis of ToM and semantic cognition studies. This allows for full*

421 *visualisation of the topography of the two networks and consideration of the relationship between*

422 *them (also see Supplementary Figure R1 and Supplementary Table R1). The independent ALE maps*

423 *were treated to a cluster-forming threshold at p<.001, and an FWE-corrected cluster-extent threshold*

424 *at p<.05. The sagittal and coronal sections are chosen as representative slices positioned over peak*

425 *coordinates at which there is the greatest conjunction in the bilateral anterior temporal lobes (left y=*

426 *12; right y= 14).*

427

428 ***Table 2*** *Conjunction and contrast analyses of the ToM (N= 113) and SCN (N= 211) experiments.*

Region of Activation	Cluster Size	Peak MNI Co-ordinates			ALE Value	Z Value
		X	Y	Z		
ToM ∩ SCN CONJUNCTION						
Left AG	15504	-46	-62	26	0.09	
Left MTG		-58	-10	-14	0.08	
Left MTG		-56	-38	0	0.07	
Left MTG		-60	-24	-8	0.06	
Left MTG		-52	-48	8	0.05	
Left IFG (pars orbitalis)	7216	-48	28	-10	0.09	
Left IFG (pars triangularis)		-52	24	6	0.07	
Left IFG (pars opercularis)		-50	18	20	0.06	
Right MTG	2624	56	0	-18	0.06	
Right Middle TP		48	14	-28	0.05	
Left SMA	2136	-4	16	58	0.06	
Left Medial SFG	1104	-8	52	34	0.06	
Left Fusiform Gyrus	976	-42	-50	-16	0.04	
Left Precuneus	800	-4	-54	26	0.05	
Right IFG (pars triangularis)	680	46	20	26	0.05	
Left Precentral Gyrus	376	-42	2	52	0.04	
Right Cerebellum	312	26	-80	-34	0.05	
Left Middle TP	8	-44	12	-34	0.03	
Left MTG	8	-44	8	-30	0.03	
ToM > SCN CONTRAST						
Left Medial SFG	8248	1.4	56.5	23.9		3.89
Left Medial SFG		-2	50	42		3.43
Right MTG	7256	54.7	-52.6	19.3		3.89
Right Precuneus	6896	1.2	-54.4	36		3.89
Left MTG	4952	-52.5	-54.4	20.7		3.89
Right MTG	4600	54.6	-2.6	-25.2		3.72
Right Fusiform Gyrus		48.5	-21.5	-15.5		3.72

Right IFG (pars triangularis)	2392	56	26	5.7	3.89
Left Cerebellum	2224	-23.9	-77.6	-36.2	3.89
Right Precentral	1648	42.4	6	44.9	3.89
Left ITG	1224	-51.3	6	-33.6	3.89
Right Gyrus Rectus	1016	3.3	49.1	-19.8	3.89
Left SMA	376	-7	17	62	3.72
Right IFG (pars triangularis)	104	36	18	24	3.89
SCN > ToM CONTRAST					
Left IFG (pars triangularis)	7048	-41.4	31.7	5.9	3.89
Left Insula		-38	18	-4	3.72
Left Fusiform Gyrus	5824	-44.1	-44.1	-17.5	0
Left ITG		-39.7	-36.7	-14.3	3.29
Left Calcarine	880	-3.6	-58.5	7	3.89
Right Middle Cingulum	696	4.3	21	42.1	3.89
Left Middle Cingulum		-5	27	38	3.19
Left Fusiform Gyrus	672	-36.5	-16.5	-25.8	3.89
Left ITG		-41.3	-8.7	-28.7	3.54
Left IPL	432	-32	-66	46	3.89
Left IPL		-34	-66	42	3.72
Left MOG		-34	-67	33	3.35
Left MOG		-34	-67	38	3.43
Right IFG (pars orbitalis)	328	34.5	34	-8	3.89
Right STG	264	63.1	-8.3	0.6	3.89
Right STG		59	-10	0	3.72
Left MTG	208	-46	-43	2	3.54
Left MTG	120	-64	-28	4	3.54

429   *Independent ALE analyses cluster forming threshold p<.001; cluster-extent FWE p<.05. The*

430   *contrast analyses were further thresholded with a cluster forming threshold at p<.001 and a minimum*

431   *cluster size of 100mm³. Anatomical labels are derived from the Automatic Anatomical Labelling Atlas.*

432   *AG = angular gyrus, MTG = middle temporal gyrus, IFG - inferior frontal gyrus, TP = temporal*

433   *pole, SMA = supplementary motor area, SFG = superior frontal gyrus, ITG = inferior temporal*

434   *gyrus, IPL = inferior parietal lobule, MOG = middle occipital gyrus, STG = superior temporal gyrus.*

435

436   **3.2. The Role of Stimulus Format (VERBAL versus NON-VERBAL)**

437   In this next set of analyses, we explored the extent to which differences between the activation

438   maps associated with ToM and semantic cognition could be explained by systematic differences in

439   the types of tasks and stimuli used in each domain. We repeated the above comparisons, this time

440   excluding contrasts involving nonverbal stimuli (i.e., only retaining those involving verbal stimuli).

441   Both samples were large enough for the purposes of meta-analysis although there were many more

442   experiments using verbal stimuli in the domain of semantic cognition than there were in the ToM

443   dataset (VERBAL ToM: n= 46; VERBAL SCN: n= 175). Nonetheless, this analysis revealed a very

444   similar pattern of conjunction to the principal set of comparisons reported in **Section 3.1** including

445   the bilateral ATL (anterior MTG/STS) and the left TPJ (See **Figure 2** and **Supplementary**

446   **Information No. 2: Supplementary Table R4**). However, there ceased to be any IFG activation for

447   ToM tasks, and thus overlap between the two domains was absent in this region. A similar observation

448   was made at the left posterior STS/MTG, and other small clusters of conjunction were no longer

449   present. This could simply be due to the substantial reduction in size of the ToM experiment sample

450   (from 113 to 46). However, we looked at the cluster analyses for the IFG and found that verbal ToM

451   experiments were significantly less likely than nonverbal ToM experiments to contribute to the

452   clusters in the bilateral IFG (see **Supplementary Information No.2: Supplementary Figure CA1**

453   and **Supplementary Table CA1** for more detail). This is contrary to expectations given that the left

454   IFG is strongly engaged in language processing (Friederici, 2011). One possible explanation,

455   however, is that there are important differences between the main experimental tasks and the

456   control/baseline tasks used in verbal ToM in terms of the semantic/syntactic operations that need to

457   be performed. Should there be greater or equivalent difficulty in the control task, then IFG activation

458   could be subtracted away (see Diveica et al., 2021 for meta-analytic evidence for the effect of task

459   difficulty on IFG activation).

460   In the corresponding contrast analyses, the differences between ToM and the SCN in the bilateral

461   ATL and left TPJ were less pronounced, yet they remained. There also continued to be more consistent

462   activation of the right TPJ for ToM. This was also true of the left anterior mPFC, and left precuneus.

463   Indeed, while the extent of the clusters changed because of the reduced sample size in the ToM

464   dataset, we continued to find more consistent involvement of the right TPJ, mPFC and left precuneus

465   in ToM as compared to semantic cognition. Given that there were more studies in the ToM than SCN

466   dataset, it is unlikely that these cross-domain differences could be attributed to lower statistical power

467   in the case of SCN. For more detail see **Supplementary Information No. 2: Supplementary**

468   **Figures R4 & R5 Panel A** and **Supplementary Table R6 & R7**).

469
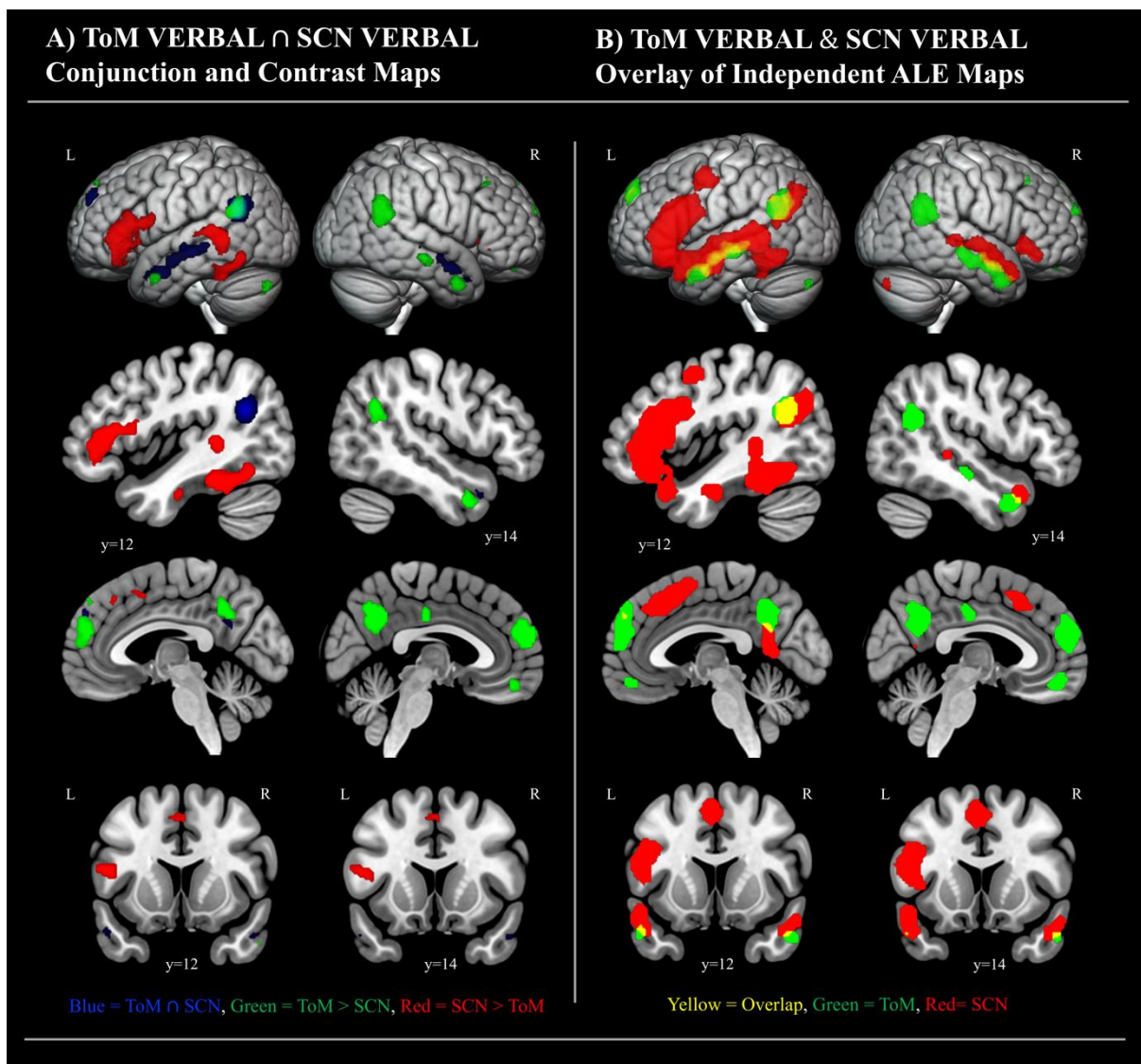
470   ***Figure 2*** *Common and differential activation for VERBAL ToM (N=46) and VERBAL SCN (N= 175).*

471   *The initial ALE maps were treated to a cluster-forming threshold at p<.001, and an FWE-corrected*

472   *cluster-extent threshold at p<.05 prior to the conjunction and contrast analyses. The contrast maps*

473   *in **Panel A** were additionally thresholded with a cluster-forming threshold at p<.001 and a minimum*

474   *cluster size of 100mm³. **Panel A** displays the conjunction alongside side statistically significant*

475   *differences. In **Panel B**, we have overlaid the binarised versions of the complete ALE maps resulting*

476   *from independent analysis of VERBAL ToM and VERBAL SCN studies. This allows for full*

477   *visualisation of the topography of the associated networks (also see Supplementary Figures R4 & R5*

478   *and Supplementary Table R6 & R7). The sagittal and coronal sections are chosen as representative*

479   *slices positioned over peak coordinates at which there is the greatest conjunction in the bilateral*

480   *anterior temporal lobes (left y= 12; right y= 14).*

481   When we limited the datasets to experiments utilising nonverbal stimuli, the results of the

482   ALE analysis for ToM remained mostly unchanged from that seen in **Section 3.1**. In the case of

483   semantic cognition, the number and extent of clusters was greatly diminished which reflects the

484   reduced sample size. Indeed, there were more experiments using nonverbal stimuli in the domain of

485   ToM than there were exploring semantic cognition (ToM: n= 71; SCN: n= 37) and, as a consequence,

486   there was no conjunction between the domains in the left TPJ. Overlap was still present in key regions

487   of interest including the left pMTG, left ITG and some small aspects of the left IFG. Notably, even

488   though visual inspection of the independent ALE maps for each domain suggests a large difference

489   in terms of bilateral ATL activation, there were no significant differences revealed by the contrast

490   analysis. The bilateral TPJ responded selectively to ToM in this analysis, while the posterior ITG was

491   only present in the SCN. The ALE maps for each domain can be found in **Supplementary**

492   **Information No. 2: Supplementary Figures R4 & R5 Panel B and Supplementary Tables R6 &**

493   **R7**. In the cluster analysis of either the ToM or semantic domain, we found that the likelihood of

494   finding activation in the respective ATL or TPJ areas did not depend on the verbal/non-verbal nature

495   of the stimuli. This finding suggests that the inability to identify convergent left TPJ activation in the

496   non-verbal SCN sample, and, consequently, overlap with non-verbal ToM, is indeed due to reduced

497   statistical power. The cluster analysis showed that non-verbal experiments did however contribute

498   more to the bilateral IFG and SFG in the ToM domain (See more detail in **Supplementary**

499   **Information No.2: Supplementary Figure CA1** and **Supplementary Table CA1**).

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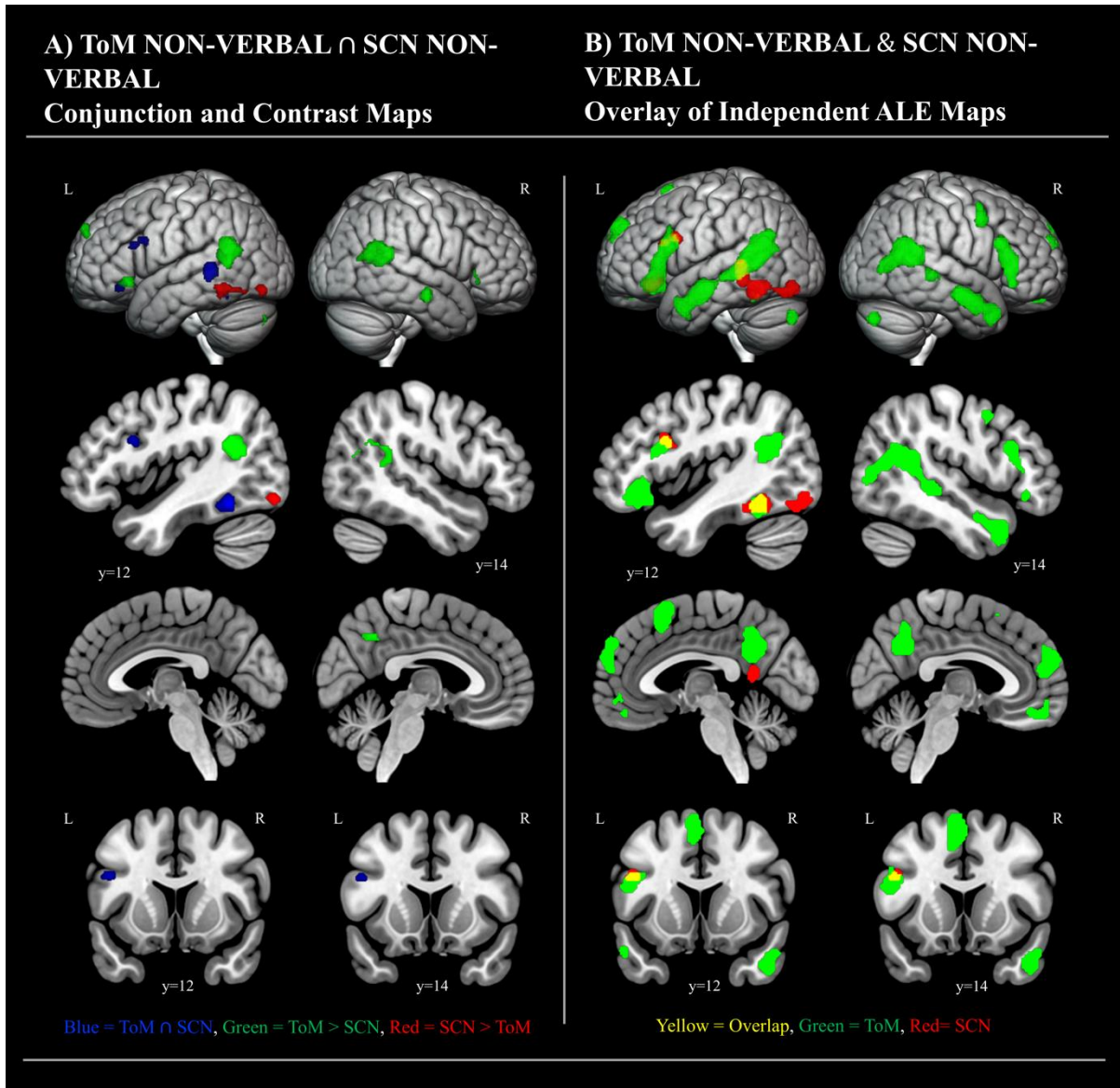
501   ***Figure 3*** *Common and differential activation for NON-VERBAL ToM (N=71) and NON-VERBAL*

502   *SCN (N= 37). The initial ALE maps were treated to a cluster forming threshold at p<.001 and an*

503   *FWE corrected cluster-extent threshold at p<.05 prior to the conjunction and contrast analyses. The*

504   *contrast maps in **Panel A** were additionally thresholded with a cluster forming threshold at p<.001*

505   *and a minimum cluster size of 100mm³. **Panel A** displays the conjunction alongside side statistically*

506   *significant differences. In **Panel B**, we have overlaid the binarised versions of the complete ALE maps*

507   *resulting from independent analysis of VERBAL ToM and VERBAL SCN studies. This allows for full*

508   *visualisation of the topography of the associated networks (also see Supplementary Figure R4 & R5*

509   *and Supplementary Table R6 & R7). The sagittal and coronal sections are chosen as representative*

510   *slices positioned over peak coordinates at which there is the greatest conjunction in the bilateral*

511   *anterior temporal lobes (left y= 12; right y= 14).*

512

513   ### 3.3. The Role of Sensory Input Modality (VISUAL versus AUDITORY)

514   We also investigated the impact of sensory input modality. Importantly, both domains were

515   dominated by experiments using visually presented stimuli. Comparisons limited to the auditory

516   experiments were not possible due to a very small sample of ToM data. Overall, the pattern and extent

517   of the common activation for VISUAL experiments (ToM: n= 106; SCN: n= 152) remained highly

518   similar to our original analysis (**Section 3.1**), with common clusters of activation in key semantic

519   areas (See **Figure 4** and **Supplementary Information No. 2: Supplementary Table R10**), including

520   the left ATL, left IFG, left pMTG and ITG/FG and the left IPL/AG. There were also clusters of

521   conjunction in the left medial SFG and precuneus. However, unlike in the initial analysis, there was

522   no right ATL activation for the visual SCN experiments, and therefore no overlap between domains

523   in the right ATL. Indeed, the cluster analyses revealed that visual relative to auditory SCN contrasts

524   were less likely to contribute to the right ATL cluster, suggesting that it is unlikely that the absence

525   of right ATL activation for visual SCN can be explained by reduced power per se. Instead, it seems

526   more likely that the auditory contrasts were driving this cluster in the case of semantic cognition. One

527   possibility is that this reflects increased effort in studies that use auditory stimuli (see **Discussion**).

528   Other minor differences to the initial analyses are a diminished area of conjunction in the left middle

529   STG and an absence of a conjunction in the right IFG (see **Supplementary Information No.2:**

530   **Supplementary Figure CA1** and **Supplementary Table CA1** for more detail).

531   As in our full analysis, the contrast analysis found more consistently identified activation in visual

532   ToM than visual semantic cognition studies in the right TPJ, right IFG, precentral gyrus, anterior

533   mPFC and precuneus. A small portion of the bilateral IFG remained more reliably engaged across

534   SCN studies, as did the MFG, anterior mPFC and left precuneus. For more detail see the VISUAL

535   and AUDITORY ToM and VISUAL and AUDITORY SCN ALE maps in **Supplementary**

536   **Information No. 2: Supplementary Figures R8 & R9** and **Supplementary Tables R11 & R12**.

537   Although they do not directly relate to the study's main questions, for sake of completeness and to

538   allow for comparisons with prior meta-analyses (Molenberghs et al., 2016; Rice, Lambon Ralph, et

539   al., 2015; Visser, Jefferies, et al., 2010) we also performed conjunctive and contrastive analyses within

540   each domain which compare each stimulus format and sensory modality (e.g., comparisons of the

541   VERBAL SCN and NON-VERBAL SCN data sets, the VISUAL SCN and AUDITORY SCN data).

542   The results of these analyses can be found in the supplementary information (see **Supplementary**

543   **Information No. 2: Supplementary Figures R6, R7 and R10 and Supplementary Tables R8, R9,**

544   **R13 and R14)**.

545

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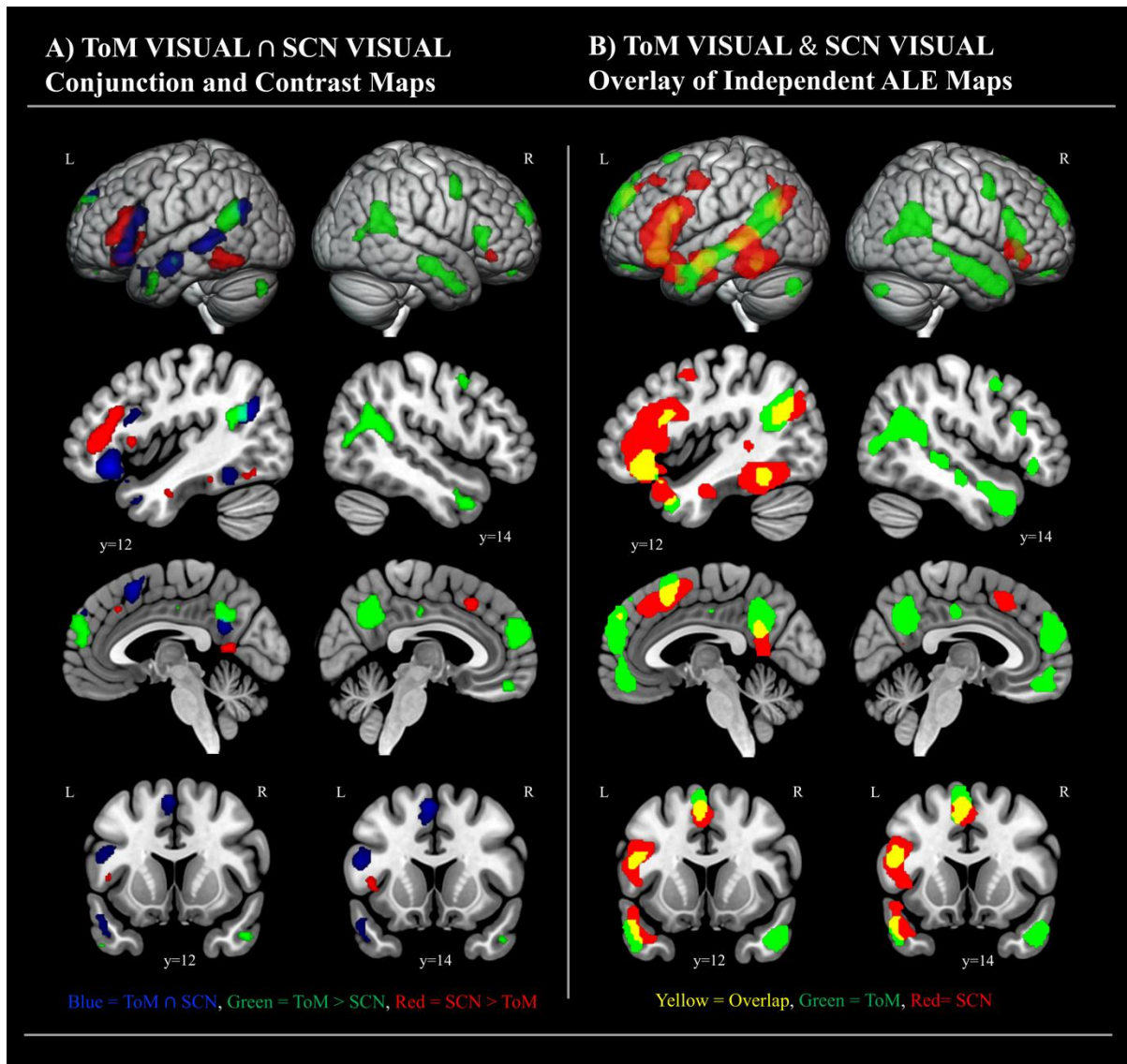
Figure 4 *Common and differential activation for VISUAL ToM (N=106) and VISUAL SCN (N= 152). The initial ALE maps were treated to a cluster-forming threshold at p<.001, and an FWE-corrected cluster-extent threshold at p<.05 prior to the conjunction and contrast analyses. The contrast maps in **Panel A** were additionally thresholded with a cluster-forming threshold at p<.001 and a minimum cluster size of 100mm³. **Panel A** displays the conjunction alongside side statistically significant differences. In **Panel B,** we have overlaid the binarised versions of the complete ALE maps resulting from independent analysis of VERBAL ToM and VERBAL SCN studies. This allows for full visualisation of the topography of the associated networks (also see Supplementary Figures R8 & R9 and Supplementary Table R11 & R12). The sagittal and coronal sections are chosen as representative*

557   *slices positioned over peak coordinates at which there is the greatest conjunction in the bilateral*

558   *anterior temporal lobes (left y= 12; right y= 14).*

559

560   **4. Discussion**

561   The present study aimed to glean a clearer understanding of the contribution of domain-

562   general systems to social cognition. To this end, we took a neuroimaging meta-analytic approach to

563   assess the degree to which ToM shares neural correlates with semantic processes. The key findings

564   were as follows:

565   1. Overall, there was a strikingly large degree of overlap between the activation likelihood maps

566   for ToM and the SCN. This was most evident in the bilateral ATL, the left STS, left MTG, left

567   TPJ, and left IFG, which are all key regions for semantic processing (Binder et al., 2009). This

568   suggests that semantic processes are integral to performing theory of mind tasks.

569   2. Most differences that emerged were mainly a matter of the extent of regional activation, which

570   is likely driven by discrepancies in the sample size contributing to each ALE map.

571   Nonetheless, there were a few notable exceptions.

572   3. The right TPJ, anterior aspects of the bilateral MTG, bilateral mPFC, and the bilateral

573   precuneus, were consistently identified in ToM but not SCN studies. Significant differences

574   remained even after controlling for methodological factors, including the type of experimental

575   stimuli, input modality and baseline condition used to probe each domain. This is consistent

576   with claims that the function of these regions (e.g., the right TPJ) are tuned towards processing

577   social stimuli (although see below).

578   4. The posterior ITG and dorsal IFG (both in the left hemisphere) were consistently identified in

579   SCN studies but not in ToM studies. This difference was even more pronounced after

580   controlling for stimulus format and modality. One possibility is that this reflects differences

581   in task difficulty, which we did not account for (see Diveica et al., 2021).

5. Activation in bilateral IFG and SFG, irrespective of domain, appears to be driven by stimulus format. Right ATL activation could be driven by input modality. However, there are other uncontrolled methodological confounds that may have also played a role (e.g., task difficulty, processing effort, experiment number differences across domains). These findings highlight the need for future studies, whose aim it is to contrast different cognitive domains, to systematically control for these types of methodological factors.

We interpret these results as generally supporting a recent proposal that, at the heart of social cognition, is a set of domain-general systems and processes dedicated to semantic cognition (Binney & Ramsey, 2020). This framework is an alternative to accounts of ToM that propose it depends chiefly upon domain-specific and highly specialised systems (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005; Scholz et al., 2009). We elaborate on these arguments and discuss each of the key findings in the following paragraphs.

4.1. *Two sides of the same coin? The relationship between semantic cognition and theory of mind*

It is argued that progress in social neuroscience theory will rapidly accelerate if the field embraces established models of other, more general domains of cognition (Amodio, 2019; Binney & Ramsey, 2020; Spunt & Adolphs, 2017). Theoretical advances in, for example, the domain of human learning and memory, are not always (immediately) incorporated within the social neuroscience literature, yet they are valuable opportunities to generate new hypotheses and more detailed models of social cognition, both in terms of mechanisms and neural bases (Amodio, 2019). Binney and Ramsey (2020) argue that reflections on theories of semantic cognition could prove particularly fruitful in this regard. They also highlight the striking similarities between the topologies of brain regions activated during neuroimaging studies of social cognition and semantic cognition, drawing particular attention to the ATL, the TPJ (including the angular gyrus and posterolateral temporal lobe), and the inferior frontal cortex. Prior to the present study, however, these activation maps had not been

607   formally compared at the level of the whole brain (see Hodgson et al., 2022 for a region-specific

608   analysis). Overall, our findings confirm there is a large degree of overlap between the brain networks

609   engaged by theory of mind and semantic cognition, particularly in the lateral frontal and temporal

610   cortex of the left hemisphere, but also bilaterally in the ATL. This suggests that at least some elements

611   of semantic cognition are integral to theory of mind. This raises questions about the nature of theory

612   of mind processes and raises the possibility that they can be considered a more generalised set of

613   cognitive mechanisms related to conceptual retrieval and cognitive inference. Moreover, it gives rise

614   to new hypotheses regarding the precise functional contribution of different brain regions to theory

615   of mind tasks, a level of specificity arguably lacking from other neurobiological accounts of theory

616   of mind (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). For example, ATL involvement likely

617   reflects access to semantic knowledge/associations (Balgova et al., 2022), whereas inferior frontal

618   and posterolateral temporal involvement of the left hemisphere could reflect control processes

619   (Diveica et al., 2021a; Satpute et al., 2014).

620

4.2 Functional fractionation of the 'social brain'

622   We observed pervasive differences between the activation likelihood maps for ToM and SCN.

623   Specifically, activation of the right TPJ, anterior aspects of the bilateral MTG, bilateral mPFC, and

624   the bilateral precuneus appear more attuned to ToM tasks. All these regions are included in

625   descriptions of putative brain regions specialized for theory of mind (Saxe, 2006; Saxe & Powell,

626   2006; Schurz et al., 2014, 2017). However, they are also considered part of the default-mode network

627   (DMN) (Andrews-Hanna et al., 2014; Buckner et al., 2008; Spreng et al., 2009; Spreng & Grady,

628   2010), a resting-state network proposed to support various forms of internally orientated cognition

629   (i.e., cognition that is decoupled from sensory processing (Margulies et al., 2016; Smallwood et al.,

630   2013)), including memory-driven cognition (Murphy et al., 2018). The DMN has been explicitly

631   linked to social cognition (Mars et al., 2012; Spreng et al. 2009; Shillbach et al. 2008) although it has

632   also been shown that regions activated by social tasks are, to some degree, distinct from what are

633   considered 'core' regions of the DMN (Jackson, 2021; Jackson et al., 2016; Mars et al., 2012). The

634   relationship between the DMN and social cognition therefore remains elusive. In the present study,

635   however, it was core DMN regions (especially those around the sagittal midline) that showed

636   differences between semantic cognition and ToM. DMN activation has been shown to be inversely

637   correlated with task difficulty and individual participants' performance in some types of cognitive

638   tasks (Eichele et al., 2008; Mayer et al., 2010) and, therefore, a possible explanation for differential

639   engagement of the DMN by semantic cognition and ToM is a general difference in task difficulty.

640   Our results shed new light on the relationship between the 'social brain' and domain-general

641   networks by highlighting significant overlap with the SCN. Important clues might also be gleaned

642   from the way in which activation patterns diverge, and the fact that this occurs most notably within

643   the right hemisphere homologues of left-lateralised SCN regions (e.g., the TPJ). One possible account

644   of these observation is that engaging in ToM recruits the SCN plus additional regions that are more

645   tuned to social processes. Alternatively, these regions may all comprise one widely distributed but

646   nonetheless functionally integrated network, that exhibits systematic variation in the involvement of

647   some of its nodes (particularly across hemispheres) owed to task-related or stimulus-related factors

648   (e.g., input modality). 'Socialness' of a task (or perhaps the degree of involvement of self- and other-

649   related processes; (Chiou et al., 2022; Platek et al., 2004; Quesque & Brass, 2019)) could be one such

650   task-related factor (Binney & Ramsey, 2020; Pexman et al., 2023). Further research is needed to

651   directly probe these factors and how they drive network involvement within and across domains. In

652   the remainder of this discussion, we expand on debates surrounding the ATL and the TPJ because

653   they are ascribed key roles in both ToM and in semantic cognition.

654

655   *4.3. The role of anterior temporal lobes in theory of mind*

656   Convergent neuropsychological and neuroimaging evidence strongly implicates the ATL in

657   semantic knowledge representations which underpin a range of meaning-imbued behaviours,

658   including language use, action understanding and interactions with objects (Patterson & Lambon

659   Ralph, 2016; Lambon Ralph et al., 2017). By extension, we argue that the contribution of the ATL to

660   ToM, and to social cognition more generally, is the supply of conceptual level information which

661   constrains inferences about the intentions and actions of other agents (Binney & Ramsey, 2020). The

662   current study revealed reliable overlap between ToM and semantic processing in the ATLs, which

663   supports this hypothesis. The present findings also complement those of prior fMRI studies that

664   directly explored the relationship between social and general semantic processing in the ATL. Across

665   all these studies, two consistent findings have emerged. First, a ventrolateral portion of the left ATL

666   responds equally to socially relevant concepts and more general concepts (both concrete and abstract),

667   and this is irrespective of whether concepts are probed via verbal or pictorial stimuli (Binney,

668   Hoffman, et al., 2016; Rice et al., 2018). The same ventrolateral region also activates during three

669   different verbal and nonverbal ToM tasks, which suggests that conceptual information is accessed

670   during ToM (Balgova et al., 2022). Second, there are some differences between social and general

671   semantic tasks within the dorsolateral ATL (Binney et al., 2016; Rice et al., 2018; also see Arioli et

672   al., 2021; Lin, Wang, et al., 2018; Lin, Yang, et al., 2018; Mellem et al., 2016; Ross & Olson, 2010;

673   Zahn et al., 2007). In the present meta-analysis there was a higher level of convergent activation for

674   ToM in the anterior MTG/STG, but the location of this difference moves around across prior studies.

675   Importantly though, the differences are small compared to the large degree of overlap. In the present

676   study, the difference between ToM and SCN was overlapping with a much larger left ATL cluster

677   which was activated consistently across both domains (also see Beauchamp, 2015; Deen et al., 2015

678   for comparisons of social perception with language and voice perception).

679   This overall pattern is consistent with the *graded semantic hub* account (Bajada et al., 2019;

680   Binney et al., 2012; Rice, Hoffman, et al., 2015), which characterises the bilateral ATL as a unified

681 representational space, all of which is engaged by the encoding and retrieval of semantic information

682 of any kind. The centre of this hub exists over the ventrolateral ATL and its engagement in semantic

683 processing is largely invariant to stimulus factors (e.g., modality). Towards the edges of this space,

684 however, there are gradual shifts in semantic function such that regions on the periphery are more

685 sensitive to certain types of semantic features (for a computational exploration of this general

686 hypothesis, see Plaut, 2002). Why exactly ToM tasks would engage the dorsolateral ATL more than

687 general semantic tasks is unclear. One possibility is that the meaning conveyed by typical ToM stimuli

688 (i.e., the state of mind of an actor in absence of explicit descriptors) is not directly observable and,

689 therefore must be inferred to a greater extent than in a typical semantic task. This may rely heavily

690 on verbally-mediated semantic information, which has been shown to engage these parts of the ATL

691 more (Binder et al., 2009; Rice, Hoffman, et al., 2015; Visser & Lambon Ralph, 2011). Another

692 possibility is that it reflects a proximity to and strong connectivity with the limbic system (via the

693 uncinate fasciculus; (Bajada et al., 2017; Binney et al., 2012; Papinutto et al., 2016) and a role of this

694 ATL region in processing semantic features related to emotion (Olson et al., 2007; Rice, Hoffman, et

695 al., 2015; Vigliocco et al., 2014). In the present study, there was no evidence of ventrolateral ATL

696 involvement in ToM or semantic processing. This can be explained by the fact that most of the studies

697 included used fMRI, and conventional forms of this technique are unable to detect blood-oxygen

698 level-dependent (BOLD) signal in these parts of the ATL (Devlin et al., 2000). ATL-optimised

699 distortion-corrected fMRI studies, on the other hand, detect robust ventral ATL activation during both

700 semantic and ToM tasks (Balgova et al., 2022; Binney et al., 2010; Castelli et al., 2000; Devlin et al.,

701 2000; Sharp et al., 2004). This methodological factor may be particularly important for understanding

702 the lack of left ATL activation for nonverbal stimuli, as prior studies have shown this is almost entirely

703 limited to ventral and ventromedial ATL structures which suffer the most from signal dropout. (Rice,

704 Lambon Ralph, et al., 2015; Visser, Embleton, et al., 2010).

705   There were also differences in the extent to which the right ATL was engaged, with a greater

706 proportion of the right anterior MTG involved in ToM. Moreover, the involvement of the right ATL

in semantic processing was dependent on including studies using auditory verbal stimuli. This confirms prior studies which also found that auditory verbal (or 'spoken') stimuli activate the ATL bilaterally, whereas written stimuli which show a left bias (Marinkovic et al., 2003; Rice, Lambon Ralph, et al., 2015). Thus, while ATL involvement in ToM appears always to be bilateral, right-sided involvement in semantic processing appears to be related to stimulus factors. This could be understood more broadly in terms of processing effort. Indeed, auditory semantic stimuli are typically sentences which require both rapid processing of individual tokens, as well as processing of combinatorial meaning, and which could work the semantic system more vigorously than other types of stimuli (see Visser, Jefferies, et al., 2010 for similar arguments). In a similar vein, the bilateral ATL activation during ToM tasks could reflect the complex, narrative structure of stimuli (e.g., animations, storyboards, vignettes, etc.). These observations are, however, not consistent with the right ATL having a distinctly social function (Bonnì et al., 2015; Gainotti, 2015; Gainotti et al., 2003; Gainotti & Marra, 2011; Pobric et al., 2016).

4.4. The Temporo-Parietal Junction

The TPJ has been associated with a variety of cognitive domains including attention, language, and episodic memory, and many of them bilaterally (Binder et al., 2009; Humphreys & Lambon Ralph, 2015; Igelström & Graziano, 2017; Özdem et al., 2017). It is also now becoming clear that these functions fractionate along an anterior-posterior, as well as a dorsal-ventral axis (Bzdok et al., 2013; Hodgson & Lambon Ralph, 2008; Humphreys & Lambon Ralph, 2015). The present study shows that STS/STG and inferior parietal involvement in ToM is bilateral (Bzdok et al., 2012; Hodgson et al., 2022; Molenberghs et al., 2016; Schurz et al., 2014, 2020). The inferior parietal lobe (including the angular gyrus) is involved in semantic processing bilaterally (Binder et al., 2009; see also Bonner et al., 2013; Kuhnke et al., 2022), whereas posterior MTG/STS involvement is left-lateralised (Jackson, 2021). Taken together, these results suggest that parts of the left TPJ serve a function common to ToM and SCN (Numssen et al., 2020). For example, the left angular gyrus has

733 been implicated in integration and storage of conceptual knowledge by some authors (Binder et al.,

734 2009; Kuhnke et al., 2020) and attributed with a more domain-general role by others (e.g., the multi-

735 sensory buffering of spatio-temporally extended representations; Humphreys, Lambon Ralph, et al.,

736 (2021; Humphreys & Tibon, (2022)). The left MTG/STS appears to be involved in processes that

737 constrain semantic retrieval and which could also be engaged during ToM (Diveica et al., 2021). The

738 right TPJ does not appear to be engaged by semantic processing which is consistent with claims that

739 it has a selective role in social and moral processing (Numssen et al., 2020; Saxe & Kanwisher, 2003;

740 Saxe & Wexler, 2005; Young et al., 2010). However, the present study cannot rule out involvement

741 in other cognitive domains.

742

4.5. Concluding remarks and future directions

744 In conclusion, we observed considerable overlap between the cortical networks engaged by

745 semantic tasks and theory of mind tasks. We propose that this reflects shared underlying processes

746 and, further, that ToM relies in part on processes related to semantic cognition (Binney & Ramsey,

747 2020). Alternatively, this overlap could, on closer inspection, turn out to reflect tightly yet separately

748 packed cognitive functions that only dissociate when investigated at higher spatial resolutions or at

749 the level of individual participants. Further research is needed to explore these alternatives.

750 Furthermore, inferences afforded by functional neuroimaging data are merely correlational and,

751 therefore, the field needs to increasingly turn to patient models such as stroke, temporal lobe epilepsy,

752 and frontotemporal dementia (Kumfor, Hazelton, et al., 2017; Kumfor, Honan, et al., 2017; Rankin,

753 2020, 2021), and non-invasive techniques like transcranial magnetic stimulation, to directly probe

754 whether certain brain regions are necessary for both social *and* semantic cognition.

761

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771

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