

## Establishing a Role of the Semantic Control Network in Social Cognitive Processing: A Meta-analysis of Functional Neuroimaging Studies

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### **Abstract**

Most leading models of socio-cognitive processing devote little discussion to the nature and neuroanatomical correlates of cognitive control mechanisms. Recently, it has been proposed that the regulation of social behaviours could rely on brain regions specialised in the controlled retrieval of semantic information, namely the anterior inferior frontal gyrus (IFG) and posterior middle temporal gyrus. Accordingly, we set out to investigate whether the neural activation commonly found in social functional neuroimaging studies extends to these ‘semantic control’ regions. We conducted five coordinate-based meta-analyses to combine results of over 500 fMRI/PET experiments and identified the brain regions consistently involved in semantic control, as well as four social abilities: theory of mind, trait inference, empathy and moral reasoning. This allowed an unprecedented parallel review of the neural networks associated with each of these cognitive domains. The results confirmed that the anterior left IFG region involved in semantic control is reliably engaged in all four social domains. This suggests that social cognition could be partly regulated by the neurocognitive system underpinning semantic control.

*Keywords:* social cognition; semantic cognition; cognitive control; empathy; theory of mind; moral reasoning; trait inference; meta-analysis.

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## 1 **1. Introduction**

2           The ability to comprehend and respond appropriately to the behaviour of others is  
3 essential for humans to survive and thrive. A major challenge for the cognitive sciences,  
4 therefore, is to characterise *how* we understand others and coordinate our behaviour to  
5 achieve mutually beneficial outcomes, and what can cause this ability to break down (Frith,  
6 2007). There is an indubitable requirement for systems that control, or regulate, the cognitive  
7 processes underpinning social interactions. This is because social interactions are intricate  
8 and fraught with the potential for misunderstandings and faux pas; first, the everyday social  
9 signals to which we are exposed are typically complex, often ambiguous and sometimes  
10 conflicting. This is compounded by the fact that the meaning of a given gesture, expression or  
11 utterance can vary across contexts (Barrett et al., 2011; Rodd, 2020). Moreover, once we  
12 have settled upon an interpretation of these signals, we are then faced with the additional  
13 challenge of selecting an appropriate response, and inhibiting others which might, for  
14 example, be utilitarian but socially insensitive or even damaging. In order to undergo social  
15 interactions that are coherent, effective and context-appropriate, we must carefully regulate  
16 both our comprehension of, and response to, the intentions and actions of others (Binney and  
17 Ramsey, 2020; Fujita et al., 2014; Gilbert and Burgess, 2008; Ramsey and Ward, 2020).

18           Despite there being a wealth of literature describing executive functions involved in  
19 general cognition (Assem et al., 2020; Diamond, 2013; Duncan, 2013, 2010; Fedorenko et  
20 al., 2013; Petersen and Posner, 2012), prominent models of socio-cognitive processing are  
21 under-specified in terms of the contribution and neural basis of cognitive control mechanisms  
22 (e.g., Adolphs, 2009, 2010; Frith & Frith, 2012; Lieberman, 2007). For example, Adolphs  
23 (2009; 2010) only very briefly refers to cognitive processes involved in ‘social regulation’  
24 and largely within the limited context of emotional regulation. Likewise, Frith and Frith  
25 (2012) refer to a “supervisory system” which has the characteristic features of executive

26 control, but its functional and anatomical descriptions lack detail important for generating  
27 testable hypotheses. However, research into specific social phenomena, such as prejudice  
28 (Amodio, 2014; Amodio and Cikara, 2021) and automatic imitation (Cross et al., 2013;  
29 Darda and Ramsey, 2019) has recently begun to give the matter of cognitive control greater  
30 attention. Of particular interest has been the contribution of the domain-general multiple-  
31 demand network (MDN), a set of brain areas engaged by cognitively-challenging tasks  
32 irrespective of the cognitive domain (Assem et al., 2020; Duncan, 2010; Fedorenko et al.,  
33 2013; Hugdahl et al., 2015). MDN activity increases with many kinds of general task  
34 demand, including working memory load and task switching, and it has been suggested that  
35 this reflects the implementation of top-down attentional control and the optimal allocation of  
36 cognitive resources to meet immediate goals (Duncan, 2013, 2010). The MDN is comprised  
37 of parts of the precentral gyrus, the middle frontal gyrus (MFG), the intraparietal sulcus  
38 (IPS), insular cortex, the pre-supplementary motor area (pre-SMA) and the adjacent cingulate  
39 cortex (Assem et al., 2020; Fedorenko et al., 2013), some of which have been implicated in  
40 controlled social processing such as, for example, working memory for social content (Meyer  
41 et al., 2012), social conflict resolution (Zaki et al., 2010), inhibition of automatic imitation  
42 (Darda and Ramsey, 2019) and mental state inference or theory of mind (ToM) (e.g.  
43 Rothmayr et al., 2011; Samson et al., 2005; Van der Meer et al., 2011). However, there are at  
44 least three key unresolved questions regarding the role of cognitive control in social  
45 cognition. First, it remains to be seen whether there could be multiple, distinguishable  
46 mechanisms of, and neural systems for, control. Second, it is unclear whether there exists a  
47 subset of control systems that are specialised towards processing social information and,  
48 third, we have little understanding as to whether certain types of control are necessary for all  
49 or only select social behavioural phenomena. Shedding light on these issues has the potential

50 to generate important new hypotheses regarding social behaviour both in the context of health  
51 and injury/disease.

52 It has recently been proposed that a relatively specialised form of cognitive control,  
53 termed *semantic control*, could be particularly important for social cognitive processing  
54 (Binney and Ramsey, 2020). This follows a broader claim that social cognition and its neural  
55 correlates can be understood as a nuanced form of *semantic cognition* which itself is defined  
56 as a set of processes involved in extracting meaning from the environment and using it to  
57 guide purposeful and context-appropriate behaviour (Binney and Ramsey, 2020; Lambon  
58 Ralph et al., 2017). This framework contrasts with approaches that look upon social  
59 processing as a distinct or even special case of cognition (i.e., domain-specific models;  
60 Barrett, 2012; Saxe, 2006; but also see Amodio, 2019; Amodio and Cikara, 2021; Schaafsma  
61 et al., 2015; Spunt and Adolphs, 2017) and, instead, posits that it is underpinned by two,  
62 more domain-general neurocognitive systems. The first system is representational in nature  
63 and supports the acquisition and long-term storage of conceptual-level knowledge about  
64 objects, people, abstract concepts, and events. The anterior temporal cortices act as a central,  
65 supramodal semantic store through interaction with modality-specific and lower-order  
66 heteromodal association cortices (Binney et al., 2010; Kuhnke et al., 2021; Lambon Ralph et  
67 al., 2017; Patterson et al., 2007; Pobric et al., 2010). The second system, the semantic control  
68 system, modulates activation of semantic knowledge to bring to the fore aspects of  
69 conceptual information that are relevant to the situational context or the task at hand while  
70 inhibiting irrelevant aspects (Chiou et al., 2018; Jefferies, 2013; Lambon Ralph et al., 2017).

71 The reasons why semantic control should be critical for social cognition and  
72 interaction are uncomplicated; we retain a vast amount of socially-relevant knowledge  
73 including knowledge about familiar people (Greven et al., 2016; Hassabis et al., 2014), about  
74 the structure of and relationship between social categories and their associated stereotypes

75 (Freeman and Johnson, 2016; Quinn and Rosenthal, 2012), and an understanding of abstract  
76 social concepts, norms and scripts (Frith and Frith, 2003; Van Overwalle, 2009). But only a  
77 limited portion of this information is relevant in a given social instance and it would be  
78 computationally inefficient to automatically retrieve it all. For example, there is no need to  
79 retrieve information about someone's personality traits, or personal interests and hobbies, if  
80 the only task is to pick them out from within a crowd. Moreover, the types and the scope of  
81 information we need to retrieve to understand and respond appropriately to certain social  
82 signals change according to the context, and irrelevant information could potentially  
83 interfere. Therefore, semantic control is essential for limiting semantic retrieval according to  
84 the circumstances and avoiding potential social errors.

85       There is a growing body of convergent computational modelling, patient,  
86 neuroimaging and neuromodulation evidence that the semantic control system is supported  
87 by a neural network that is distinct from that underpinning semantic representation (e.g.,  
88 Corbett et al., 2009; Davey et al., 2016, 2015; Jackson, 2021; Jefferies et al., 2008; Jefferies  
89 and Lambon Ralph, 2006; Teige et al., 2018). Specifically, semantic control engages regions  
90 of the MDN, as well as the semantic control network (SCN) which comprises the anterior  
91 IFG and the posterior middle temporal gyrus (pMTG) (Badre et al., 2005; Davey et al., 2016;  
92 Jackson, 2021; Noonan et al., 2013). Moreover, while the domain-general MDN is engaged  
93 by semantic tasks, and particularly those with high control demands (Jackson, 2021;  
94 Thompson et al., 2018), there is evidence that both the anatomy of the SCN and MDN and  
95 their functional contributions to controlled semantic processing are at least partially distinct  
96 (Gao et al., 2020). In particular, fMRI studies reveal that the mid- to posterior IFG (pars  
97 triangularis and pars opercularis), nodes of the MDN, have been shown to increase activity in  
98 response to increased 'semantic selection' demands, a process that is engaged when  
99 automatic retrieval of semantic knowledge results in competition between multiple

100 representations which must be resolved (for example, hearing the word *bank* might elicit  
101 retrieval of the concept of a riverside and a financial institution)(Badre and Wagner, 2007;  
102 Nagel et al., 2008; Thompson-Schill et al., 1997). However, this mid- to posterior IFG region  
103 is also engaged by other non-semantic forms of response competition (Badre et al., 2005;  
104 Barredo et al., 2015) and tests of inhibitory function such as the Stroop task (Huang et al.,  
105 2020; January et al., 2009; Nee et al., 2007). In contrast, activation of the anterior IFG (pars  
106 orbitalis) appears to be more selective to semantic control demands and driven specifically by  
107 an increased need for ‘controlled semantic retrieval’, a mechanism that is engaged when  
108 automatic semantic retrieval fails to activate semantic information necessary for the task at  
109 hand, and a further goal-directed semantic search needs to be initiated (Badre and Wagner,  
110 2007; Krieger-Redwood et al., 2015).

111 To date, there have been but a few neuroimaging investigations that have directly  
112 questioned the involvement of the SCN in social cognitive processing. Two recent fMRI  
113 studies compared activation during semantic judgements made on social and non-social  
114 stimuli and found that the IFG and pMTG were engaged by both stimulus types (Binney et  
115 al., 2016; Rice et al., 2018). Further, Satpute et al., (2014) found that controlled retrieval, but  
116 not selection of social conceptual information engages the anterior IFG. However, we are not  
117 aware of any prior studies that attempt to examine the engagement of the SCN specifically  
118 during tasks that are commonly viewed as social in nature (e.g., ToM tasks). As a starting  
119 point, rather than conducting a novel individual experiment, the present study adopted a  
120 meta-analytic approach to extract reliable trends from large numbers of studies. Meta-  
121 analyses of functional neuroimaging data overcome the limitations of individual studies  
122 (Cumming, 2014; Eickhoff et al., 2012), which are frequently statistically underpowered  
123 (Button et al., 2013) and vulnerable to effects of idiosyncratic design and analytic choices  
124 (Botvinik-Nezer et al., 2020; Carp, 2012) so that it becomes difficult to distinguish between

125 replicable and spurious findings and to generalize the results. Our principal aim was to  
126 determine whether the distributed neural activation commonly associated with functional  
127 neuroimaging studies of social cognition extends to the neural networks underpinning  
128 semantic control (i.e., SCN and MDN). In order to localise the brain network sensitive to  
129 semantic control demands (i.e., semantic retrieval and/or selection), and then compare and  
130 contrast it to networks implicated in social cognition, we performed an update of Noonan et  
131 al.'s (2013) meta-analysis of semantic control (also see Jackson, 2021a).

132 We took the approach of investigating multiple sub-domains of social cognition in  
133 parallel because this should allow an assessment of the extent to which inferences are  
134 generalisable, rather than specific to certain types of social tasks and/or abilities. We chose to  
135 focus on four particular areas of research that target abilities frequently identified as key  
136 facets of the human social repertoire - ToM, empathy, trait inference, and moral reasoning  
137 (Lieberman, 2007; Van Overwalle, 2009) – and, for each, we conducted separate meta-  
138 analyses of the available functional imaging data to determine the brain regions consistently  
139 implicated. In the case of trait inference, this was the first neuroimaging meta-analysis to  
140 include studies that used stimuli other than faces (see Section 2, and also Bzdok et al., 2011,  
141 and Mende-Sieddecki et al., 2013, for contrasting approaches). In the other three cases, we  
142 performed updates of prior meta-analyses (Eres et al., 2018; Molenberghs et al., 2016;  
143 Timmers et al., 2018).

144 Further, we conducted an exploratory conjunction analysis aimed at identifying brain  
145 areas reliably implicated in all four social sub-domains and, thus, a core network for social  
146 cognitive processing (Bzdok et al., 2012; Schurz et al., 2020; Van Overwalle, 2009). We  
147 hypothesised that this core network would include parts of the MDN and the SCN. It is of  
148 note that, across all four social sub-domains, we took a different approach to study inclusion  
149 and exclusion criteria than that taken by some prior meta-analyses of general social cognition

150 (e.g., Van Overwalle, 2009). In particular, we excluded studies investigating processes  
151 associated primarily with the self because social cognition is, although perhaps only in the  
152 strictest sense, about understanding other people. We also excluded studies in which tasks  
153 could be completed based on relatively simple perceptual processing and without a need for  
154 deeper cognitive and inferential processes (e.g., emotion discrimination tasks, automatic  
155 imitation). This was done in an attempt to constrain our inferences to be about the  
156 neurobiology underpinning cognitive rather than primarily perceptual social processes (for  
157 further detail on this distinction, see Adolphs, 2010, and Binney & Ramsey, 2020).

158         Finally, as a secondary aim, the present study used the meta-analytic approach to  
159 assess whether there are differences in the neural networks engaged by implicit and explicit  
160 social processing (also see Dricu & Frühholz, 2016; Eres et al., 2018; Fan et al., 2011;  
161 Molenberghs et al., 2016; Timmers et al., 2018). This was aimed at addressing a pervasive  
162 distinction in the social neuroscientific literature between automatic and controlled processes  
163 (Adolphs, 2010; Happé et al., 2017; Lieberman, 2007), and followed an assumption that  
164 implicit paradigms engage only automatic processes, whereas controlled processes are  
165 recruited during explicit paradigms (Sherman et al., 2014); automatic processes are described  
166 as unintentional, effortless, and fast, whereas controlled processes are deliberate, effortful,  
167 and thus slower (Lieberman, 2007; Shiffrin and Schneider, 1977). Some authors have argued  
168 that automatic and controlled social processes are mutually exclusive of one another and  
169 draw upon distinct cortical networks, with the former engaging lateral temporal cortex, the  
170 amygdala, ventromedial frontal cortex and the anterior cingulate, and the latter engaging  
171 lateral and medial prefrontal and parietal cortex (Forbes and Grafman, 2013; Lieberman,  
172 2007). However, these dual-process models have been criticised for over-simplifying both the  
173 distinction and the relationship between automatic and controlled processes (Amodio, 2019;  
174 Cunningham and Zelazo, 2007; Ferguson et al., 2014; Fidler and Hütter, 2014; Fujita et al.,

175 2014; Melnikoff and Bargh, 2018). An alternative proposal, that we describe above, makes a  
176 different distinction - one between representation and control. This neurocognitive model  
177 proposes that social processing relies on a single-route architecture wherein the degree to  
178 which cognitive processing has certain attributes (e.g., speed or effort) does not reflect one  
179 system versus another. Instead, it is proposed that it reflects the degree to which the control  
180 system needs to exert influence, upon otherwise automatic activation within the  
181 representational system, in order to meet the demands of a task in an appropriate and efficient  
182 manner (Binney and Ramsey, 2020; Jefferies, 2013). If the dual route model is correct,  
183 explicit but not implicit social paradigms should differentially engage brain regions  
184 associated with cognitive control demands, including the SCN and MDN. If the single-route  
185 model is correct, then there should be no qualitative difference in terms of the network of  
186 regions activated by implicit paradigms (ergo automatic processing) and explicit paradigms  
187 (ergo controlled processing), although there may be differences in the magnitude of regional  
188 activation.

189 To summarise, the aims of the present study were as follows: 1) explore the  
190 involvement of domain-general control systems in social cognition; more specifically,  
191 determine whether social cognitive processing reliably engages brain areas implicated in the  
192 controlled retrieval and selection of conceptual knowledge; and 2) examine the evidence for  
193 dual-route and single-route models of controlled social cognition.

194

## 195 **2. Methods**

196 *Preregistration and Open Science statement.* Following open science initiatives  
197 (Munafò et al., 2017), the current study was pre-registered via the Open Science Framework  
198 (OSF; [osf.io/fktb8/](https://osf.io/fktb8/)). We adhered to our pre-registered protocols with a few minor exceptions  
199 (see Section S1 of Supplementary Information (SI) 1 for details). All the raw datasets are

200 openly-available on the OSF project page and are accompanied by a range of study  
201 characteristics including details that are not the focus of the present study but may be of  
202 interest in future research (please see Section S1 of SI 1 for a detailed description). Moreover,  
203 the input data and output files of all analyses can be accessed via the OSF page.

204

205 In accordance with our pre-registered aims, we performed a comprehensive review of  
206 published functional neuroimaging studies investigating four social abilities – Theory of  
207 mind (ToM), trait inference, empathy and moral reasoning - and independent coordinate-  
208 based meta-analyses aimed at characterising the brain-wide neural networks underpinning  
209 each. In the case of three of these domains (ToM, empathy and moral reasoning), we updated  
210 earlier meta-analyses (Eres et al., 2018; Molenberghs et al., 2016; Timmers et al., 2018),  
211 capitalizing on additional data, and also implementing recommendations for best practice that  
212 became available in a year subsequent to these prior studies (Müller et al., 2018). In the case  
213 of trait inference, as far as we are aware, this was the first neuroimaging meta-analysis to  
214 include studies that explored potential sources of information beyond face stimuli (see Bzdok  
215 et al., 2011; Mende-siedlecki et al., 2013, for contrasting approaches). To localise the brain  
216 areas underpinning semantic retrieval and selection, we also updated a meta-analysis of  
217 functional imaging studies of semantic control by Noonan et al. (2013). This involved the  
218 inclusion of additional data, and improvements in meta-analytic tools which corrected  
219 previous implementation errors that led to the use of liberal statistical thresholds (Eickhoff et  
220 al., 2017).

221 To directly address our first aim, we assessed the degree of overlap between the neural  
222 networks supporting semantic control and those involved in social information processing via  
223 a set of formal conjunctions and contrasts analyses. To address our second aim, where  
224 possible, we contrasted brain-wide activation associated with explicit versus implicit social

225 cognitive paradigms. Tasks that drew the participant's attention to the behaviour/cognitive  
226 process of interest were categorised as explicit, while tasks that used non-specific instructions  
227 (e.g., they involved passive observation of stimuli) or employed orthogonal tasks (e.g., age  
228 judgement) were categorised as implicit. Finally, where sufficient relevant information was  
229 available, we explored the influence of task difficulty on patterns of brain activation.

230 All of the meta-analyses reported below were conducted following best-practice  
231 guidelines recommended by Müller et al. (2018). This, as well as several refinements to  
232 inclusion/exclusion criteria, contributed to methodological differences between the present  
233 meta-analyses and those prior meta-analyses upon which the 'updates' were based. A  
234 summary of similarities and differences is provided in Table S1 (SII) and further details are  
235 given in the sections below.

236

## 237 ***2. 1. Literature Selection and Inclusion Criteria***

### 238 **2. 1. 1. General Approach and Criteria**

239 Where possible, relevant functional neuroimaging studies were initially identified  
240 based on their inclusion in a recent prior neuroimaging meta-analysis. These lists were  
241 supplemented via a search on the Web of Science (WoS) online database  
242 ([www.webofknowledge.com](http://www.webofknowledge.com)) for original reports published in the years subsequent, and by  
243 searching through reference lists of said articles. Each WoS search used the terms ['fMRI' or  
244 'PET'], as well as terms uniquely chosen for a given cognitive domain (see Table 2).

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250 Table 2. Terms used to search the Web of Science database for relevant articles.

<b>Cognitive domain</b>	<b>Search terms</b>
Semantic control	'semantic', 'comprehension', 'conceptual knowledge', 'selection', 'retrieval', 'inhibition', 'control', 'elaboration', 'fluency', 'ambiguity', 'metaphor', 'idiom'
ToM	'theory of mind', 'ToM', 'mentalising', 'mentalizing'
Trait inference	'social judgement', 'social evaluation', 'social attribution', 'trait inference', 'impression formation'
Empathy	'empathy', plus 'empath*' - corresponding variations (e.g. 'empathic')
Moral cognition	'morality', 'moral', 'moral decision making', 'moral emotion', 'harm', 'guilt'

251 *N.b.*, For all five cognitive domains, the search followed the following format: [fMRI OR  
252 PET] AND [term1 OR term2 OR ... OR termX].

253

254 A general set of inclusion criteria applied to all our analyses were as follows:

- 255 1) Only studies that employed task-based fMRI or PET to obtain original data were  
256 included. Studies employing other techniques (e.g., EEG/MEG), meta-analyses and  
257 review articles were excluded.
- 258 2) Studies were only included if they reported whole-brain activation coordinates that  
259 were localised in one of two standardised spaces – Talairach (TAL) or Montreal  
260 Neurological Institute (MNI) – or these coordinates were made available on request  
261 (see Section 1 of SI1). Coordinates reported in TAL space were converted into MNI  
262 space using the Lancaster transform (tal2icbm transform (Lancaster et al., 2007)  
263 embedded within the GingerALE software (version 3.0.2; <http://brainmap.org/ale>).

264 Studies exclusively reporting results from region-of-interest or small volume  
265 correction analyses were excluded because these types of analysis violate a key  
266 assumption of coordinate-based meta-analyses (Eickhoff et al., 2012; Müller et al.,  
267 2018).

268 3) Studies were only included if they reported activation coordinates that resulted from  
269 univariate contrasts clearly aimed at identifying the process of interest (e.g., ToM).  
270 We included contrasts between an experimental task and either a comparable active  
271 control task or a low-level baseline such as rest or passive fixation. Contrasts against  
272 low-level baselines were included in the primary analyses because they can reveal  
273 activity associated with domain-general cognitive processes that is subtracted out by  
274 contrasts between active conditions. This could include semantic processes that are  
275 common to both social and non-social tasks. However, contrasts against low-level  
276 baselines also yield activity associated with differences in perceptual stimulation and  
277 attentional demand. To address this caveat, we repeated the analyses whilst excluding  
278 this subset of contrasts. The results can be found on the project's OSF page  
279 ([osf.io/fktb8/](https://osf.io/fktb8/)). We excluded contrasts that make comparisons between components of  
280 the process of interest (e.g., affective vs. cognitive ToM; utilitarian vs. deontological  
281 moral judgements) because we were interested in the common, core processes that  
282 would be subtracted out by these contrasts (but see the following paragraph).

283 4) Multiple contrasts from a single group of participants (e.g., separate contrasts against  
284 one of two different baseline conditions) were included in a single meta-analysis as  
285 long as they independently met all other inclusion criteria for the primary analyses.  
286 This allowed maximum use of all available data and enabled us to evaluate the effect  
287 of using different types of baseline, for example (see above). However, it is important  
288 to adjust for this (Müller et al., 2018), and accordingly, we adopted an approach to

289 controlling for within-group effects (Turkeltaub et al., 2012); specifically, sets of  
290 activation coordinates from different contrasts, but the same participant group, were  
291 pooled. This means that when we refer to the numbers of experiments, we have  
292 counted multiple contrasts from a single participant sample as one single experiment.  
293 This partially explains why the number of experiments in our analyses is lower than  
294 in those of some prior meta-analyses. However, in formal contrast analyses that  
295 compare different conditions (e.g., instructional cue, task difficulty), contrasts like  
296 these would be separated, and care was also taken to minimize the difference in the  
297 number of experiments on either side of the contrast. For example, if a study reported  
298 two contrasts – one implicit and one explicit - based on the same participant group,  
299 only the peaks from the implicit task would be included in the contrast/conjunction  
300 analyses if there were a greater number of explicit than implicit tasks overall (see  
301 Figure S8).

302 5) Only studies that tested healthy participants were included. Contrasts including  
303 clinical populations or pharmacological interventions were excluded.

304 6) Only research articles published in English were included.

305

### 306 2.1.2. Theory of Mind

307 This meta-analysis was built upon that of Molenberghs et al. (2016) and only included  
308 studies that were specifically designed to identify the neural network underpinning ToM  
309 processes (i.e., they employed tasks involving inferences about the mental states of others,  
310 including their beliefs, intentions, and desires). Therefore, studies that looked at passive  
311 observation of actions, social understanding, mimicry or imitation were not included, unless  
312 tasks included a ToM component. Unlike Molenberghs et al., (2016), we excluded studies  
313 investigating irony comprehension (e.g., Wang et al., 2006) because ToM might not always

314 be necessary to detect non-literal meaning in language (Ackerman, 1983; Bosco et al., 2018;  
315 Pexman, 2008) and studies that employed interactive games (e.g., Rilling et al., 2008). These  
316 latter studies are commonly designed to investigate the degree to which ToM is engaged  
317 under different task conditions rather than distinguish activation associated with ToM from  
318 that related to other processes. Moreover, unlike Molenberghs et al. (2016), we excluded  
319 studies that employed trait inference tasks as these were considered separately (see Section  
320 2.1.3).

321 Molenberghs et al.'s (2016) search was inclusive of fMRI studies published prior to  
322 July 2014 and yielded 144 independent experiments (1789 peaks) contributing to their  
323 analysis. We performed a WoS search for further original fMRI and PET studies conducted  
324 between August 2014 and March 2020, and a search of PET studies published prior to July  
325 2014. We then applied our inclusion criteria to both newly identified studies and those  
326 analysed by Molenberghs and colleagues (see Table S1 for further differences in criteria). In  
327 the end, we found 136 experiments with a total number of 2158 peaks and 3452 participants  
328 that met our criteria for inclusion (see Figure S1 of SI1 for more details regarding the  
329 literature selection process; and Table S1 of SI2 for a full list of the included experiments).

330

### 331 2.1.3. Trait inference

332 Studies were included in the meta-analysis if they employed tasks that required the  
333 participants to infer the personality traits of others based on prior person knowledge or  
334 another's appearance and/or behaviour. Whereas the types of mental states typically inferred  
335 in ToM tasks are transitory in nature (e.g., relating to immediate goals or the intentions  
336 behind a specific instance of behaviour), traits are coherent and enduring dispositional  
337 characteristics of others (i.e., personality traits; Van Overwalle, 2009). Previous meta-  
338 analyses (Molenberghs et al., 2016; Schurz et al., 2014) of ToM have included tasks

339 requiring trait inferences. However, it has been suggested that personality trait inferences  
340 differ from mental state inferences in terms of likelihood and speed of processing, and hold a  
341 higher position in the hierarchical organisation of social inferential processes (Korman and  
342 Malle, 2016; Malle and Holbrook, 2012). In line with this proposal, we maintained a  
343 distinction and performed separate analyses. Moreover, previous imaging meta-analyses of  
344 trait inference were limited to studies that used face stimuli (Bzdok et al., 2011; Mende-  
345 siedlecki et al., 2013). However, trait inferences can be made on the basis of many different  
346 sources of information, including physical appearance, behaviour and prior knowledge about  
347 others (Uleman et al., 2007). To our knowledge, the present attempt is the first to include  
348 studies that required participants to make trait inferences based on facial photographs,  
349 behavioural descriptions *or* prior person knowledge. We excluded any studies that asked  
350 participants to make inferences about transitory mental states, including basic emotions. We  
351 also excluded studies that did not use a subtraction approach, but rather investigated brain  
352 activity that varied parametrically with the levels of a pre-defined trait dimension (e.g. Engell  
353 et al., 2007). Finally, we excluded studies that included emotional face stimuli to avoid  
354 conflating brain activity related to trait inference with that associated with emotion  
355 recognition and processing.

356 We performed a WoS search of studies published before March 2020 and reference-  
357 tracing to identify relevant studies for inclusion in the meta-analysis. A total of 40  
358 experiments with 523 peaks and 732 participants were found to meet the criteria for inclusion  
359 (Figure S2 - SI1; Table S2 - SI2).

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#### 364 2.1.4. Empathy

365 This meta-analysis was built upon that of Timmers et al. (2018) and only included  
366 studies that were specifically designed to identify the neural network underpinning empathy  
367 by employing tasks asking participants to observe, imagine, share and/or evaluate the  
368 emotional or sensory state of others. The task definition was kept identical to previous meta-  
369 analyses on empathy (Fan et al., 2011; Timmers et al., 2018). We also made a distinction  
370 between tasks eliciting empathic responses to other people's pain and those investigating  
371 empathic responses to others' affective states.

372 Timmers et al. (2018) included studies published before December 2017, totalling 128  
373 studies with 179 contrasts (1963 peaks). We identified additional original studies conducted  
374 between January 2018 and March 2020 via a WoS search and subsequently applied our  
375 inclusion criteria to all, including those analysed by Timmers et al. (2018) (see Table 1 for  
376 further differences in criteria). This resulted in a yield of 164 experiments with a total number  
377 of 2704 peaks and 4423 participants (Figure S3 - SI1; Table S3 – SI2). Empathy for pain was  
378 independently investigated in 93 of these experiments, empathy for affective states was  
379 independently explored in 70 experiments, and 9 experiments concurrently explored both  
380 empathy for pain and emotions in the same contrasts.

381

#### 382 2.1.5. Moral reasoning

383 This analysis updated a previous meta-analysis conducted by Eres et al., (2018) and  
384 included studies that employed tasks designed to investigate judgements and decision-making  
385 based on moral values. In line with Eres et al., (2018), studies that did not specifically have a  
386 morality component were not included. For example, studies investigating judgements  
387 regarding adherence to social expectations but not moral values (e.g., Bas-Hoogendam et al.,  
388 2017) were excluded.

389 Eres et al., (2018)'s search was restricted to fMRI studies and covered the period  
390 before February 2016 yielding 123 contrasts (989 peaks). We expanded this list via a WoS  
391 search for original fMRI and PET studies published between March 2016 and March 2020,  
392 and a search for PET studies published before March 2016, and then applied our inclusion  
393 criteria (see Table 1 for differences in criteria). This resulted in a yield of 69 experiments  
394 with a total number of 909 foci and 1609 participants (Figure S4 - SI1; Table S4 – SI2).

395

#### 396 2.1.6. Semantic Control

397 In this meta-analysis, we sought to extend an earlier meta-analysis conducted by  
398 Noonan et al. (2013). In line with theirs, this analysis only included studies that were  
399 specifically investigating semantic processing, and that reported contrasts that reflected high  
400 > low semantic control, or comparisons between a task requiring semantic control and an  
401 equally demanding executive decision in a non-semantic domain. We excluded studies with a  
402 focus upon priming without an explicit semantic judgment (e.g., primed lexical decision),  
403 bilingualism, episodic memory, or sleep consolidation.

404 Noonan et al., (2013)'s search covered the period between January 1994 and August  
405 2009 and yielded 53 studies (395 peaks) that met their criteria for inclusion in their analysis.  
406 We performed a WoS search for original studies published between September 2009 and  
407 March 2020, and reference-tracing, and then applied our inclusion criteria to both newly  
408 identified studies and those analysed by Noonan et al. (2013). This produced a yield of 96  
409 experiments with a total number of 981 peaks and 2052 participants that met the criteria for  
410 inclusion in our analysis (Figure S5 - SI1; Table S5 – SI2).

411

## 412 **2.2. Data Analysis**

413 We performed coordinate-based meta-analyses using the revised activation likelihood  
414 estimation (ALE) algorithm (Eickhoff et al., 2012, 2009; Turkeltaub et al., 2012)  
415 implemented in the GingerALE 3.0.2 software (<http://brainmap.org/ale>). We used the  
416 GingerALE software to conduct two types of analysis. The first were independent dataset  
417 analyses, which were used to identify areas of consistent activation across particular sets of  
418 experiments. These analyses were performed only on the experiment samples with a  
419 recommended minimum of 17 experiments in order to have sufficient power to detect  
420 consistent effects and circumvent the possibility of results being driven by single experiments  
421 (Eickhoff et al., 2016). The ALE meta-analytic method treats reported activation coordinates  
422 as the centre points of three-dimensional Gaussian probability distributions which take into  
423 account the sample size (Eickhoff et al., 2009). First, the spatial probability distributions of  
424 all coordinates reported were aggregated, creating a voxel-wise modelled activation (MA)  
425 map for each experiment. Then, the voxel-wise union across the MA maps of all included  
426 experiments was computed, resulting in an ALE map that quantifies the convergence of  
427 results across experiments (Turkeltaub et al., 2012). The version of GingerALE used in the  
428 present study tests for above-chance convergence between experiments (Eickhoff et al.,  
429 2012) thus permitting random-effects inferences.

430 Following the recommendations of Eickhoff et al. (2016), for the main statistical  
431 inferences, the individual ALE maps were thresholded using cluster-level family-wise error  
432 (FWE) correction of  $p < 0.05$  with a prior cluster-forming threshold of  $p < 0.001$ . Cluster-  
433 level FWE correction has been shown to offer the best compromise between sensitivity to  
434 detect true convergence and spatial specificity (Eickhoff et al., 2016). This was  
435 complemented by a highly conservative voxel-level FWE correction of  $p < 0.05$  which,  
436 despite the decreased sensitivity to true effects, allows the attribution of significance to each

437 voxel above the threshold, offering increased spatial specificity (Eickhoff et al., 2016). The  
438 FWE-corrected cluster-level and voxel-height thresholds were estimated using a permutation  
439 approach with 5000 repetitions (Eickhoff et al., 2012). None of the meta-analyses that we  
440 updated had used the recommended cluster-level FWE or the FWE height-based correction  
441 methods.

442 The second set of analyses, conjunction and contrast analyses, were also performed in  
443 GingerALE and were aimed at identifying similarities and differences in neural activation  
444 between the different sets of studies. The conjunction images were generated using the  
445 voxel-wise minimum value (Nichols et al., 2005) of the included ALE maps to highlight  
446 shared activation. Contrast images were created by directly subtracting one ALE map from  
447 the other to highlight unique neural activation associated with each dataset (Eickhoff et al.,  
448 2011). Then, the differences in ALE scores were compared to a null-distribution estimated  
449 via a permutation approach with 5000 repetitions. The contrast maps were thresholded using  
450 an uncorrected cluster-forming threshold of  $p < 0.001$  and a minimum cluster size of 200  
451  $\text{mm}^3$ .

452 In addition, we performed post-hoc analyses to investigate if the clusters of  
453 convergence revealed by the ALE analyses were driven by experiments featuring specific  
454 characteristics of interest (i.e., type of instructional cue, task difficulty). To this end, we  
455 examined the list of experiments that contributed at least one peak to each ALE cluster and  
456 compared the number of contributing experiments featuring the characteristic of interest (e.g.,  
457 explicit vs implicit processing) by conducting Fisher's exact tests of independence and post-  
458 hoc pairwise comparisons (using False Discovery Rate correction for multiple comparisons)  
459 in RStudio Version 1.2.5001 (RStudio Team, 2020).

460 A full list of the confirmatory and exploratory analyses we conducted can be found in  
461 Section 3 of SI1.

462

### 463 **3. Results**

#### 464 **3.1. *The “Social Brain”***

##### 465 3.1.1. Theory of Mind

466 Convergent activation across all 136 ToM experiments was found in 13 clusters (see  
467 Figure 1a and Table S1.1.1 – S1.3) located within the bilateral middle temporal gyrus (MTG)  
468 (extending anteriorly towards the temporal poles and also in a posterior and superior direction  
469 towards the superior temporal gyrus (STG) and angular gyrus (AG) in both hemispheres),  
470 bilateral IFG, bilateral dorsal precentral gyrus, ventromedial prefrontal cortex (vmPFC),  
471 dorsomedial prefrontal cortex (dmPFC), pre-SMA, precuneus, left fusiform gyrus and left  
472 and right cerebellum. All these clusters survived both the height-based and extent-based  
473 thresholding. A cluster in the posterior cingulate cortex (PCC) survived height-based  
474 thresholding but did not survive extent-based thresholding. These results are largely  
475 consistent with those of Molenberghs et al. (2016), with the difference being that they did not  
476 find activation in SMA, left fusiform gyrus or cerebellum. In order to address concerns  
477 regarding the validity of some other popular ToM tasks (Heyes, 2014; Quesque and Rossetti,  
478 2020), we conducted a separate supplementary meta-analysis that was limited to the subset of  
479 ToM experiments that employed false belief tasks (see Section 3.1 of SI1, Table S1.1.2). This  
480 analysis revealed convergent activation in similar temporo-parietal and medial frontal regions  
481 to the inclusive ToM analysis but did not implicate the lateral frontal cortex.

482

##### 483 3.1.2. Trait inference

484 The ALE meta-analysis revealed convergent activation across 40 experiments in 8  
485 clusters (Figure 1b, Table S1.2) implicating the bilateral IFG, dmPFC, vmPFC, PCC, right  
486 pMTG (extending to AG), left AG and left anterior MTG. Voxels from all clusters, except for

487 those in the right pMTG and vmPFC, survived the more conservative height-based  
488 thresholding.

489

### 490 3.1.3. Empathy

491 The ALE meta-analysis of all 164 empathy experiments revealed 16 clusters of  
492 convergent activation (Figure S6a; Table S1.3.1), including in the bilateral IFG (extending  
493 towards the insula), SMA, dmPFC, bilateral posterior inferior temporal gyrus (ITG), right  
494 pMTG, bilateral supramarginal gyrus (SMG), left inferior parietal lobule (IPL), bilateral  
495 occipital cortex, left amygdala, left thalamus, left caudate and brainstem. These clusters  
496 survived both the height-based and extent-based thresholding, except for the anterior dmPFC,  
497 right pMTG and brainstem clusters, which survived extent-based thresholding only. Two  
498 clusters, one in the right cerebellum and one in the right hippocampus survived height-based  
499 thresholding but did not survive cluster extent-based thresholding. These areas were also  
500 implicated by Timmers et al. (2018). In contrast, however, we did not find convergent  
501 activation in the left posterior fusiform gyrus, left SMG (although we found a cluster slightly  
502 more posterior and inferior), left anterior ITG, right TP, precuneus, middle cingulate gyrus,  
503 right superior parietal lobule, and right amygdala.

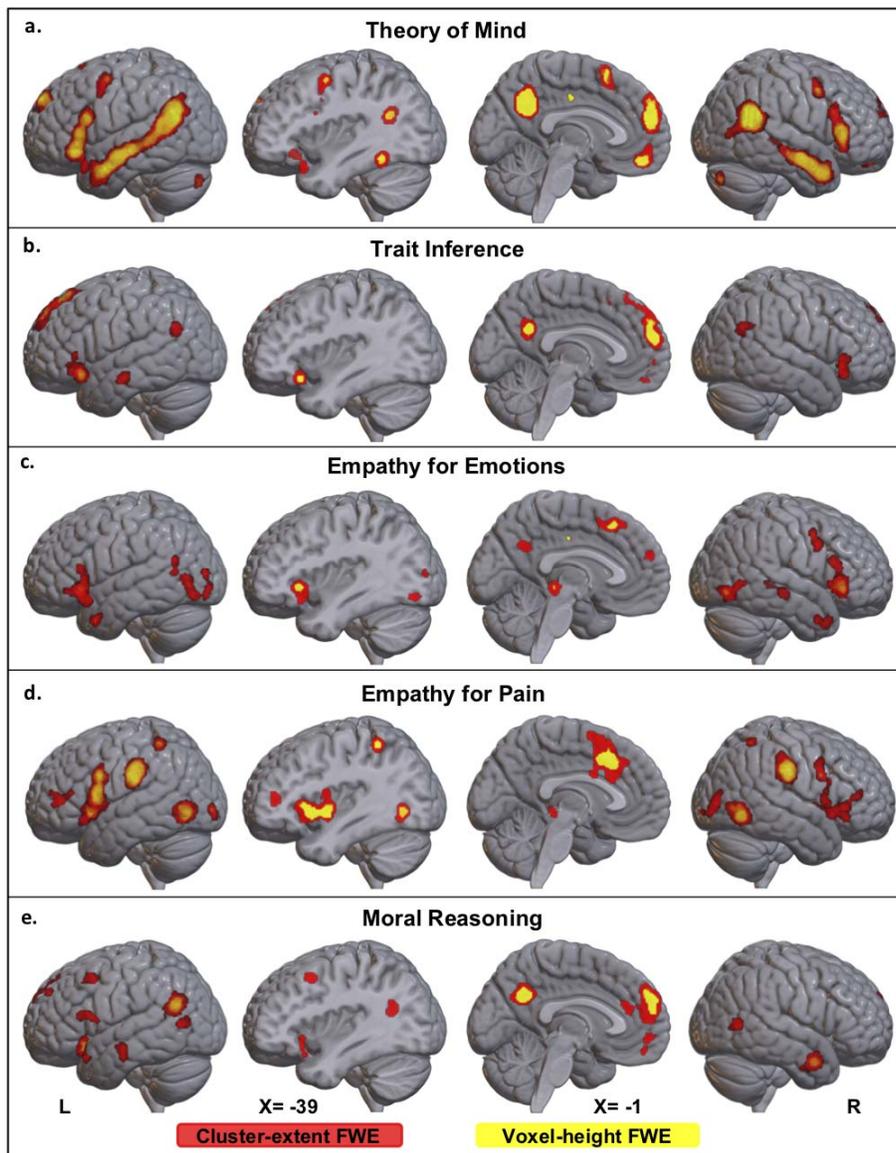
504 The separate ALE maps for empathy for pain and empathy for affective states are  
505 displayed in Figure 1c and d. A conjunction analysis found activation common to empathy  
506 for pain (Table S1.3.2) and empathy for affective states (Table S1.3.3) in the bilateral insula  
507 (extending to the IFG), SMA, right precentral gyrus, right ITG, bilateral occipital cortex and  
508 the brainstem (Figure S6b; Table S1.3.4). Formal contrasts revealed that empathy for pain  
509 and empathy for emotions also engage highly distinct brain areas (Figure S6b; Table S1.3.4).  
510 Clusters with increased convergence for empathy for pain were found in left IFG (pars  
511 triangularis), right MFG, bilateral insula, middle cingulate gyrus, bilateral SMG, right IPL

512 and bilateral pITG. In contrast, increased convergence in empathy for affective states was  
513 revealed in left IFG (pars orbitalis), PCC, left pMTG, right temporal pole and left anterior  
514 MTG. Given these significant differences in their underlying neural networks, empathy for  
515 pain and empathy for emotions were considered separately for all subsequent analyses.

516

#### 517 3.1.4. Moral reasoning

518 Convergent activation across all 69 experiments studying moral reasoning was found in  
519 11 clusters (Figure 1e, Table S1.4) located in the left IFG, left insula (extending towards the  
520 superior temporal pole), mPFC, medial orbitofrontal cortex (OFC), precuneus, bilateral  
521 pMTG, and the bilateral anterior MTG. Only four clusters - left insula, mPFC, precuneus and  
522 left pMTG - survived height-based thresholding. These results are mostly consistent with  
523 those obtained by Eres (2018), with the difference that we did not find convergent activation  
524 in the left amygdala and right AG, and found additional clusters of convergent activation in  
525 left MFG, bilateral anterior MTG, and right pMTG.



526 Figure 1. Binary whole-brain ALE maps showing statistically significant convergent  
527 activation resulting from independent meta-analyses of ToM studies (N=136), trait  
528 inference (N= 40), empathy for pain (N=80) and emotions (N=75) and moral  
529 reasoning (N=69). The ALE maps were thresholded using an FWE corrected cluster-  
530 extent at  $p < .05$  with a cluster-forming threshold of  $p < .001$  (red) and an FWE  
531 corrected voxel-height threshold of  $p < .05$  (yellow). The lateral views, which show  
532 projections on the cortical surface, are accompanied by brain slices at the sagittal

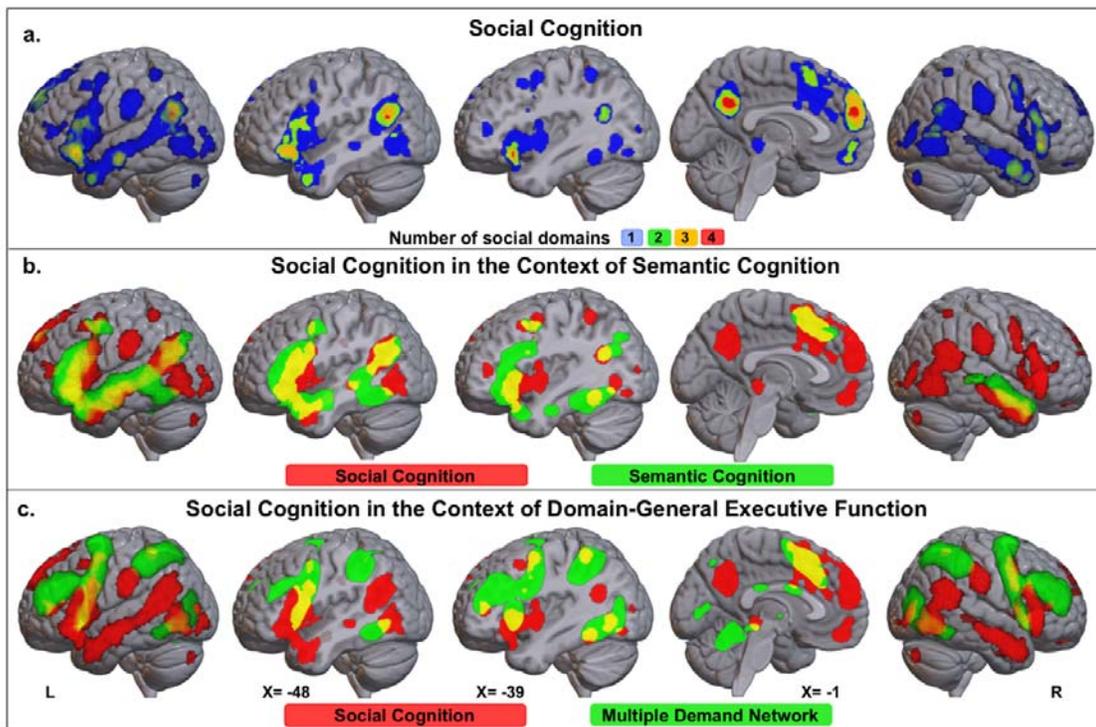
533 midline and also coplanar with the peak of the left IFG cluster observed across all  
534 social domains ( $X = -39$ ; Table S1.5).

535

### 536 3.1.5. A common network for multiple sub-domains of social cognition

537 To identify brain areas consistently activated across multiple sub-domains of social  
538 cognition, we performed an overlay conjunction analysis of the cluster-extent FWE-corrected  
539 ALE maps associated with ToM, trait inference, empathy (for pain and/or emotions) and  
540 moral reasoning (see Figure 2a, Table S1.5). Convergent activation across all four socio-  
541 cognitive sub-domains was found in the left IFG (pars orbitalis), mPFC, precuneus and left  
542 pSTG. Overlapping areas of activation across three of four social sub-domains included right  
543 IFG, left IFG (pars triangularis and pars opercularis), SMA, medial OFC, left MTG, right  
544 anterior MTG and right PMTG. Overlap between two of four maps was found in right  
545 posterior IFG, bilateral precentral gyrus, right AG, right PMTG, left TP and left PMTG.  
546 Because the conservative thresholding used in this analysis could have excluded smaller  
547 clusters that nonetheless overlap across the sub-domains, we repeated the conjunction using  
548 ALE maps treated with a more liberal statistical threshold of  $p < .001$  uncorrected. This  
549 revealed additional overlapping activation for all four social domains in the right IFG (pars  
550 orbitalis) and bilateral ATL (Figure S7). These brain areas have been implicated in a variety  
551 of social-cognitive abilities by multiple previous meta-analyses (Alcalá-López et al., 2018).

552 The extent to which brain regions engaged in social cognition overlap with those engaged  
553 in general semantic cognition (including both representation and control processes) is  
554 illustrated in Figure 2b. Figure 2c shows that the brain regions engaged in social cognition  
555 are largely non-overlapping with the network engaged by domain-general executive  
556 processes (i.e., the MDN).



557

558 Figure 2. The neural network engaged in social cognitive processing: (a) An overlay  
559 conjunction of the ALE maps resulting from independent meta-analyses of ToM studies,  
560 trait inference, empathy for pain/emotions, and moral reasoning. The map displays the  
561 number of social domains showing convergent activation in each voxel. The ALE maps  
562 were thresholded using an FWE corrected cluster-extent threshold at  $p < .05$  with a  
563 cluster-forming threshold of  $p < .001$ . (b) The binarized social cognition map (red)  
564 generated by the overlay conjunction is displayed overlaid with a binarized ALE map of  
565 convergent activation across  $N = 415$  semantic  $>$  non-semantic contrasts generated in  
566 Jackson, 2021 (green); overlap is shown in yellow. (c) The binarized social cognition map  
567 (red) generated by the overlay conjunction is displayed overlaid with a mask of the  
568 multiple-demand network (MDN) generated in Fedorenko et al., 2013 (green) by  
569 contrasting hard  $>$  easy versions of seven diverse cognitive tasks; overlap is shown in  
570 yellow. The lateral views, which show projections on the cortical surface, are

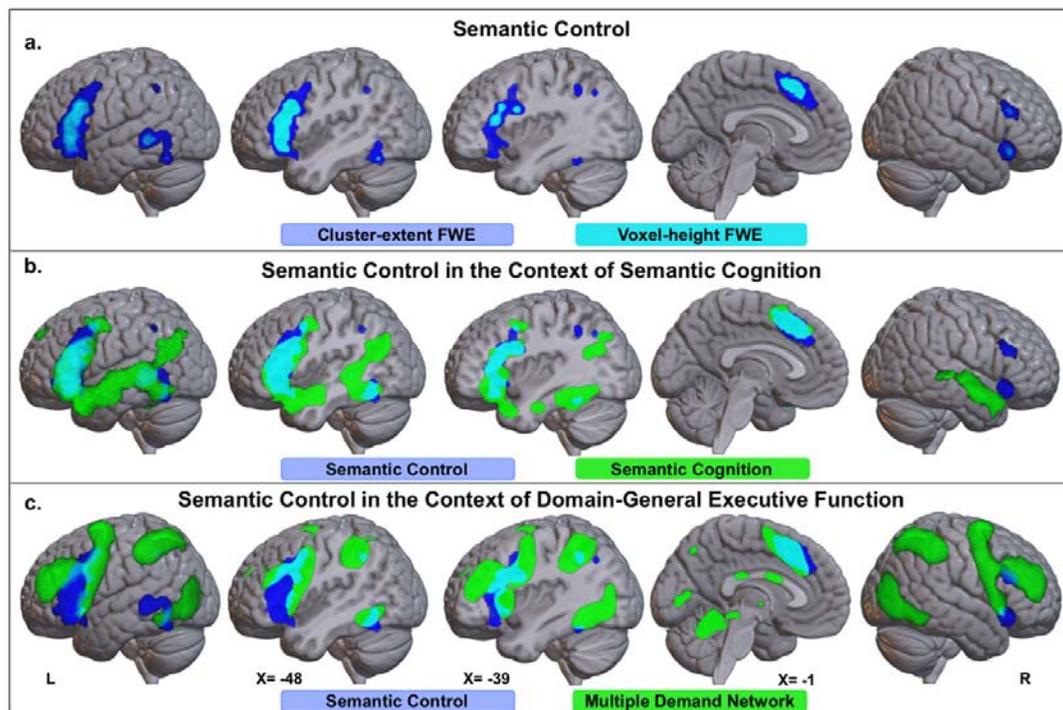
571 accompanied by brain slices at the sagittal midline and also coplanar with the peak of the  
572 left STG (X = -48) and left IFG (X = -39) clusters that overlapped across all four social  
573 domains (Table S1.5).

574

### 575 **3.2. The semantic control network**

576 The ALE meta-analysis of all 96 semantic control experiments revealed convergent  
577 activation in a distributed network consisting of frontal, temporal and parietal areas (Figure  
578 3a, Table S2). The largest cluster was located in the left frontal lobe and extended from the  
579 IFG (pars orbitalis) to MFG. In the right frontal lobe, convergent activation was limited to  
580 two clusters with peaks in pars orbitalis and pars triangularis of the IFG. Consistent activation  
581 was also found in the medial frontal cortex with the peak in SMA. The left temporal cluster  
582 extended from the posterior portion of the MTG, which showed the highest level of  
583 convergence, to the fusiform gyrus. All these clusters survived both the height-based and  
584 extent-based thresholding. In addition, two left IPL clusters survived only the cluster-extent  
585 FWE correction. In contrast to Noonan et al., (2013), we did not find convergent activation in  
586 ACC, bilateral SFG, left AG, right IPL/SPL, and left anterior MTG.

587 Figure 3b illustrates the extent to which brain regions engaged in semantic control  
588 overlap with those engaged in general semantic cognition (including both representation and  
589 control processes), while Figure 3c illustrates their overlap with the network engaged by  
590 domain-general executive processes (i.e., the MDN).



591

592 Figure 3. The neural network engaged in semantic control: (a) Binarized ALE maps showing  
593 statistically significant convergent activation across 96 experiments contrasting high >  
594 low semantic control thresholded using cluster-extent FWE correction of  $p < .05$  with a  
595 cluster-forming threshold of  $p < .001$  (blue) and voxel-height FWE correction of  $p < .05$   
596 (cyan). (b) The binarized semantic control map (blue) overlaid with a binarized ALE map  
597 of convergent activation across  $N = 415$  semantic > non-semantic contrasts generated in  
598 Jackson, 2021 (green); overlap is shown in cyan. (c) The binarized semantic control map  
599 (blue) overlaid with a mask of the multiple-demand network (MDN) generated in  
600 Federenko et al., 2013 (green) by contrasting hard > easy versions of seven diverse  
601 cognitive tasks; overlap is shown in cyan. The lateral views, which show projections on  
602 the cortical surface, are accompanied by brain slices at the sagittal midline and also  
603 coplanar with the peak of the left STG ( $X = -48$ ) and left IFG ( $X = -39$ ) clusters that  
604 overlapped across all four social domains (Table S1.5).

### 605 ***3.3. Neural substrates shared by semantic control and social cognition***

#### 606 3.3.1. ToM

607 Overlap between the neural network underpinning semantic control (i.e., SCN & regions  
608 of the MDN) and the ToM network was found in 8 clusters located in the left IFG (including  
609 pars orbitalis and triangularis and extending to the precentral gyrus) and, to a smaller extent,  
610 the right IFG, the left dorsal precentral gyrus, SMA, left pMTG, left superior temporal pole  
611 and the left fusiform gyrus (Figure 4a, Table S3.1.1). The results of the conjunction between  
612 semantic control and false belief reasoning can be found in Section 3.1 of SI1 and Table  
613 S3.1.2. This analysis revealed overlapping activation in the pMTG, but not in the SMA or  
614 lateral frontal cortex.

615

#### 616 3.3.2. Trait Inference

617 Brain areas involved in both semantic control and trait inference included bilateral IFG  
618 (pars orbitalis), SMA and dmPFC (Figure 4b, Table S3.2).

619

#### 620 3.3.3. Empathy for emotions

621 The neural network underpinning semantic control overlapped with the areas engaged in  
622 empathy for emotions in bilateral IFG (pars orbitalis and pars triangularis), SMA, left pMTG  
623 and right insula (Figure 4c, Table S3.3).

624

#### 625 3.3.4. Empathy for pain

626 Overlapping activation between empathy for pain and semantic control was revealed in  
627 left IFG (pars orbitalis and pars triangularis), right IFG (pars orbitalis), left precentral gyrus,  
628 bilateral insula, SMA and left posterior ITG (extending towards pMTG) (Figure 4d, Table  
629 S3.4).

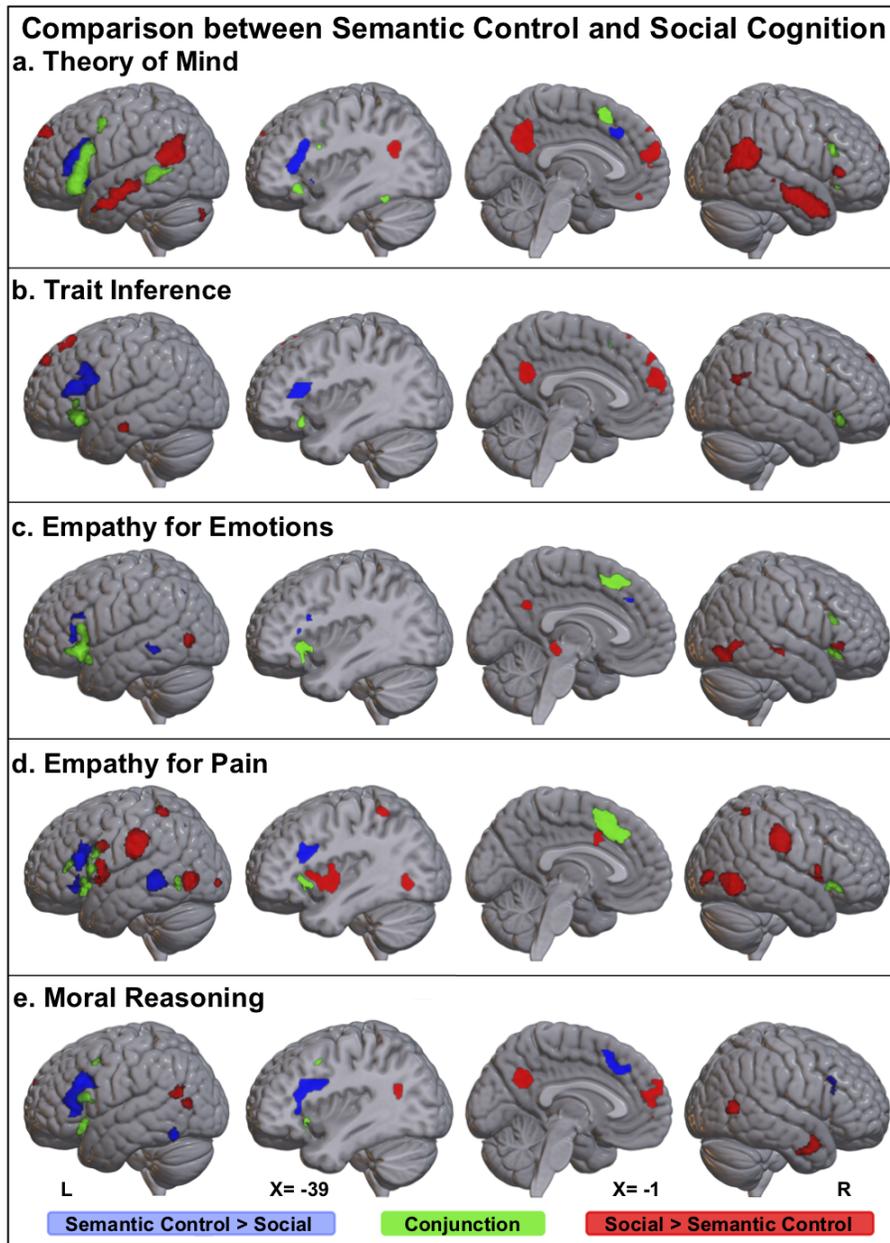
630

631 3.3.5. Moral reasoning

632 Overlapping activation in response to semantic control and moral reasoning included left  
633 insula (extending to pars orbitalis of the IFG), pars opercularis of the left IFG and the left  
634 precentral gyrus (Figure 4e, Table S3.5).

635

636 Overall, the neural network engaged in semantic control overlapped with the neural  
637 networks underpinning all four social domains in the left IFG and, in particular, pars orbitalis.  
638 Except for moral reasoning, overlapping activation was also found in the right IFG (pars  
639 orbitalis) and SMA. In the left pMTG, we found a large area of overlap between semantic  
640 control and ToM and some evidence of overlap between semantic control and empathic  
641 processing.



642 Figure 4. Results of the contrast (blue, red) and conjunction (green) analyses between the  
643 ALE maps associated with semantic control and each social domain: a) Theory of Mind  
644 b) Trait Inference c) Empathy for Emotions d) Empathy for Pain and e) Moral Reasoning.  
645 The contrast maps were thresholded with a cluster-forming threshold of  $p < .001$  and a  
646 minimum cluster size of  $200 \text{ mm}^3$ . The lateral views, which show projections on the  
647 cortical surface, are accompanied by brain slices at the sagittal midline and also coplanar

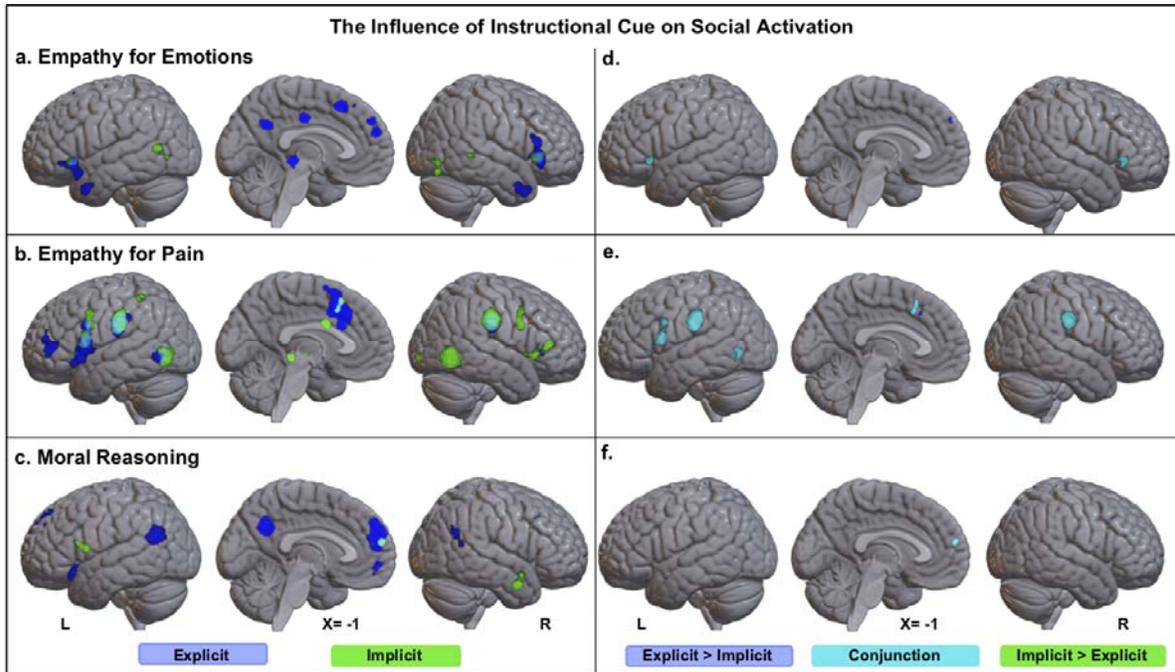
648 with the peak of the left IFG cluster ( $X = -39$ ) that overlapped across all four social  
649 domains (Table S1.5).

650

### 651 **3.4. *Explicit versus implicit social cognition***

652 Further to the meta-analyses above, we compared activation associated with implicit and  
653 explicit paradigms for studying empathy for emotions, empathy for pain and moral reasoning.  
654 The results of independent analyses are displayed in Figure 5 a-c and Tables S4.1.1 – S4.1.6).  
655 Conjunctions and formal contrasts are displayed in Figure 5 d-f and Tables S4.2.1 – S4.2.3).  
656 The only difference between activation associated with explicit and implicit paradigms, as  
657 identified by these formal comparisons, was in the case of empathy, with a small cluster in  
658 the dmPFC showing increased convergence for explicit as compared to implicit empathy (see  
659 Section 3.3.1. of Supplementary Information). In addition, we conducted exploratory cluster  
660 analyses to investigate whether the explicit and implicit experiments contributed similarly to  
661 each of the significant ALE clusters found for each social domain. In summary, these  
662 analyses (Figure S8) revealed that in the case of all social domains, implicit and explicit  
663 experiments contributed equally to most clusters (see Section 3.3.2. of Supplementary  
664 Information for a more detailed description).

665



666 Figure 5. The left panel displays the binary ALE maps showing statistically significant  
667 convergent activation resulting from independent meta-analyses on explicit (blue) and  
668 implicit (green) studies on a) Empathy for Emotions, b) Empathy for Pain and c)  
669 Moral Reasoning. The ALE maps were thresholded using an FWE corrected cluster-  
670 extent threshold of  $p < .05$  with a cluster-forming threshold of  $p < .001$ . The right  
671 panel displays the results of the contrast (dark blue, green) and conjunction (cyan)  
672 analyses between the ALE maps associated with explicit and implicit instructions.  
673 The contrast maps were thresholded at  $p < .001$  and using a minimum cluster size of  
674  $200 \text{ mm}^3$ . The lateral views, which show projections on the cortical surface, are  
675 accompanied by brain slices at the sagittal midline.

676

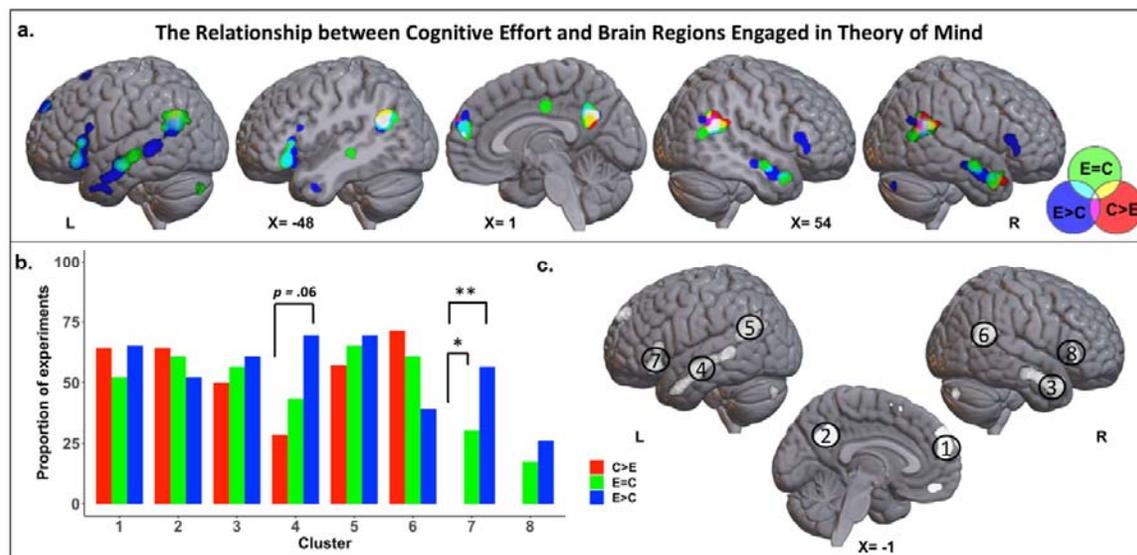
### 677 *3.5. The relationship between cognitive effort and brain regions engaged during social* 678 *cognitive tasks*

679 The above-reported conjunction analyses suggest that social cognition engages  
680 regions associated with semantic control. In these analyses, we took a pooled approach which

681 involved collapsing over many different comparisons between social and non-social tasks and  
682 ignoring subtler differences between experimental and baseline conditions. The key  
683 advantage of this approach is that it identifies activation that is generalisable across highly  
684 variable experimental conditions. However, ignoring experimental differences precludes a  
685 determination of more specific factors driving a given region's involvement. In particular, it  
686 is not possible to directly infer from the above results that semantic control regions are  
687 specifically being engaged by the cognitive control demands of social tasks. Therefore, to  
688 address this issue, we performed a set of exploratory analyses to determine whether the IFG  
689 and pMTG regions are sensitive to the degree of cognitive effort required to complete social  
690 tasks. While these analyses cannot disentangle semantic control from other forms of control,  
691 they represent a further initial step towards confirming a role of semantic control regions in  
692 social regulatory processes. To this end, we took experiments that used explicit paradigms  
693 and, on the basis of reported inferential statistics regarding participants' reaction/decision  
694 times, categorised them according to whether the experimental condition was more difficult  
695 than the control condition ( $E > C$ ), experimental and control conditions ( $E = C$ ) were equally  
696 difficult, or the experimental condition was easier than the control condition ( $C > E$ ). In the  
697 subsequent set of analyses we worked with the premise that in the case of  $E = C$  experiments  
698 and  $C > E$  experiments, activation associated with cognitive effort that is common to both the  
699 experimental and control conditions is subtracted away (along with activation specific to the  
700 control condition). In contrast,  $E > C$  experiments preserve activation associated with  
701 cognitive effort that is specific to the experimental condition. Therefore, a contrast analysis  
702 pitting  $E > C$  experiments against either  $C > E$  or  $E = C$  experiments will reveal activation  
703 associated with cognitive effort specific to the social domain. A conjunction will reveal  
704 activation associated with social processing irrespective of task difficulty.

705           There was only enough information regarding behavioural data to allow for  
706 sufficiently powered analyses in the case of ToM (Figure S9) where there were 26 E>C ToM  
707 experiments and 25 E=C ToM experiments. The results of the independent ALE analyses are  
708 reported in Tables S5.1 – S5.3. A conjunction analysis of E>C and E=C experiments yielded  
709 common activation in the left IFG (pars orbitalis and pars triangularis), dmPFC, precuneus,  
710 bilateral anterior MTG, right pMTG and left SMG (cyan in Figure 6a; Table S5.3) which we  
711 interpret as regions engaged in ToM irrespective of task difficulty. Interestingly, a contrast of  
712 E>C with E=C ToM experiments revealed differential activation in the left pMTG, an area  
713 implicated in semantic control. The full reports of these analyses, including prerequisite  
714 independent ALE analyses on the E>C ToM and E=C ToM experiments, can be found in  
715 Tables S5.1 – S5.4. For completeness, we also analysed C>E ToM experiments, but the  
716 sample size (N=14) was smaller than required to be sufficiently powered (Eickhoff et al.,  
717 2016) and therefore the result should be interpreted with caution (Figure 6a, Table S5.4).  
718 Secondly, we conducted exploratory analyses to assess whether E>C, E=C or C>E ToM  
719 experiments were equally likely to contribute to each activation cluster (Figure 6b).  
720 The clusters were identified in an independent ALE analysis of ToM experiments  
721 limited to those for which the behavioural information was known (Figure 6c; Table  
722 S5.5). We expected clusters within brain areas that have a cognitive control function  
723 to have a disproportionate contribution from experiments in which the experimental  
724 task was more difficult than the control condition. To assess this, we conducted  
725 Fisher’s exact tests and then interrogated significant main effects through post-hoc  
726 pairwise comparisons and using false-discovery-rate adjustments for multiple  
727 comparisons. This cluster analysis revealed that E>C, E=C and C>E experiments  
728 contributed equally to mPFC ( $p = 0.67$ ), precuneus ( $p = 0.8$ ), right anterior MTG ( $p =$   
729  $0.85$ ), left pMTG ( $p = 0.74$ ), right pMTG ( $p = 0.15$ ) and right IFG ( $p = 0.15$ ).

730 Contributions to the left IFG cluster depended on the difficulty category ( $p < .001$ )  
731 and pairwise comparisons indicated that the C>E experiments contributed  
732 significantly less peaks compared to E>C ( $p = .001$ ) and E=C ( $p = .046$ ) experiments.  
733 Contributions to the left anterior MTG cluster also depended on the difficulty  
734 category ( $p = .043$ ) and pairwise comparisons indicated that the C>E experiments  
735 contributed fewer peaks compared to E>C, but this effect did not survive correction  
736 for multiple comparisons ( $p = .06$ ). These results suggest that the left IFG is



737 particularly sensitive to cognitively-challenging ToM processing.  
738 Figure 6. Results of exploratory analyses investigating the effect of task difficulty on ToM  
739 activation: (a) Binary ALE maps showing statistically significant convergent  
740 activation resulting from independent meta-analyses of three subsets of explicit ToM  
741 studies characterized by experimental conditions that were harder than the control  
742 task (E>C; N=26; blue), experimental and control conditions that were equally  
743 difficult (E=C; N=27; green) and control conditions that were harder than the  
744 experimental condition (C>E; N=14; red) as indexed by participant reaction times.  
745 The ALE maps were thresholded using an FWE corrected cluster-extent threshold at  $p$

746 < .05 with a cluster-forming threshold of  $p < .001$ . The lateral views, which show  
747 projections on the cortical surface, are accompanied by brain slices at the sagittal  
748 midline and also coplanar with the peak of the left IFG cluster ( $X = -39$ ) that  
749 overlapped across all four social domains (Table S1.5) and the right pSTG cluster  
750 from the ToM meta-analysis (Table S1.1.1). (b) The results of the cluster analyses  
751 where bars represent the proportion of experiments in each difficulty category  
752 contributing to clusters of interest resulting from an ALE analysis of  $N = 60$  ToM  
753 meta-analysis which included E>C, E=C and C>E experiments. (c) Binary ALE map  
754 showing statistically significant convergent activation across ToM experiments  
755 limited to those for which the behavioural information was known – this map  
756 represented the basis of the cluster analysis. The ALE map was thresholded using an  
757 FWE corrected cluster-extent threshold at  $p < .05$  with a cluster-forming threshold of  
758  $p < .001$ ; \*\*  $p < .001$  \*  $p < .05$ .

759

#### 760 **4. Discussion**

761 Although many contemporary theories of social cognition acknowledge the  
762 importance of control, or regulatory processes (Adolphs, 2010; Amodio and Cikara, 2021;  
763 Frith and Frith, 2012), many key questions remain about their exact nature and neural  
764 underpinnings. These include a) whether multiple forms of cognitive control contribute to  
765 social cognition, b) whether these mechanisms are best understood in terms of domain-  
766 general processes or systems specialised for social information processing and, c) whether  
767 they are ubiquitously involved or selectively engaged according to certain task demands  
768 (Binney and Ramsey, 2020). In the present study, we set out to specifically investigate  
769 whether brain regions implicated in the controlled retrieval and selection of conceptual  
770 knowledge - namely the IFG and pMTG comprising the SCN (Jefferies, 2013; Lambon Ralph

771 et al., 2017) - contribute to social processing. We simultaneously applied this question to  
772 multiple sub-domains of social cognition so that we could assess the extent to which  
773 involvement is general, or specific to certain types of social tasks and/or abilities. And we  
774 adopted a formal meta-analytic approach to extracting reliable trends from across a large  
775 number of functional neuroimaging studies and overcome the limitations of individual  
776 experiments (Cumming, 2014; Eickhoff et al., 2012). We found that theory of mind, trait  
777 inference, empathy, and moral reasoning commonly engage a core social network that  
778 includes the left IFG, left pMTG/AG, mPFC and precuneus. Moreover, the left IFG  
779 (particularly the pars orbitalis) region greatly overlapped with that implicated in an  
780 independent meta-analysis of neuroimaging studies of semantic control. Further, exploratory  
781 analyses suggest that both the left anterior IFG and the left posterior MTG (at a position just  
782 anterior to the ‘temporoparietal junction’) are sensitive to executive demands of social tasks.  
783 We interpret our overall findings as supportive of the hypothesis that the SCN supports social  
784 cognition via a process of controlled retrieval of conceptual knowledge. This aligns with a  
785 broader proposal in which social cognition is described as a flavour of domain-general  
786 semantic cognition and relies on the same basic cognitive and brain systems (Binney &  
787 Ramsey, 2020).

788

#### 789 ***4.1. Cognitive control in social cognition***

##### 790 4.1.1. The contribution of semantic control

791 A form of cognitive control known as semantic control could be crucial for effective  
792 goal-directed social behaviour (Binney and Ramsey, 2020; Satpute et al., 2014). In a broad  
793 sense, semantic control refers to a set of executive processes involved in the attribution of  
794 meaning to stimuli and experiences, and in the production of meaning-imbued behaviour  
795 (Corbett et al., 2015; Lambon Ralph et al., 2017). However, a key distinction has been drawn

796 between a) top-down goal-directed retrieval and b) post-retrieval selection of goal-relevant  
797 semantic knowledge (Badre et al., 2005; Jefferies, 2013; Thompson-Schill et al., 1997), and it  
798 has been suggested that both of these two semantic control mechanisms contribute  
799 significantly to interpersonal interactions (Binney and Ramsey, 2020; Satpute and  
800 Lieberman, 2006). Studies of semantic cognition suggest that ‘selection’ is engaged when  
801 bottom-up, automatic activation of conceptual knowledge results in multiple competing  
802 semantic representations and/or responses. Social interactions frequently involve subtle or  
803 ambiguous cues, such as neutral facial expressions and bodily gestures, and/or conflicting  
804 cues (e.g., sarcasm). This causes semantic competition that can only be resolved by taking  
805 into account the wider situational and linguistic context and/or prior knowledge about the  
806 speaker (Aviezer et al., 2008; Pexman, 2008). Controlled retrieval processes, on the other  
807 hand, are engaged when automatic semantic retrieval fails to activate the semantic  
808 information necessary for the task at hand. This may occur frequently in social interactions,  
809 and particularly with less familiar persons, because of a preponderance of surface features  
810 (e.g., physical characteristics) over less salient features (e.g., personality traits, preferences,  
811 and mental states). To avoid exchanges that are deemed superficial at best, controlled  
812 retrieval must be used to bring to the fore person-specific but also context-relevant semantic  
813 information.

814         There is now over a decade’s worth of multi-method evidence that semantic control is  
815 underpinned by the left IFG and the left pMTG (Jefferies, 2013; Lambon Ralph et al., 2017).  
816 Research is now aimed at understanding the neural mechanisms by which these regions  
817 modulate semantic processing. One recent proposal is that it involves coordination of  
818 spreading activation across the semantic representational system (Chiou et al., 2018).  
819 According to the hub-and-spoke theory of semantic representation (Lambon Ralph et al.,  
820 2017), coherent concepts are represented conjointly by a central supramodal semantic ‘hub’

821 located in the ATLS, as well as multiple distributed areas of association cortex (i.e. ‘spokes’)  
822 that represent modality-specific information (e.g. visual features, auditory features, verbal  
823 labels, etc). Chiou et al., (2018) showed that the left IFG could be imposing cognitive control  
824 by flexibly changing its effective connectivity with the hub and spoke regions according to  
825 task characteristics; the IFG displayed enhanced functional connectivity with the ‘spoke’  
826 region that processes the most task-relevant information modality. A similar proposal has  
827 been made for the contribution of domain-general cognitive control systems to social  
828 information processing. Zaki et al. (2010) found that, in the presence of conflicting social  
829 cues, IFG activity becomes functionally coupled with the brain areas associated with  
830 processing the particular cue type the participant chose to rely on to make inferences about  
831 emotional states. On this basis, they proposed that cognitive control areas upregulate  
832 activation within systems that represent social cues that are currently most relevant to the  
833 task. Consistent with this, a further study found evidence to suggest that the left IFG  
834 downregulates neural activation associated with task-irrelevant self-referential information  
835 when the task required reference to others (and vice versa) (Soch et al., 2017).

836         An important feature of semantic processing is the ability to accommodate new  
837 information that emerges over extended periods of time and update our internal  
838 representation of the current “state of affairs” in the external world according to contextual  
839 changes. This is particularly important for navigating social dynamics which are liable to  
840 abrupt and sometimes extreme changes in tone. For instance, imagine being in a bar and  
841 having your attention drawn to someone standing suddenly and picking up a glass. One might  
842 reasonably infer that this person is thirsty. That is until they proceed to walk towards a group  
843 of noisy sports fans rather than the bartender. In this case, you will likely adapt your  
844 interpretation and engage in a pre-emptive defensive stance. Recent research suggests that  
845 this ability to update depends, at least in part, on the IFG, as well as the mPFC and ventral

846 IPL (also see Section 4.2.2) (Branzi et al., 2020). Likewise, Lavoie et al., (2016) showed that,  
847 during a ToM task, activation of the left IFG and pMTG is associated with contextual  
848 adjustments of mental state inferences (and also more general physical inferences) although  
849 not the representation of mental states specifically. Left IFG activation has also been  
850 observed when newly-presented information requires one to update the initial impression  
851 formed of another person (e.g., Mende-Siedlecki et al., 2013b, 2013a; Mende-Siedlecki and  
852 Todorov, 2016).

853

#### 854 4.1.2. The wider contribution of executive processes

855         According to Lambon Ralph, Jefferies, and colleagues, the executive component of  
856 semantic cognition comprises both semantic control and other domain-general processes  
857 (Lambon Ralph et al., 2017; Binney & Ramsey, 2020). The latter includes top-down  
858 attentional control and working memory systems that support goal-driven behaviour  
859 irrespective of the task domain (i.e., perceptual, motor or semantic). These processes recruit  
860 nodes of the MDN (Duncan, 2010), which include the precentral gyrus, MFG, IPS, insular  
861 cortex, pre-SMA and adjacent cingulate cortex (Assem et al., 2020; Fedorenko et al., 2013).  
862 In terms of organisation, the SCN appears to be nested among domain-general executive  
863 systems (Wang et al., 2020) and could play a role in mediating interactions between the  
864 MDN and the semantic representational system (Davey et al., 2016; Lambon Ralph et al.,  
865 2017). In line with this general perspective, we expected MDN regions to be reliably engaged  
866 by all four social sub-domains explored in the present meta-analyses. While there was  
867 evidence of engagement of the MFG, the pre-SMA, ACC, insula and IPS in some of the  
868 social sub-domains, MDN regions were not part of the core social processing network  
869 identified by the overlay conjunction analysis. This could reflect the fact that the majority of  
870 contrasts included in our meta-analyses employed high-level control conditions that were

871 well-matched to the experimental conditions in terms of general task requirements, and thus,  
872 most activation associated with general cognitive demands had been subtracted away.  
873 Consistent with this notion is the fact that studies contrasting social tasks with lower-level  
874 control conditions (e.g., passive fixation) find more extensive MDN activation in ToM  
875 (Mason et al., 2008; Mier et al., 2010), trait inference (Chen et al., 2010; Hall et al., 2012),  
876 empathy (De Greck et al., 2012; Tamm et al., 2017) and moral reasoning (Reniers et al.,  
877 2012). The role of the MDN in social cognition is otherwise becoming well-established, and  
878 it has been found to be sensitive to difficulty manipulations in social tasks, showing increased  
879 activation in response to conflicting social cues (Cassidy and Gutchess, 2015; Mitchell,  
880 2013), social stimuli that violate expectations (Cloutier et al., 2011; Hehman et al., 2014; Ma  
881 et al., 2012; Weissman et al., 2008) and increasing social working memory load (Meyer et al.,  
882 2012).

883         Finally, it is important to note that, although both MDN and the SCN co-activate in  
884 social and semantic tasks, the nature of their specific contributions *and* their anatomy are at  
885 least partially dissociable. The MDN is associated with the implementation of top-down  
886 constraints to facilitate goal-driven aspects of processing that is not limited to the semantic  
887 domain (Duncan, 2013; Fedorenko et al., 2013; Gao et al., 2020; Whitney et al., 2012). In  
888 contrast, the engagement of the anterior ventrolateral IFG (pars orbitalis) and the left pMTG  
889 appear specific to the semantic domain and, in particular, controlled semantic retrieval (Badre  
890 and Wagner, 2007; Gao et al., 2020; Hodgson et al., 2021; Whitney et al., 2012). Unlike the  
891 MDN, they do not appear to respond to challenging non-semantic tasks (Gao et al., 2020;  
892 Noonan et al., 2013; Whitney et al., 2012). Further, tasks associated with low conceptual  
893 retrieval demands but a requirement for response inhibition engage the MDN but do not  
894 engage the SCN, even if conceptual knowledge is used to guide responses (Alam et al.,  
895 2018).

896

897 4.1.3. Double-route vs single-route cognitive architecture of social cognition

898 A secondary aim of the present study was to address a pervasive distinction in the  
899 social neuroscientific literature between automatic and controlled processes (Adolphs, 2010;  
900 Happé et al., 2017; Lieberman, 2007). Some authors have argued that automatic and  
901 controlled social processes are mutually exclusive of one another and draw upon distinct  
902 cortical networks (Forbes & Grafman, 2013; Lieberman, 2007; Satpute & Lieberman, 2006).  
903 The alternative is a single-route architecture where the degree to which behaviours have  
904 particular attributes (e.g. speed, effort, intentionality) does not reflect the involvement of one  
905 system and not another, but quantitative differences in the extent to which the control system  
906 interacts with the representational system in order to produce context-/task- appropriate  
907 responses (Binney and Ramsey, 2020). Our results are consistent with the latter perspective.  
908 The brain regions reliably activated in response to explicit instructions and those associated  
909 with implicit instructions revealed more overlap than discrepancy across empathy and moral  
910 reasoning tasks. Notably, this overlap included brain areas associated with executive  
911 functions: the bilateral IFG in the case of empathy for emotions and bilateral IFG and dmPFC  
912 in the case of empathy for pain. Moreover, cluster analyses of the ALE maps associated with  
913 the four social domains suggest that studies using explicit and implicit paradigms (which are  
914 assumed to engage controlled and automatic processing respectively) contributed equally to  
915 most activation clusters, including those in brain regions associated with control processes.  
916 Contrary to the predictions of dual-process models, these findings suggest that common  
917 neural networks contribute to both explicit and implicit social processing (also see Van  
918 Overwalle & Vandekerckhove, 2013). Furthermore, exploratory analyses suggest that both  
919 the left anterior IFG and the pMTG are sensitive to executive demands of social tasks.  
920 Overall, we argue that these results support the existence of a single-route cognitive

921 architecture wherein the contribution made by control mechanisms to implicit and explicit  
922 social processing reflects cognitive effort demanded by the task at hand. This follows similar  
923 proposals put forth specifically in the domain of ToM (Carruthers, 2017, 2016).

924

#### 925 ***4.2. Beyond cognitive control***

926 Our findings converged upon four further regions that have been strongly linked with  
927 key roles in social cognition: the mPFC (including the anterior cingulate), the precuneus, the  
928 ‘temporoparietal junction’ (TPJ), and the ATL. We briefly discuss the putative role of each of  
929 these regions below.

930

##### 931 4.2.1. The ‘Temporo-parietal Junction’

932 A region often referred to as the ‘temporo-parietal junction’ (TPJ) has been subject to  
933 an elevated status within the social neurosciences. In particular, the right TPJ has been  
934 attributed with a key role in representing the mental states of others (Saxe and Wexler, 2005).  
935 In line with previous meta-analyses (Bzdok et al., 2012; Molenberghs et al., 2016; Schurz et  
936 al., 2020, 2014, 2013), our results reveal a bilateral TPJ region that is reliably involved in  
937 ToM tasks. In the left hemisphere, an overlapping area is also implicated in trait inference,  
938 empathy for emotions and moral reasoning which is suggestive of a broader role of the left  
939 TPJ in social cognition. In contrast, the right TPJ showed more limited overlap, being reliably  
940 engaged only by ToM and trait inference tasks, which is suggestive of a more selective role  
941 of the right TPJ in social cognition.

942 The TPJ encompasses a large area of cortex that is poorly defined anatomically and  
943 seems to include parts of the AG, SMG, STG and MTG (Schurz et al., 2017). Moreover, this  
944 area is functionally heterogeneous and has been associated with a variety of cognitive  
945 domains including but not limited to attention, language, numerosity, episodic memory,

946 semantic cognition and social perception (Binder et al., 2009; Decety and Lamm, 2007; Deen  
947 et al., 2015; Humphreys and Lambon Ralph, 2015a; Igelström and Graziano, 2017; Özdem et  
948 al., 2017; Quadflieg and Koldewyn, 2017). While there is some indication that the function of  
949 the TPJ may be dependent on the hemisphere (e.g., Numssen et al., 2021), many cognitive  
950 domains, including ToM, are associated with bilateral TPJ activation. Our results at least  
951 seem to suggest dissociable roles of pMTG and a more posterior TPJ region; while the left  
952 pMTG is activated within both semantic control and ToM studies, a separate and more  
953 posterior STG (TPJ) area located closer to SMG/AG was reliably engaged by all of the social  
954 tasks, but not studies of semantic control. Furthermore, the results suggest that the left pMTG  
955 is sensitive to the difficulty of ToM tasks while the bilateral pSTG (TPJ) region is not.

956         This finding is generally in line with previous research suggesting a functional  
957 dissociation between the left pMTG and the left ventral IPL/AG regions. From one  
958 perspective, the activation of both regions appears to be positively associated with semantic  
959 tasks (Binder et al., 2009). However, the left pMTG shows increased activation to difficult  
960 relative to easier semantic tasks (Jackson, 2021; Noonan et al., 2013), unlike the ventral  
961 IPL/AG which has been shown to deactivate to semantic tasks when they are contrasted  
962 against passive/resting conditions where there may be greater opportunity for spontaneous  
963 semantic processing or ‘mind-wandering’ (Humphreys et al., 2015; Humphreys and Lambon  
964 Ralph, 2015b). Moreover, Davey et al., (2015) found that TMS applied to pMTG disrupted  
965 processing of weak semantic associations more than for strong associations, whereas TMS  
966 applied to AG had the opposite effect. Based on these and similar observations it has been  
967 suggested that the ventral IPL/AG has a role in the automatic retrieval of semantic  
968 information.

969

970 4.2.2. The Default Mode Network

971           The pSTG/AG and the mPFC and precuneus regions we identified as part of the core  
972 social cognition network are also considered part of the default-mode network (DMN)  
973 (Buckner et al., 2008; Spreng and Andrews-Hanna, 2015). The DMN is a resting-state  
974 network, meaning that it is a group of regions consistently co-activated without the  
975 requirement of an explicit task. It is proposed that it is ideally suited for supporting self-  
976 generated internally-oriented, as opposed to externally-oriented, cognition (i.e., it is  
977 decoupled from sensory processing; Margulies et al., 2016; Smallwood et al., 2013). Some of  
978 these regions (e.g., the AG and mPFC) have been also implicated in processes that allow the  
979 integration of information over time (Huey et al., 2006; Humphreys et al., 2020; Ramanan et  
980 al., 2018; Ramanan and Bellana, 2019). These purported functions are all presumably  
981 important for social and more general semantic processing (see Section 4.1.1.) and likely  
982 involve domain-general mechanisms (also see Van Overwalle, 2009). However, the degree to  
983 which regions implicated in the DMN and those implicated in social and/or semantic  
984 cognition do or do not overlap is contentious and much is left to be gleaned regarding the  
985 relationship between these systems (Jackson et al., 2021, 2019; Mars et al., 2012).

986

#### 987 4.2.3. The anterior temporal lobe

988           Our findings implicate the lateral anterior temporal lobe (ATL), and particularly the  
989 dorsolateral STG/temporal pole (BA 38) and middle anterior MTG/STS, in all the socio-  
990 cognitive domains investigated, except for empathy for pain. Exploratory cluster analyses  
991 revealed that ATL engagement is not dependent on instructional cue or task difficulty, and  
992 thus it appears to serve a role other than control.

993           A key contribution of the ATL to social-affective behaviour has been recognised by  
994 comparative and behavioural neurologists for well over a century, owed at first to the  
995 acclaimed work of Brown and Schafer (1888) and, later, Klüver and Bucy, (1939) who

996 provide detailed reports of profound social and affective disturbances in non-human primates  
997 following a bilateral, full depth ATL resection. These observations are mirrored in  
998 descriptions of neurogenerative patients that associate progressive ATL damage with a wide  
999 range of socio-affective deficits ( Binney et al., 2016; Chan et al., 2009; Ding et al., 2020;  
1000 Perry et al., 2001), including impaired emotion recognition (Lindquist et al., 2014; Rosen et  
1001 al., 2004) and empathy (Rankin et al., 2005), impaired capacity for ToM (Duval et al., 2012;  
1002 Irish et al., 2014), and a loss of person-specific knowledge (Gefen et al., 2013; Snowden et  
1003 al., 2012, 2004). Over the past 10 years, there been a growing acceptance of the central role  
1004 played by the ATL within the social neurosciences (Olson et al., 2013) and it now features  
1005 prominently in some neurobiological models of face processing (Collins & Olson, 2014),  
1006 ToM (Frith & Frith, 2006), moral cognition (Moll et al., 2005), and emotion processing  
1007 (Lindquist et al., 2012). It has also been pinpointed as a key source of top-down influence on  
1008 social perception (Freeman & Johnson, 2016). One influential account of social ATL  
1009 function proposes a domain-specific role in the representation of social knowledge, including  
1010 person knowledge, and other more abstract social concepts (Olson et al., 2013; Thompson et  
1011 al., 2003; Zahn et al., 2007a).

1012 A parallel line of research focused upon general semantic cognition has given rise to  
1013 an alternative, more domain-general account of ATL function; there is a large body of  
1014 convergent multi-method evidence from patient and neurotypical populations in support of a  
1015 role of the ATL in the formation and storage of all manner of conceptual-level knowledge  
1016 (Lambon Ralph et al., 2017). Research efforts have therefore recently begun to ask whether  
1017 the purported roles of the ATL in both social and semantic processes can be reconciled under  
1018 a single unifying framework (Binney et al., 2016; Rice et al., 2018). Some clues already exist  
1019 in the aforementioned work of Klüver and Bucy (1939), who observed a broader symptom  
1020 complex comprising multimodal semantic impairments, including visual and auditory

1021 associative agnosias, that might explain rather than just co-present with social-affective  
1022 disturbances. More recent work that leverages the higher spatial resolution of functional  
1023 neuroimaging in humans has revealed a ventrolateral ATL region that responds equally to all  
1024 types of concepts, including social, object and abstract concepts, be they referenced by verbal  
1025 and/or non-verbal stimuli (Binney et al., 2016; Rice et al., 2018). Activation of the dorsal-  
1026 polar ATL, on the other hand, appears to be more sensitive to socially-relevant semantic  
1027 stimuli (Binney et al., 2016; Rice et al., 2018; Zahn et al., 2007b). These observations support  
1028 a proposal in which the broadly-defined ATL region can be characterised as a domain-  
1029 general supramodal semantic hub with graded differences in relative specialisation towards  
1030 certain types of conceptual information (Binney et al., 2012; Binney et al., 2016; Lambon  
1031 Ralph et al., 2017; Plaut, 2002; Rice et al., 2015). Our results reveal that the temporal poles  
1032 are reliably activated across four social domains – moral reasoning, empathy for emotions,  
1033 ToM and trait inference. They do not, however, provide support for the involvement of the  
1034 ventrolateral ATL. We argue this is likely due to technical and methodological limitations of  
1035 the fMRI studies included in the meta-analyses (see Visser et al., 2010). Most notably this  
1036 includes vulnerability to susceptibility artefacts that cause BOLD signal drop-out and  
1037 geometric distortions around certain brain areas, including the ventral ATLs (Jezzard and  
1038 Clare, 1999; Ojemann et al., 1997). Studies that have used PET, which is not vulnerable to  
1039 such artefacts, or techniques devised to overcome limitations of conventional fMRI (Devlin  
1040 et al., 2000; Embleton et al., 2010), reveal activation in both the temporal poles and the  
1041 ventral ATL in response to social stimuli (Balgova et al., in prep; Binney et al., 2016; Castelli  
1042 et al., 2002).

1043

1044 **4.3. Limitations**

1045           Because semantic control demands were not explicitly manipulated in the social  
1046 contrasts we included, our results cannot directly confirm our hypothesis regarding the  
1047 specific contribution made by the SCN in social cognition. Our conclusions rely on an  
1048 assumption that overlap reflects a generalised neurocomputation upon which both semantic  
1049 control and social processing rely. The alternative explanation is that overlapping activation  
1050 reflects tightly yet separately packed cognitive functions which may only dissociate when  
1051 investigated at an increased spatial resolution (Henson, 2006; Humphreys et al., 2020).  
1052 Moreover, we chose to pool across heterogeneous samples of studies to investigate the  
1053 cognitive domains of interest. The advantage of this approach is that it identifies activation  
1054 that is generalisable across highly variable experimental conditions and washes out spurious  
1055 findings associated with idiosyncratic properties of stimuli and/or paradigms. However, the  
1056 preponderance of specific experimental procedures in each literature addressed still  
1057 unintentionally led to systematic differences in the characteristics of the studies used to  
1058 define the different cognitive domains. For example, the semantic control dataset included  
1059 studies that employed verbal stimuli almost exclusively, while the majority of empathy  
1060 studies employed non-verbal stimuli. Some of the differences between the associated  
1061 networks (e.g, in lateralization) might therefore be attributable to verbal processing demands.  
1062 As is the case with all meta-analyses, therefore, some aspects of our results should be treated  
1063 with caution.

1064           Another limitation of this study is that most of the experiments included used control  
1065 conditions that were highly matched to their experimental conditions in terms of the demand  
1066 for domain-general processes such as cognitive control and semantic processing, and  
1067 therefore they may have subtracted away much of the activation we were aiming to explore.  
1068 Despite this, we did find consistent activation of the SCN, particularly the left IFG, across all  
1069 four social domains. This may be because, although a considerable subset of included

1070 experiments had high-matching control conditions, not all may have properly controlled for  
1071 semantic control demands specifically. An alternative explanation is that processing socially-  
1072 relevant conceptual knowledge may impose greater demands on the SCN. Consistent with  
1073 this, it has been shown that processing social concepts relative to non-social concepts led to  
1074 increased activation of the SCN even when controlling for potentially confounding  
1075 psycholinguistic factors (Binney et al., 2016).

1076

1077

#### 1078 ***4.4. Concluding remarks and future directions***

1079         Regions of the SCN are engaged by several types of complex social tasks, including  
1080 ToM, empathy, trait inference and moral reasoning. This finding sheds light on the nature and  
1081 neural correlates of the cognitive control mechanisms which contribute to the regulation of  
1082 social cognition and specifically implicates processes involved in the goal-directed retrieval  
1083 of conceptual knowledge. Importantly, our current findings and our broader set of hypotheses  
1084 can be generalised to multiple social phenomena, thereby contributing a unified account of  
1085 social cognition. Future research will need to establish a causal relationship between the SCN  
1086 and successful regulation of social processing. This could be done by directly probing  
1087 whether SCN regions are sensitive to manipulations of semantic control demands within a  
1088 social task. Similarly, the capacity for neurostimulation of SCN regions to disrupt social task  
1089 performance needs to be investigated.

1090         Elucidating the neural bases of social control and representation may help us  
1091 understand the precise nature of social impairments resulting from damage to different neural  
1092 systems. For example, our framework (Binney & Ramsey, 2020) predicts that damage to  
1093 representational areas such as the ATL will impair social information processing irrespective  
1094 of task difficulty or the need to integrate context. In contrast, we expect that damage to

1095 control areas would lead to impaired social processing specifically when it requires selecting  
1096 from amongst alternative interpretations of social cues, and/or retrieving social information  
1097 that is only weakly associated with a person or a situation. Damage to perisylvian frontal  
1098 and/or temporo-parietal areas (comprising the SCN) leads to semantic aphasia, a disorder  
1099 characterized by impaired access and use of conceptual knowledge (Corbett et al., 2009;  
1100 Jefferies et al., 2008, 2007; Jefferies and Lambon Ralph, 2006; Noonan et al., 2010). This  
1101 contrasts with ATL damage which leads to semantic dementia, a condition associated with a  
1102 loss or degradation of semantic knowledge (including social knowledge; Hodges and  
1103 Patterson, 2007; Lambon Ralph et al., 2010; Lambon Ralph and Patterson, 2008; Patterson et  
1104 al., 2007; Rogers et al., 2004). As far as we are aware, the extent to which brain damage that  
1105 leads to semantic aphasia also affects social abilities has not yet been formally investigated.  
1106 Some insight can be found in neurodegenerative patients with prominent frontal lobe damage,  
1107 where social impairments can be linked to deficits in executive function (Healey and  
1108 Grossman, 2018; Kamminga et al., 2015). More generally, it will be interesting to discover  
1109 whether a distinction between knowledge representation and cognitive control can inform our  
1110 understanding of the precise nature of atypical or disordered social cognition in, for example,  
1111 the context of dementia, acquired brain injury, autism spectrum conditions and schizophrenia.

1112

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