Overlapping Neural Correlates Underpin Theory of Mind and Semantic Cognition: Evidence from a Meta-Analysis of 344 Functional Neuroimaging Studies

Eva Balgova[1,2], Veronica Diveica[1,3], Rebecca L. Jackson[4] & Richard J. Binney[1*]

[1]*Cognitive Neuroscience Institute, Department of Psychology, Bangor University, UK*

[2]*Department of Psychology, Aberystwyth University, UK*

[3]*Montreal Neurological Institute, Department of Neurology and Neurosurgery, McGill University,, Canada*

[4]*Department of Psychology & York Biomedical Research Institute, University of York, UK*

Abstract

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

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

*To whom correspondence may be addressed: R.Binney@Bangor.ac.uk

1. Introduction

The capacity to understand and respond appropriately to the thoughts and actions of others is of vital importance to our daily lives. When this ability breaks down, there are profound consequences for an individual's ability to thrive in society (Frith, 2007; Frith & Frith, 2007). Therefore, a key challenge for neuroscience is to develop a full account of the cognitive and brain basis of social interaction.

The dominant mode within social neuroscience has been to seek out specialised neural subsystems dedicated to processing social (as opposed to more general kinds of) information (Apperly et al., 2005; Happé et al., 2017; Saxe & Powell, 2006; Spunt & Adolphs, 2017). This approach has uncovered evidence for the existence of category-selective cortex; regions that preferentially activate during the perception of certain social stimuli, such as faces (Kanwisher & Yovel, 2006), bodies (Downing & Kanwisher, 2010), and dyadic social interactions (Landsiedel et al., 2022). It has been argued that more complex inferential processes such as mental state attribution, or Theory of Mind, also engage highly specialised social brain areas (Apperly et al., 2005; Brüne & Brüne-Cohrs, 2006; Dodell-Feder et al., 2011; Gweon et al., 2012; Jacoby et al., 2016; Jenkins et al., 2014; Koster-Hale & Saxe, 2013; Ross & Olson, 2010; Saxe & Baron-Cohen, 2006; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005; Scholz et al., 2009; Simmons et al., 2010). However, the extent to which 'higher-order' systems (e.g., declarative memory; cognitive control) exhibit domain-specificity of this kind is hotly debated (e.g., Apperly et al., 2005; Binney & Ramsey, 2020; Ramsey & Ward, 2020). One factor keeping this debate from being resolved is that, to date, the role of domain-general systems in social cognition has received comparatively little attention and is not well understood. Consequently, neurobiological accounts of human social behaviour fall short of being comprehensive.

Recently, however, there has been increased interest in the involvement of a set of distributed domain-general networks in social processing. This includes the 'multiple-demand network' (MDN) and the 'default mode network' (DMN; Darda & Ramsey, 2019; Diveica et al., 2021; Zaki et al.,

2010; Duncan, 2010; Fedorenko, 2014; Fedorenko et al., 2013; Hughes et al., 2019; Jackson et al., 2022; Mars et al., 2012; Schilbach et al., 2006; Spreng & Grady, 2010), both of which include regions previously linked to social processing. These lines of enquiry have not only broadened the scope of the cortical regions believed to contribute to social cognition, but they also provide support for theories that recast social cognition as fundamentally built upon a set of more generalisable systems and processes (for more on this debate, see Amodio, 2019; Binney & Ramsey, 2020; Lockwood et al., 2020). More recently, it has been argued that a third network, known as the semantic cognition network (SCN; Humphreys et al., 2015; Jackson et al., 2019), has a crucial role in supporting social cognition (Balgova et al., 2022; Binney & Ramsey, 2020; Diveica et al., 2021).

Semantic cognition (supported by the SCN) refers to the acquisition and flexible retrieval of conceptual-level knowledge that transforms sensory inputs into meaningful, multimodal experiences. Conceptual knowledge critically underpins our capacity to use our sensory information to recognise and interact with objects, words, people, and events in our environment (Patterson et al., 2007; Lambon Ralph et al., 2017). The SCN is comprised of the IFG and posterolateral temporal cortex (inclusive of the pMTG and pITG), which play a particular role in control-related processes, and the ATL which underpins semantic representation processes (Jackson, 2021; Jefferies, 2013; Noonan et al., 2013; Lambon Ralph et al., 2017). Research has only recently begun to explore the SCN's relationship to social cognition. However, Binney and Ramsey (2020) suggest it could prove to be productive to understand social cognition as, essentially, an example of semantic cognition. This is because social interaction is, at its core, a process of *meaningful* exchange between persons; for example, it involves understanding the communicative intent of a speaker, and/or understanding how an actor's interaction with their environment reflects their thoughts, beliefs, or intentions. This 'primary systems' view of social cognition is supported by the high degree of overlap in anterior temporal lobe (ATL), frontal, temporoparietal and midline cortical structures in the networks recruited by social and semantic tasks in both functional neuroimaging reviews (Binney & Ramsey, 2020; also see Diveica et al., 2021 and Hodgson et al., 2022) and direct fMRI comparisons of social and non-

social stimuli (Balgova et al., 2022; Binney, Hoffman et al., 2016; Paunov et al., 2019; Rice et al., 2018 see also Deen et al., 2015; Paunov et al., 2019). Moreover, there is preliminary evidence for a relationship between social and semantic cognition within the neuropsychological and comparative neuroscience literature; in the context of ATL damage, there appears to be a tight coupling of general semantic deficits and social impairments (Bertoux et al., 2020; Irish et al., 2014; Klüver & Bucy, 1937; Miller et al., 2012; Souter et al., 2021; for a review see Olson et al., 2013 and Rouse et al., 2023).

The present study is the first attempt to use a meta-analytic approach to simultaneously investigate the whole brain networks associated with social and semantic cognition and explore the extent to which they are overlapping. Meta-analyses of functional imaging data allow the extraction of reliable findings from across large numbers of studies, thereby circumventing the limitations of individual studies (Cumming, 2014; Eickhoff et al., 2012) which include low statistical power (Button et al., 2013) and vulnerability to idiosyncratic design/analysis choices (Botvinik-Nezer et al., 2020; Carp, 2012). We chose to focus on one key aspect of social cognition, namely mental state attribution or 'theory of mind' (ToM). This is a logical starting place for three reasons. First, ToM is considered central to social cognition as it is fundamental to successful social interactions (Apperly, 2012; Brüne & Brüne-Cohrs, 2006; Frith & Frith, 2005; Heleven & van Overwalle, 2018; van Hoeck et al., 2014). Second, it is a well-established area of research with a large body of literature, as is requisite for meta-analytic investigation. Third, ToM abilities enable one to describe, explain, predict, and infer the intentions, beliefs, and affective states of others (Adolphs, 2009; Brüne & Brüne-Cohrs, 2006; Frith & Frith, 2007, 2012; Frith & Frith, 2010; Happé et al., 2017; Premack & Woodruff, 1978). As such, ToM includes inferential processes that allow one to go beyond what is directly observable through the senses, thus appearing to be comparable to, and perhaps explained by, more domain-general semantic processes that are specialized for the extraction of meaning from sensory inputs (Binney & Ramsey, 2020).

In the present study, we explored the relationship between the regions consistently engaged in ToM and the SCN. Most neural accounts of ToM implicate the temporoparietal junction (TPJ) alongside medial prefrontal cortex (mPFC) and the precuneus. Some accounts also include the posterior superior temporal sulcus (pSTS) and the ATL (Amodio & Frith, 2006; Mar, 2011; Molenberghs et al., 2016; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005; Saxe, 2006; Saxe & Powell, 2006; Schurz et al., 2014, 2017). It is key to note that the term 'TPJ' is less frequently used in the semantic cognition literature than in social neuroscience, and the corresponding definition can be vague and heterogeneous. For present purposes, we interpret the label TPJ to refer to a large area that includes the posterolateral temporal cortex and the inferior parietal lobe, including the angular gyrus (AG) (Hodgson et al., 2022; Seghier, 2013, 2022; Seghier et al., 2010). Some accounts of semantic cognition include the AG and argue it is involved in the integration and storage of conceptual knowledge (Kuhnke et al., 2020). However, the AG has also been attributed to other domain-general processes that extend beyond semantic processing (Cabeza et al., 2012; Geng & Vossel, 2013; Humphreys, Lambon Ralph, et al., 2021; Humphreys & Tibon, 2022)). In the present study, we specifically anticipated overlap in the ATL and the TPJ as both regions are frequently implicated in putatively domain-specific social processes as well as semantic cognition (Balgova et al., 2022; Diveica et al., 2021; Humphreys, Lambon Ralph et al., 2021; Olson et al., 2013; Seghier et al., 2010).

We further aimed to investigate a potential hemispheric dissociation between social and semantic cognition at these sites. In semantic cognition, the role of the ATL is viewed as bilateral (albeit with a leftwards asymmetry when probed with verbal semantic information; Lambon Ralph et al., 2001; Rice, Hoffman, et al., 2015), whereas the role of the ATL in social cognition has been ascribed right lateralisation (Younes et al., 2022; Zahn et al., 2009). Evidence for this distinction is limited, however, because claims that the right, but not the left ATL, is key for social processing are based chiefly upon patient studies (Borghesani et al., 2019; Gainotti, 2015; Gorno-tempini et al., 2003; Irish et al., 2014). Individual fMRI studies, on the other hand, typically indicate bilateral involvement or possibly a leftward asymmetry (Balgova et al., 2022; Binney, Hoffman, et al., 2016;

Rice et al., 2018; Ross & Olson, 2010 but see Zahn et al., 2002; also see Arioli et al., 2021; Catricalà et al., 2020; Lin, Yang, et al., 2018; Pobric et al., 2016; Rice, Lambon Ralph, et al., 2015). The laterality of TPJ involvement in social cognition is unclear. In neuroimaging studies, it is often observed bilaterally (Molenberghs et al., 2016; Schurz et al., 2014), but selectivity of this region for ToM is argued to be limited to the right hemisphere by some authors (Perner et al., 2006; Saxe & Wexler, 2005) while others have reported greater selectivity in the left (Aichhorn et al., 2006, 2009). In semantic cognition, activation of regions within the TPJ tends to be left lateralised (Handjaras et al., 2017; Kuhnke et al., 2022; Seghier, 2013; Seghier et al., 2010). Collectively, these findings paint a complex picture regarding how the ToM and semantic networks converge and diverge at these ATL and TPJ sites.

These laterality differences may be of critical importance to differentiating semantic and social cognition networks. Alternatively, they could reflect a methodological confound which is that their typical neuroimaging assessments tend to use different types of stimuli. A key aim of this study, therefore, was to investigate whether methodological factors give rise to a skewed pattern of activity in each domain. Most fMRI studies probing semantic cognition have used verbal stimuli (e.g., words/sentences) (Rice, Lambon Ralph, et al., 2015; Visser, Jefferies, et al., 2010). In contrast, nonverbal stimuli such as animations, vignettes, or free-viewing movie paradigms are popular in the ToM literature (Diveica et al., 2021; Molenberghs et al., 2016). Although both semantic cognition and ToM are typically viewed as modality-independent processes (Gallagher et al., 2000), these prevalent methodological differences could mar between-domain comparisons because activation patterns within each domain shift according to the stimulus presentation format. For example, a meta-analysis of fMRI studies found that non-verbal compared to verbal ToM tasks, evoke greater activation in the left precentral gyrus and left and right IFG, and lower activation in the mPFC, precuneus, and bilateral TPJ (Molenberghs et al., 2016). Similarly, Visser et al.'s (2010) meta-analysis of semantic cognition found that the laterality of ATL activation depends on whether stimuli were presented in the auditory versus visual modality (also see Krieger-Redwood et al., 2015; Rice,

Lambon Ralph, et al., 2015). Thus, left unaccounted for, these kinds of systematic methodological differences could create the appearance of divergence between the two task-associated networks when there is, in fact, a common system with meaningful covariation driven by properties of the stimuli. In the present study, we controlled for stimulus format (verbal, non-verbal) and input modality (visual, auditory) to disentangle pervasive from context dependent network differences. In the same vein, we controlled for inter-domain differences in the types of baseline/control tasks used (e.g., active versus passive) and screened for the presence of social stimuli in the studies of semantics.

In summary, to determine the degree to which ToM and semantic cognition share an underlying neural basis, we performed a systematic comparison between an update of Molenberghs et al.'s (2016) large-scale neuroimaging meta-analysis of ToM (previously reported in Diveica et al., 2021) and a comprehensive meta-analysis of semantic cognition and the SCN (Jackson, 2021) with a primary focus on the ATL and TPJ. Moreover, we assessed the effect of stimulus format and sensory input modality on network overlap. To our knowledge, this is the first direct comparison of these two large-scale networks via these means (see Hodgson et al., 2022 for a region-specific analysis).

2. Materials and Methods

Data Availability statement. Following open science initiatives (e.g., Munafò et al., 2017), the raw data sets, including study characteristics and the input and output files of all analyses, are openly available on the Open Science Framework (OSF) project page (https://osf.io/ydnxh/).

2. 1. Literature selection and inclusion criteria

We leveraged a Theory of Mind (ToM) dataset curated by (Diveica et al., 2021), and a Semantic Cognition (SCN) dataset compiled by (Jackson, 2021). Both these studies performed a comprehensive and up-to-date literature review and followed best practice guidance for conducting meta-analyses (Müller et al., 2018). Below, we provide a brief description of each of these original datasets.

The general semantics analysis (257 studies, 415 contrasts, 3606 peaks) reported by Jackson (2021) was designed to capture all aspects of semantic cognition, including activation of conceptual level knowledge, as well as engagement of control processes that guide context- or task-appropriate retrieval of concepts. Studies were included if they compared a (more) semantic with a non- (or less-) semantic task or meaningful (or known) with meaningless (or unknown) stimuli. It included studies published between 2008 and 2019. The ToM analysis (136 experiments, 2158 peaks, 3452 participants) reported by Diveica et al. (2021) included studies published between 2014 and 2020 that employed a primary task involving inferences about the mental states of others, including their beliefs, intentions, and desires (but not sensory or emotional states). These studies were also required to compare the ToM task to a non-ToM task. Studies that looked at the passive observation of actions, social understanding, mimicry or imitation were not included unless the primary task included a clear ToM component. Studies investigating irony comprehension, those that employed trait inference tasks, and those that employed interactive games were also excluded. Both Jackson and Diveica et al. excluded contrasts that made comparisons between sub-components of the process of interest (but see the final paragraph in this Section). For example, Diveica et al. excluded affective ToM > cognitive ToM contrasts and from the semantic cognition studies, and Jackson excluded abstract semantics > concrete semantics contrasts. This was critical for the present study because we were interested in common, core semantic/ToM processes that are subtracted out by these contrasts.

For these two datasets to be compared, it was essential to ensure that a similar, if not identical set of general exclusion criteria (i.e., those pertaining to the sample demographics, the imaging method, etc.) were applied. To this end, we initially planned to use the general inclusion/exclusion criteria described by Diveica et al. (2021) and reapply them to both the ToM and SCN datasets. In practice, we needed to implement a few minor modifications to these criteria. Below we summarise the final set of general criteria that we applied in the present study and highlight discrepancies from the approaches of Diveica et al. (2021) and Jackson (2021):

1. We included only peer-reviewed articles in English, and studies that employed task-based fMRI or PET, and only those that report whole-brain activation coordinates localised in one of two standardised stereotactic spaces (Talairach (TAL) or Montreal Neurological Institute (MNI)). Coordinates reported in TAL space were converted into MNI space using the Lancaster transform (tal2icbm transform (Lancaster et al., 2007) embedded within the GingerALE software version 3.0.2; http://brainmap.org/ale). Results from region-of-interest or small-volume correction analyses were excluded.
2. We included only studies that tested healthy adults to control for age-related changes in neural networks supporting cognition (e.g., see Hoffman & Morcom, 2018). A deviation from Diveica et al. (2021) was that we only considered studies reporting data from participants aged 18-40 years. If the age range of participants in a given study was not stated, we included the results in our datasets as long as the mean age of the participants was less than 40 years (if stated) and there was no clear indication that adults outside the range of 18-40 were included in the sample. This was a similar criterion to that used by Jackson (2021).
3. Diveica et al. (2021) included contrasts between the experimental task (i.e., ToM processing) and either an active control condition or rest/passive fixation. Jackson (2020) only included contrasts against active baselines. Therefore, we added additional contrasts involving rest/passive fixation into the SCN dataset. In the present study, active control conditions were characterised as either a high-level or low-level baseline; thus, over and above Diveica et al. (2021) and Jackson (2020), the present study differentiated low-level active baselines (e.g., visual stimulation with a string of hashmarks as a control for sentence reading) from rest/passive fixation. With these extra steps, we aimed to better account for methodological differences across domains (see more detail in **Section 2.3.1**).
4. Where present, multiple contrasts from the same group of participants were included if they met all the other inclusion criteria. We controlled for within-group effects by pooling contrasts into a single experiment (Müller et al., 2018; Turkeltaub et al., 2012) like Diveica et al. (2021)

and Jackson (2020). This means that, when we refer to the numbers of experiments that constituted the units of input, we have counted contrasts from a single participant sample as one single experiment. In follow-up contrast analyses that compared different conditions (e.g., stimulus format or input modality), initially pooled contrasts related to these different conditions were separated (see more detail in **Section 2.2**). While Diveica and colleagues excluded the contrast with a smaller number of peaks after separating, we retained both of these contrasts to maximise the use of all available data.

Two further adjustments were made to the SCN dataset to make it optimally comparable to the ToM dataset. As discussed above, both Jackson and Diveica et al. excluded contrasts that made comparisons between sub-components of the process of interest and thus could subtract away core processes associated with ToM and semantic cognition. In the case of ToM, this left only those contrasts comparing ToM tasks with non-ToM tasks. Jackson, however, also included a small number of contrasts that compared more semantic tasks with less semantic tasks (e.g., an identity classification task using faces with varying degrees of familiarity used by Rotshtein et al., (2005) or a task contrasting personal familiar and famous familiar faces used by Sugiura et al., (2006)). In the present study, we excluded these because they could subtract out some core processes or common regions. While this was likely of little consequence in Jackson's (2021) study, the inclusion of these contrasts could, in principle, weaken the comparison of SCN data with the ToM data. An exception was applied to contrasts that pitted intelligible sentences against scrambled sentences because they were an important source of data in the verbal and auditory domain, and we reasoned that, while there is meaning present in both stimuli types at the single word level, the critical difference was meaningfulness at the sentence level. Finally, we identified and excluded a small number of experiments in Jackson's SCN dataset (n=4) that used contrasts that could be viewed as probing ToM-related processing.

The final ToM dataset used in the present study comprised 114 experiments from 2800 participants, 159 contrasts, and 1893 peaks. The final SCN dataset used in the present study comprised 214 experiments, including data from 3934 participants, 410 contrasts, and 3803 peaks.

2.2. Categorising Contrasts by Stimulus Format and Sensory Input Modality

In line with our secondary aim of accounting for the effects of stimulus format and sensory input modality on network overlap, individual contrasts from both the ToM and SCN datasets were further categorised as being chiefly within the verbal domain or the non-verbal domain. Verbal paradigms used spoken or written language stimuli. Examples of non-verbal paradigms include those using pictures (e.g., of objects or actions), animations, videos, or environmental sounds (see Rice et al., 2015 for a similar approach). Moreover, contrasts were independently categorised according to whether stimuli were presented in the visual or auditory modality (see Molenberghs et al., 2016; Visser et al., 2010 for similar approaches). In cases where both types of stimuli (e.g., verbal and non-verbal) were used in the same task, the contrast was excluded (e.g. Sommer et al., (2010)).The reader is referred to **Table 1** and the **Supplementary Information** for the number of studies and a list of excluded contrasts in each of these categories.

2.3. Further Methodological Considerations

Following the application of general inclusion/exclusion criteria and the categorization described in **Section 2.2**, we took additional steps to further characterize the two revised datasets and evaluate the potential for other confounds to influence their comparison. As we shall describe below, this led to further refinement which improved the suitability of the datasets for addressing our key research questions.

2.3.1. Controlling for type of baseline

In semantic cognition research, it is widely accepted that the results of neuroimaging studies are affected, in important ways, by the choice of baseline task; a failure to perform adequate matching of baselines to experimental conditions in terms of perceptual input, response and attentional/executive demands, decreases sensitivity of subtractive designs to activation in brain areas associated with cross-modal integration, semantic processing and response selection (Price et al., 2005). Indeed, the use of passive rest or simple fixation as a baseline results in failure to reveal task-positive activation in anterior temporal areas (Binder et al., 2009; Price et al., 2005; Visser, Jefferies, et al., 2010), because minimal baseline task demands increase the opportunity for spontaneous semantic processing (associated with daydreaming and inner speech) to occur at an equal or greater depth/magnitude than that associated with more focused task-related semantic processing (Andrews-Hanna et al., 2014; Binder et al., 2009, 2016; Chiou et al., 2020; Humphreys et al., 2015; Visser, Jefferies, et al., 2010). While it is not typically discussed in the literature, this is also an important consideration for neuroimaging studies of social cognition because various forms of social inference are likely to occur during a state of mind-wandering (see, e.g., Diaz et al., 2013).

We observed that our SCN and ToM datasets differed considerably in the types of baselines used and that there was a higher degree of variability among semantic cognition studies (see **Table 1** and the **Supplementary Information**). This could have led to a confound in the inter-domain comparisons, namely a difference in the sensitivity to activation associated with cross-modal processing. To explore these issues, we (a) quantified these differences using three categories of baseline and (b) mapped the effect of including/excluding contrasts that used these baselines on the outcomes of ALE analysis within each domain. The results of this preliminary analysis informed our final approach to defining the datasets used for the inter-domain comparisons (see below). Previous attempts to deal with this issue have only distinguished between two types of baselines (e.g., Visser et al., 2010), but with a view to capturing greater specificity in these effects, we operationalized three, as follows:

1. High-level baselines were defined as those including an active task designed to approximate the demands of the main/experimental task without engaging the process of interest (ToM or semantic processing). This includes being generally well-matched to the experimental task in terms of perceptual (visual, auditory) properties, and means of behavioural output (overt/covert).
2. Low-level baselines were defined as having a task that required active engagement but one that differed from the main task in numerous ways, including perceptual properties, means of behavioural output, or difficulty.
3. Finally, the third category of baselines were those which required only passively watching a blank screen or maintaining visual fixation.

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

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

level and passive baselines (**Supplementary Figure R2a and Supplementary Table R1**). Overall, these outcomes are consistent with an expectation that the inclusion of passive baselines would occlude activation within parts of the SCN (Binder et al., 2009, 2016; Humphreys et al., 2015; Visser, Jefferies, et al., 2010). Exclusion of lower-level baselines, on the other hand, might be an overly conservative approach that prohibits the detection of activation that is common across domains. We, therefore, opted to exclude only contrasts involving rest/passive baselines from the cross-domain comparisons reported in the Results section.

2.3.2. Controlling for the 'socialness' of semantic stimuli

20 studies (48 contrasts) in Jackson's (2021) original SCN data set, having otherwise met our revised exclusion/inclusion criteria, involved a task or stimuli that were, to some degree, social in nature. For example, some studies used social or emotion concepts, and others probed person knowledge through famous faces (e.g., Elfgren et al., 2006; Grabowski et al., 2001; Leveroni et al., 2000). These studies required further consideration, particularly because of an ongoing debate concerning whether social semantics and general semantics depend upon independent or overlapping representational systems (Arioli et al., 2020; Binney et al., 2016; Binney & Ramsey, 2020; Olson et al., 2013; Pexman et al., 2023). It is possible that ToM tasks engage social concepts and therefore the same regions engaged by social semantic processing (e.g., the dorsal ATL; Binney & Ramsey, 2020; Ross & Olson, 2010; Zahn et al., 2007) without relying on general semantic areas. In this case, if we were to pool social semantic contrasts and general semantic contrasts, then we might obtain an exaggerated picture of the extent to which the ToM network overlaps with the general processing semantic network. However, there was also a pragmatic reason for including these studies: they are a key source of data related to non-verbal semantic processing (see **Table 1**) and excluding them could compromise our ability to remove the confounding effect of stimuli type. To account for this, we examined the effect of including/excluding these studies in our general semantic dataset. These results are fully reported in the **Supplementary Information No 2.** Briefly, the overall pattern remained

almost the same when the social contrasts were excluded, apart from losing a small cluster in the right IFG and slightly less extensive left temporopolar activation. These differences are likely to be due to the reduction in the number of studies included and concern brain regions that were not the focus of the present study, and thus are not central to the conclusions made. Therefore, we decided to retain the social contrasts as part of our SCN dataset and include them in the cross-domain comparisons reported in the **Results** section.

Table 1. *The number of experiments, contrasts, and peaks split according to the stimulus format, input modality, type of baseline, and presence of social content.*

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

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

2.3. Data Analysis

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

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

(Nichols et al., 2005). Contrast images were created by directly subtracting one ALE map from the other (Eickhoff et al., 2011). Differences in ALE scores were compared to a null distribution that was estimated via a permutation approach with 5000 repetitions. The contrast maps were thresholded using an uncorrected cluster-forming threshold of $p < .001$, and a minimum cluster size of 100 mm^3. Thresholded ALE maps were plotted on a MNI152 template brain using MRICroGL (https://www.nitrc.org/projects/mricrogl). We used FSL maths commands and FSL VIEW (https://www.nitrc.org/projects/fsl) to binarise the ALE maps for better visual clarity when displaying the conjunction.

In a final step, we conducted post hoc cluster analyses that afforded a complementary approach to evaluating whether clusters of activation identified in the two independent ALE analyses of the SCN and ToM data were driven by certain methodological characteristics (i.e., input modality and stimulus format). We examined the list of experiments that contributed to each cluster by at least one peak and computed the likelihood of contribution of a given experiment type. For these purposes, we used Fisher's exact tests of independence and post-hoc pairwise comparisons in R studio Version 1.4.1106 (https://www.rstudio.com).

In summary, our analysis pipeline proceeded as follows. To address our primary question about similarities in the brain networks underpinning semantic and social cognition, we conducted independent ALE analyses on the ToM and SCN datasets which generated whole-brain activation maps. These maps were then used to create conjunction and contrast analyses aimed at identifying overlap and differences in the topology of activation between the two domains. We repeated these analyses having divided the SCN and ToM datasets into subsets containing experiments that used VERBAL stimuli on one hand, and NON-VERBAL stimuli on the other. This allowed examination of the effect of stimulus format. Then we split the datasets into subsets containing experiments that used VISUAL and AUDITORY stimuli and repeated the analyses to investigate the impact of sensory input modality. Finally, we performed cluster analyses to check whether the likelihood of finding

activation within each cluster identified in the primary ALE analyses of the ToM and GS data depends on experiment type (VERBAL, NON-VERBAL, VISUAL, AUDITORY).

3. Results

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

Our principal analyses explored the extent to which neural networks engaged by ToM and semantic cognition tasks overlap (and diverge). Overall, the results reveal extensive areas of overlap including at key areas of interest (see **Figure 1** and **Table 2;** also see the independent ALE analysis results for each separate domain in **Supplementary Information No. 2: Supplementary Figure R1** and **Supplementary Table R1**). Specifically, there was a conjunction of ToM and SCN activity within the bilateral ATL that covered the temporal pole (TP) and the banks of the anterior STS, the MTG and STG in both hemispheres. In the left but not the right hemisphere, the area of overlap extended along the whole length of the MTG/STG towards the lateral temporoparietal junction (including the AG) as well as medial portions of the IPL. There was also a conjunction of activation in the left posterior ventral temporal lobe (ITG/FG), and in the lateral frontal cortex including pars orbitalis, triangularis and opercularis of the left IFG and the ventral precentral gyrus. There were smaller clusters on the bank of the right inferior frontal sulcus (pars triangularis), the left dorsomedial frontal cortex and left inferior precuneus.

In the context of this large overlap, the contrast analyses revealed key differences between ToM and SCN (**Figure 1**). On the lateral surface of the bilateral ATL the activation for ToM included an area of anterior MTG that the SCN did not. Moreover, in the right IPL/AG (within the TPJ), activation was only consistently identified for ToM. While both ToM and semantic cognition elicit reliable activation in the left TP, as well as the IPL/AG (TPJ), the contrast analyses revealed that voxels in this same areas had significantly higher ALE values for ToM compared to the SCN. Beyond our key areas of interest, compared to the semantic studies, ToM studies also showed higher convergence of

activation in the right IFG, right precentral gyrus, bilateral anterior mPFC, left precuneus and left cerebellum. On the other hand, SCN experiments also showed increased convergence of activation in the ventral portion of the left pMTG stretching to the posterior ITG and FG, in the left MFG/IFG spreading towards the insula, and in the left inferior precuneus and right dorsal mPFC.

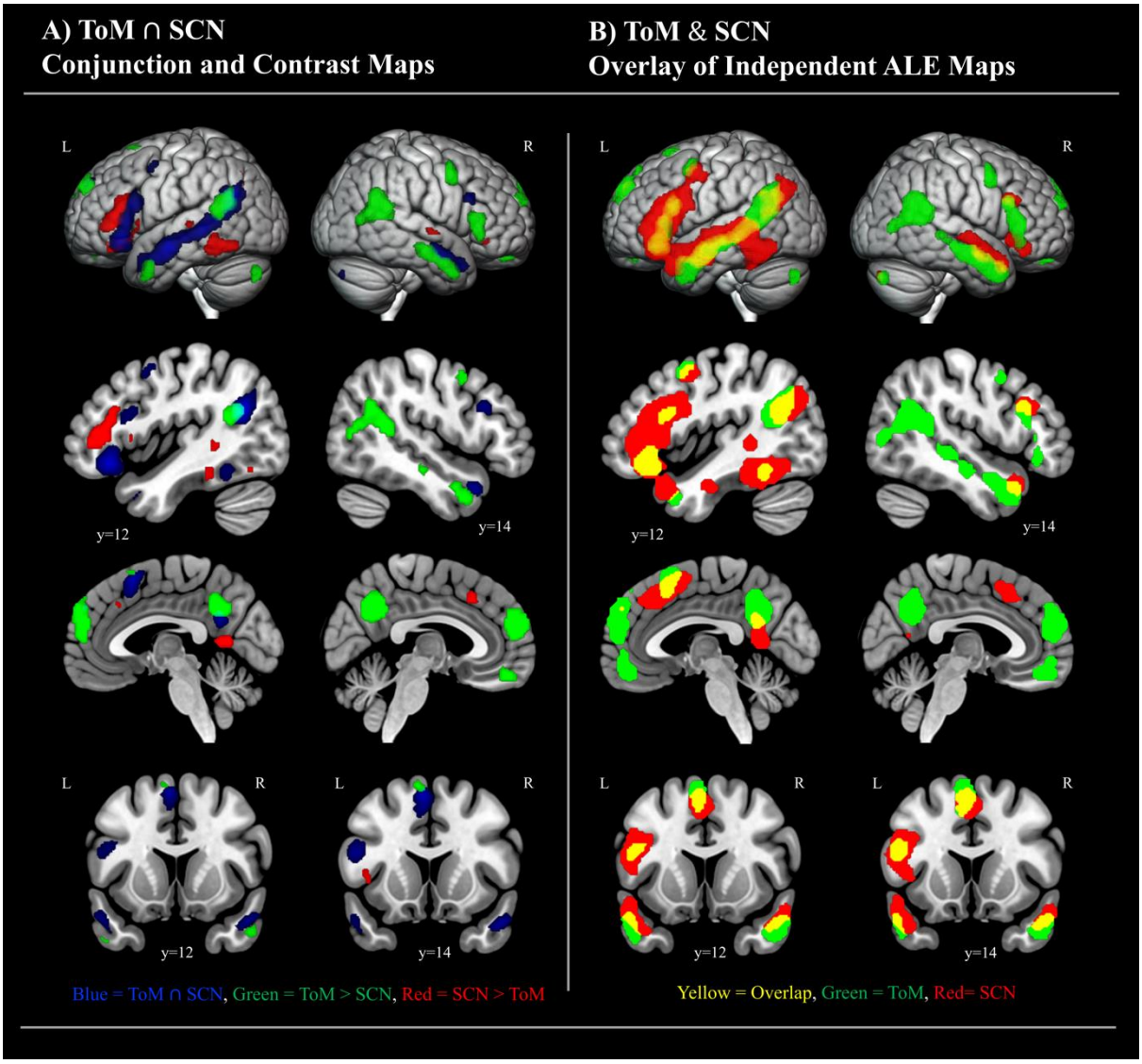

Figure 1 *Common and differential activation for ToM (N=113) and SCN (N= 211).* ***Panel A*** *displays the conjunction alongside statistically significant differences revealed by the contrast analyses. The contrast maps in* ***Panel A*** *were thresholded with a cluster forming threshold at p<.001 and a minimum cluster size of 100mm^3. In* ***Panel B,*** *we have overlaid the binarised versions of the complete ALE maps resulting from independent analysis of ToM and semantic cognition studies. This allows for full visualisation of the topography of the two networks and consideration of the relationship between them (also see Supplementary Figure R1 and Supplementary Table R1). The independent ALE maps were treated to a cluster-forming threshold at p<.001, and an FWE-corrected cluster-extent threshold at p<.05. The sagittal and coronal sections are chosen as representative slices positioned over peak*

coordinates at which there is the greatest conjunction in the bilateral anterior temporal lobes (left y= 12; right y= 14).

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

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

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

Independent ALE analyses cluster forming threshold p<.001; cluster-extent FWE p<.05. The contrast analyses were further thresholded with a cluster forming threshold at p<.001 and a minimum cluster size of 100mm^3. Anatomical labels are derived from the Automatic Anatomical Labelling Atlas. AG = angular gyrus, MTG = middle temporal gyrus, IFG - inferior frontal gyrus, TP = temporal pole, SMA = supplementary motor area, SFG = superior frontal gyrus, ITG = inferior temporal gyrus, IPL = inferior parietal lobule, MOG = middle occipital gyrus, STG = superior temporal gyrus.

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

In this next set of analyses, we explored the extent to which differences between the activation maps associated with ToM and semantic cognition could be explained by systematic differences in the types of tasks and stimuli used in each domain. We repeated the above comparisons, this time excluding contrasts involving nonverbal stimuli (i.e., only retaining those involving verbal stimuli). Both samples were large enough for the purposes of meta-analysis although there were many more experiments using verbal stimuli in the domain of semantic cognition than there were in the ToM dataset (VERBAL ToM: n= 46; VERBAL SCN: n= 175). Nonetheless, this analysis revealed a very similar pattern of conjunction to the principal set of comparisons reported in **Section 3.1** including the bilateral ATL (anterior MTG/STS) and the left TPJ (See **Figure 2** and **Supplementary Information No. 2: Supplementary Table R4**). However, there ceased to be any IFG activation for ToM tasks, and thus overlap between the two domains was absent in this region. A similar observation was made at the left posterior STS/MTG, and other small clusters of conjunction were no longer present. This could simply be due to the substantial reduction in size of the ToM experiment sample (from 113 to 46). However, we looked at the cluster analyses for the IFG and found that verbal ToM experiments were significantly less likely than nonverbal ToM experiments to contribute to the clusters in the bilateral IFG (see **Supplementary Information No.2: Supplementary Figure CA1** and **Supplementary Table CA1** for more detail). This is contrary to expectations given that the left IFG is strongly engaged in language processing (Friederici, 2011). One possible explanation, however, is that there are important differences between the main experimental tasks and the control/baseline tasks used in verbal ToM in terms of the semantic/syntactic operations that need to be performed. Should there be greater or equivalent difficulty in the control task, then IFG activation could be subtracted away (see Diveica et al., 2021 for meta-analytic evidence for the effect of task difficulty on IFG activation).

In the corresponding contrast analyses, the differences between ToM and the SCN in the bilateral ATL and left TPJ were less pronounced, yet they remained. There also continued to be more consistent activation of the right TPJ for ToM. This was also true of the left anterior mPFC, and left precuneus.

Indeed, while the extent of the clusters changed because of the reduced sample size in the ToM dataset, we continued to find more consistent involvement of the right TPJ, mPFC and left precuneus in ToM as compared to semantic cognition. Given that there were more studies in the ToM than SCN dataset, it is unlikely that these cross-domain differences could be attributed to lower statistical power in the case of SCN. For more detail see **Supplementary Information No. 2: Supplementary Figures R4 & R5 Panel A** and **Supplementary Table R6 & R7**).

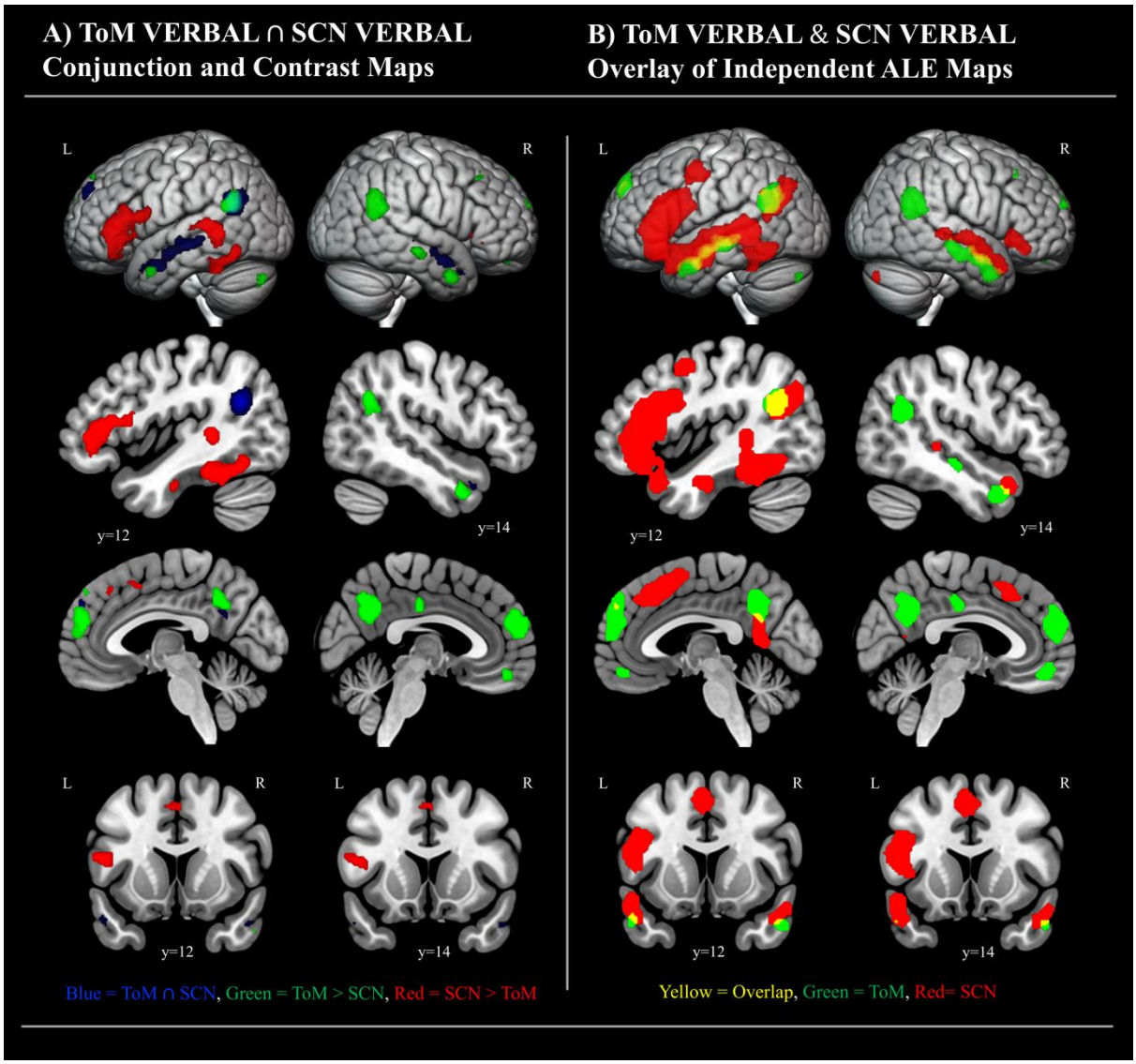

Figure 2 *Common and differential activation for VERBAL ToM (N=46) and VERBAL SCN (N= 175). The initial ALE maps were treated to a cluster-forming threshold at p<.001, and an FWE-corrected cluster-extent threshold at p<.05 prior to the conjunction and contrast analyses. The contrast maps*

*in **Panel A** were additionally thresholded with a cluster-forming threshold at p<.001 and a minimum cluster size of 100mm^3. **Panel A** displays the conjunction alongside side statistically significant differences. In **Panel B,** we have overlaid the binarised versions of the complete ALE maps resulting from independent analysis of VERBAL ToM and VERBAL SCN studies. This allows for full visualisation of the topography of the associated networks (also see Supplementary Figures R4 & R5 and Supplementary Table R6 & R7). The sagittal and coronal sections are chosen as representative slices positioned over peak coordinates at which there is the greatest conjunction in the bilateral anterior temporal lobes (left y= 12; right y= 14).*

When we limited the datasets to experiments utilising nonverbal stimuli, the results of the ALE analysis for ToM remained mostly unchanged from that seen in **Section 3.1**. In the case of semantic cognition, the number and extent of clusters was greatly diminished which reflects the reduced sample size. Indeed, there were more experiments using nonverbal stimuli in the domain of ToM than there were exploring semantic cognition (ToM: n= 71; SCN: n= 37) and, as a consequence, there was no conjunction between the domains in the left TPJ. Overlap was still present in key regions of interest including the left pMTG, left ITG and some small aspects of the left IFG. Notably, even though visual inspection of the independent ALE maps for each domain suggests a large difference in terms of bilateral ATL activation, there were no significant differences revealed by the contrast analysis. The bilateral TPJ responded selectively to ToM in this analysis, while the posterior ITG was only present in the SCN. The ALE maps for each domain can be found in **Supplementary Information No. 2: Supplementary Figures R4 & R5 Panel B and Supplementary Tables R6 & R7**. In the cluster analysis of either the ToM or semantic domain, we found that the likelihood of finding activation in the respective ATL or TPJ areas did not depend on the verbal/non-verbal nature of the stimuli. This finding suggests that the inability to identify convergent left TPJ activation in the non-verbal SCN sample, and, consequently, overlap with non-verbal ToM, is indeed due to reduced statistical power. The cluster analysis showed that non-verbal experiments did however contribute

more to the bilateral IFG and SFG in the ToM domain (See more detail in **Supplementary Information No.2: Supplementary Figure CA1** and **Supplementary Table CA1**).

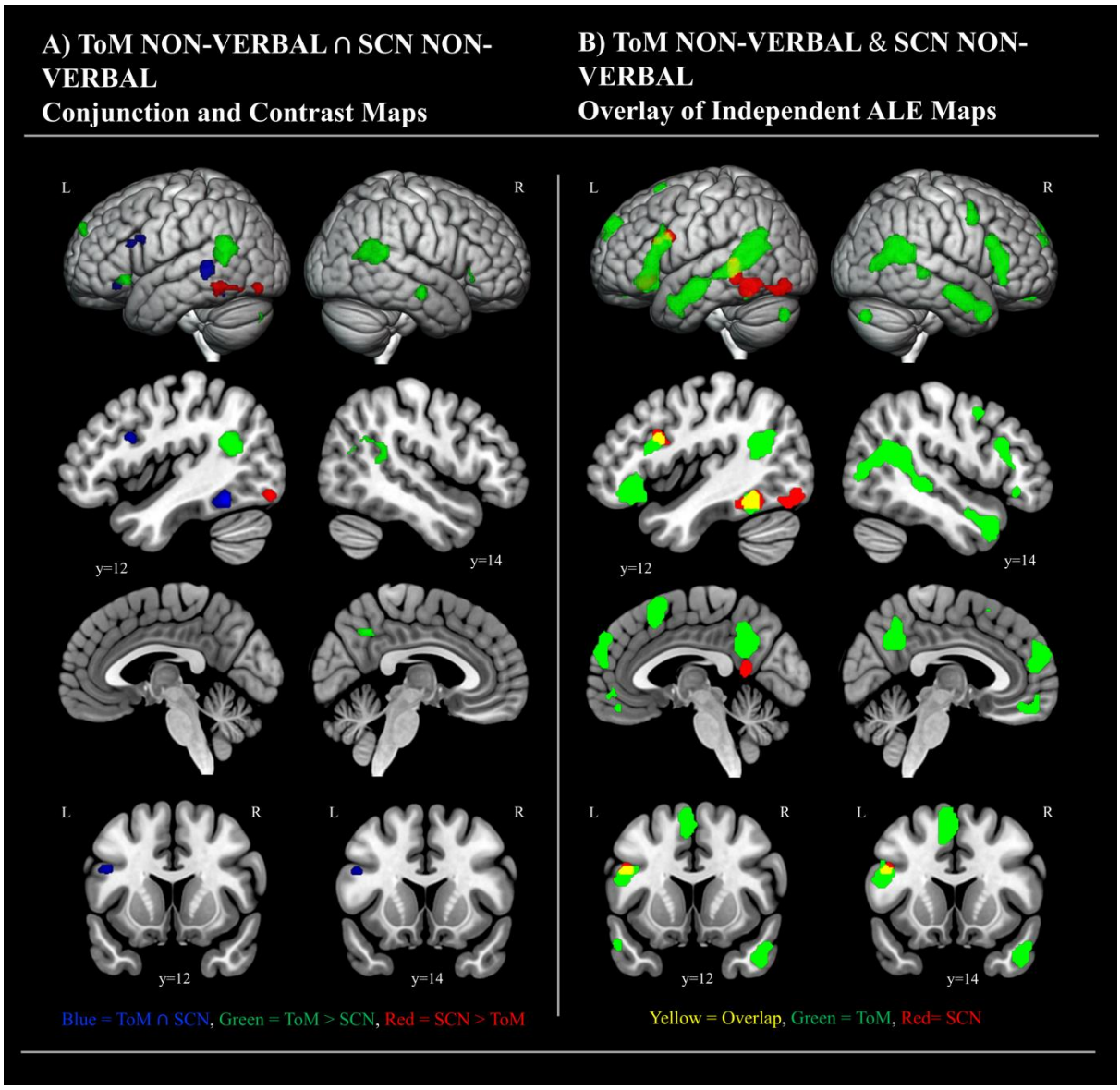

Figure 3 *Common and differential activation for NON-VERBAL ToM (N=71) and NON-VERBAL SCN (N= 37). The initial ALE maps were treated to a cluster forming threshold at p<.001 and an FWE corrected cluster-extent threshold at p<.05 prior to the conjunction and contrast analyses. The contrast maps in* ***Panel A*** *were additionally thresholded with a cluster forming threshold at p<.001 and a minimum cluster size of 100mm^3.* ***Panel A*** *displays the conjunction alongside side statistically significant differences. In* ***Panel B,*** *we have overlaid the binarised versions of the complete ALE maps*

resulting from independent analysis of VERBAL ToM and VERBAL SCN studies. This allows for full visualisation of the topography of the associated networks (also see Supplementary Figure R4 & R5 and Supplementary Table R6 & R7). The sagittal and coronal sections are chosen as representative slices positioned over peak coordinates at which there is the greatest conjunction in the bilateral anterior temporal lobes (left y= 12; right y= 14).

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

We also investigated the impact of sensory input modality. Importantly, both domains were dominated by experiments using visually presented stimuli. Comparisons limited to the auditory experiments were not possible due to a very small sample of ToM data. Overall, the pattern and extent of the common activation for VISUAL experiments (ToM: n= 106; SCN: n= 152) remained highly similar to our original analysis (**Section 3.1**), with common clusters of activation in key semantic areas (See **Figure 4** and **Supplementary Information No. 2: Supplementary Table R10**), including the left ATL, left IFG, left pMTG and ITG/FG and the left IPL/AG. There were also clusters of conjunction in the left medial SFG and precuneus. However, unlike in the initial analysis, there was no right ATL activation for the visual SCN experiments, and therefore no overlap between domains in the right ATL. Indeed, the cluster analyses revealed that visual relative to auditory SCN contrasts were less likely to contribute to the right ATL cluster, suggesting that it is unlikely that the absence of right ATL activation for visual SCN can be explained by reduced power per se. Instead, it seems more likely that the auditory contrasts were driving this cluster in the case of semantic cognition. One possibility is that this reflects increased effort in studies that use auditory stimuli (see **Discussion**). Other minor differences to the initial analyses are a diminished area of conjunction in the left middle STG and an absence of a conjunction in the right IFG (see **Supplementary Information No.2: Supplementary Figure CA1** and **Supplementary Table CA1** for more detail).

As in our full analysis, the contrast analysis found more consistently identified activation in visual ToM than visual semantic cognition studies in the right TPJ, right IFG, precentral gyrus, anterior

mPFC and precuneus. A small portion of the bilateral IFG remained more reliably engaged across SCN studies, as did the MFG, anterior mPFC and left precuneus. For more detail see the VISUAL and AUDITORY ToM and VISUAL and AUDITORY SCN ALE maps in **Supplementary Information No. 2: Supplementary Figures R8 & R9** and **Supplementary Tables R11 & R12**.

Although they do not directly relate to the study's main questions, for sake of completeness and to allow for comparisons with prior meta-analyses (Molenberghs et al., 2016; Rice, Lambon Ralph, et al., 2015; Visser, Jefferies, et al., 2010) we also performed conjunctive and contrastive analyses within each domain which compare each stimulus format and sensory modality (e.g., comparisons of the VERBAL SCN and NON-VERBAL SCN data sets, the VISUAL SCN and AUDITORY SCN data). The results of these analyses can be found in the supplementary information (see **Supplementary Information No. 2: Supplementary Figures R6, R7 and R10 and Supplementary Tables R8, R9, R13 and R14)**.

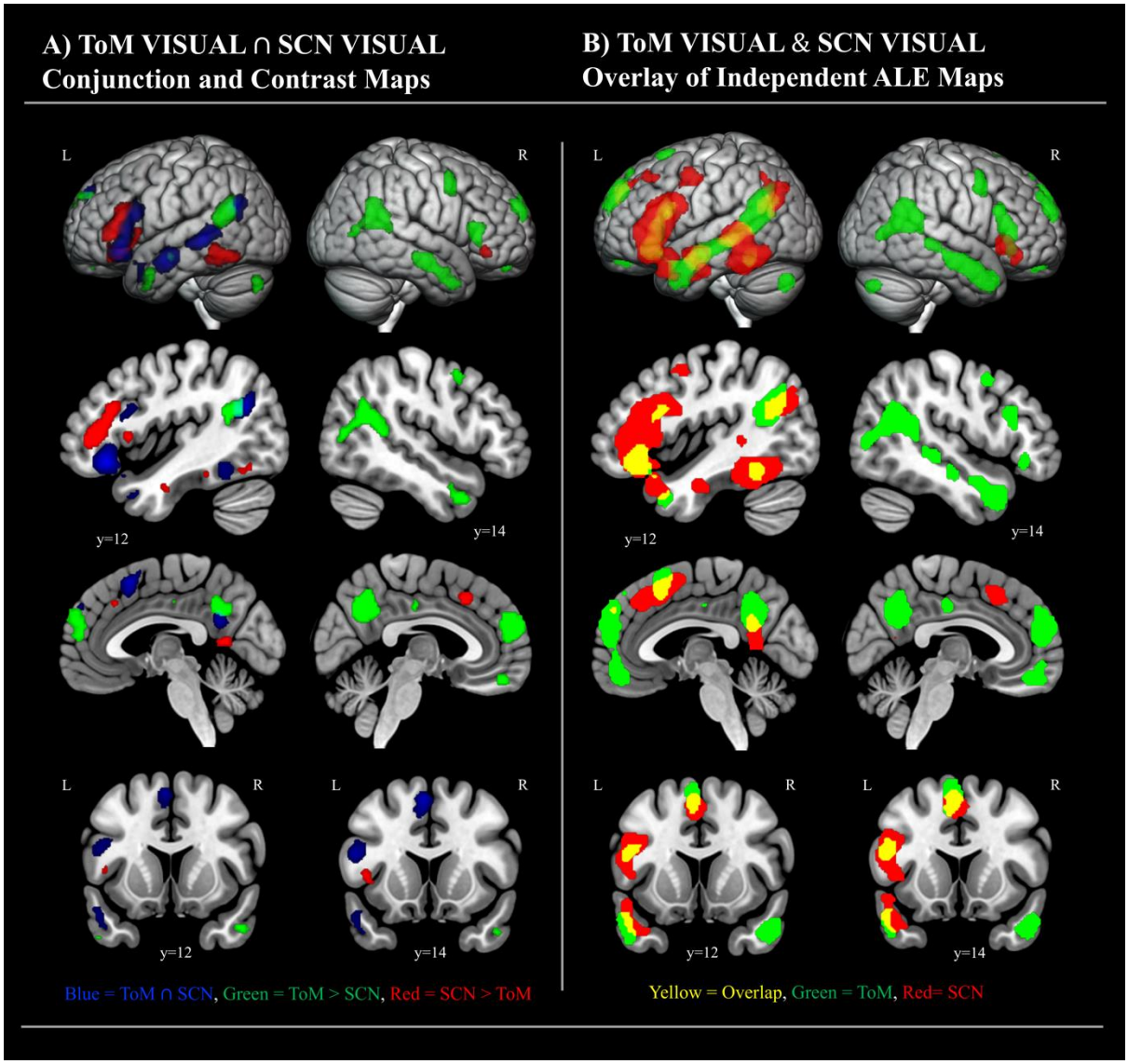

Figure 4 *Common and differential activation for VISUAL ToM (N=106) and VISUAL SCN (N= 152). The initial ALE maps were treated to a cluster-forming threshold at p<.001, and an FWE-corrected cluster-extent threshold at p<.05 prior to the conjunction and contrast analyses. The contrast maps in* ***Panel A*** *were additionally thresholded with a cluster-forming threshold at p<.001 and a minimum cluster size of 100mm^3.* ***Panel A*** *displays the conjunction alongside side statistically significant differences. In* ***Panel B,*** *we have overlaid the binarised versions of the complete ALE maps resulting from independent analysis of VERBAL ToM and VERBAL SCN studies. This allows for full visualisation of the topography of the associated networks (also see Supplementary Figures R8 & R9 and Supplementary Table R11 & R12). The sagittal and coronal sections are chosen as representative*

slices positioned over peak coordinates at which there is the greatest conjunction in the bilateral anterior temporal lobes (left y= 12; right y= 14).

4. Discussion

The present study aimed to glean a clearer understanding of the contribution of domain-general systems to social cognition. To this end, we took a neuroimaging meta-analytic approach to assess the degree to which ToM shares neural correlates with semantic processes. The key findings were as follows:

1. Overall, there was a strikingly large degree of overlap between the activation likelihood maps for ToM and the SCN. This was most evident in the bilateral ATL, the left STS, left MTG, left TPJ, and left IFG, which are all key regions for semantic processing (Binder et al., 2009). This suggests that semantic processes are integral to performing theory of mind tasks.
2. Most differences that emerged were mainly a matter of the extent of regional activation, which is likely driven by discrepancies in the sample size contributing to each ALE map. Nonetheless, there were a few notable exceptions.
3. The right TPJ, anterior aspects of the bilateral MTG, bilateral mPFC, and the bilateral precuneus, were consistently identified in ToM but not SCN studies. Significant differences remained even after controlling for methodological factors, including the type of experimental stimuli, input modality and baseline condition used to probe each domain. This is consistent with claims that the function of these regions (e.g., the right TPJ) are tuned towards processing social stimuli (although see below).
4. The posterior ITG and dorsal IFG (both in the left hemisphere) were consistently identified in SCN studies but not in ToM studies. This difference was even more pronounced after controlling for stimulus format and modality. One possibility is that this reflects differences in task difficulty, which we did not account for (see Diveica et al., 2021).

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

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

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

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

formally compared at the level of the whole brain (see Hodgson et al., 2022 for a region-specific analysis). Overall, our findings confirm there is a large degree of overlap between the brain networks engaged by theory of mind and semantic cognition, particularly in the lateral frontal and temporal cortex of the left hemisphere, but also bilaterally in the ATL. This suggests that at least some elements of semantic cognition are integral to theory of mind. This raises questions about the nature of theory of mind processes and raises the possibility that they can be considered a more generalised set of cognitive mechanisms related to conceptual retrieval and cognitive inference. Moreover, it gives rise to new hypotheses regarding the precise functional contribution of different brain regions to theory of mind tasks, a level of specificity arguably lacking from other neurobiological accounts of theory of mind (Saxe & Kanwisher, 2003; Saxe & Wexler, 2005). For example, ATL involvement likely reflects access to semantic knowledge/associations (Balgova et al., 2022), whereas inferior frontal and posterolateral temporal involvement of the left hemisphere could reflect control processes (Diveica et al., 2021a; Satpute et al., 2014).

4.2 Functional fractionation of the 'social brain'

We observed pervasive differences between the activation likelihood maps for ToM and SCN. Specifically, activation of the right TPJ, anterior aspects of the bilateral MTG, bilateral mPFC, and the bilateral precuneus appear more attuned to ToM tasks. All these regions are included in descriptions of putative brain regions specialized for theory of mind (Saxe, 2006; Saxe & Powell, 2006; Schurz et al., 2014, 2017). However, they are also considered part of the default-mode network (DMN) (Andrews-Hanna et al., 2014; Buckner et al., 2008; Spreng et al., 2009; Spreng & Grady, 2010), a resting-state network proposed to support various forms of internally orientated cognition (i.e., cognition that is decoupled from sensory processing (Margulies et al., 2016; Smallwood et al., 2013)), including memory-driven cognition (Murphy et al., 2018). The DMN has been explicitly linked to social cognition (Mars et al., 2012; Spreng et al. 2009; Shillbach et al. 2008) although it has

also been shown that regions activated by social tasks are, to some degree, distinct from what are considered 'core' regions of the DMN (Jackson, 2021; Jackson et al., 2016; Mars et al., 2012). The relationship between the DMN and social cognition therefore remains elusive. In the present study, however, it was core DMN regions (especially those around the sagittal midline) that showed differences between semantic cognition and ToM. DMN activation has been shown to be inversely correlated with task difficulty and individual participants' performance in some types of cognitive tasks (Eichele et al., 2008; Mayer et al., 2010) and, therefore, a possible explanation for differential engagement of the DMN by semantic cognition and ToM is a general difference in task difficulty.

Our results shed new light on the relationship between the 'social brain' and domain-general networks by highlighting significant overlap with the SCN. Important clues might also be gleaned from the way in which activation patterns diverge, and the fact that this occurs most notably within the right hemisphere homologues of left-lateralised SCN regions (e.g., the TPJ). One possible account of these observation is that engaging in ToM recruits the SCN plus additional regions that are more tuned to social processes. Alternatively, these regions may all comprise one widely distributed but nonetheless functionally integrated network, that exhibits systematic variation in the involvement of some of its nodes (particularly across hemispheres) owed to task-related or stimulus-related factors (e.g., input modality). 'Socialness' of a task (or perhaps the degree of involvement of self- and other-related processes; (Chiou et al., 2022; Platek et al., 2004; Quesque & Brass, 2019)) could be one such task-related factor (Binney & Ramsey, 2020; Pexman et al., 2023). Further research is needed to directly probe these factors and how they drive network involvement within and across domains. In the remainder of this discussion, we expand on debates surrounding the ATL and the TPJ because they are ascribed key roles in both ToM and in semantic cognition.

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

Convergent neuropsychological and neuroimaging evidence strongly implicates the ATL in semantic knowledge representations which underpin a range of meaning-imbued behaviours, including language use, action understanding and interactions with objects (Patterson & Lambon Ralph, 2016; Lambon Ralph et al., 2017). By extension, we argue that the contribution of the ATL to ToM, and to social cognition more generally, is the supply of conceptual level information which constrains inferences about the intentions and actions of other agents (Binney & Ramsey, 2020). The current study revealed reliable overlap between ToM and semantic processing in the ATLs, which supports this hypothesis. The present findings also complement those of prior fMRI studies that directly explored the relationship between social and general semantic processing in the ATL. Across all these studies, two consistent findings have emerged. First, a ventrolateral portion of the left ATL responds equally to socially relevant concepts and more general concepts (both concrete and abstract), and this is irrespective of whether concepts are probed via verbal or pictorial stimuli (Binney, Hoffman, et al., 2016; Rice et al., 2018). The same ventrolateral region also activates during three different verbal and nonverbal ToM tasks, which suggests that conceptual information is accessed during ToM (Balgova et al., 2022). Second, there are some differences between social and general semantic tasks within the dorsolateral ATL (Binney et al., 2016; Rice et al., 2018; also see Arioli et al., 2021; Lin, Wang, et al., 2018; Lin, Yang, et al., 2018; Mellem et al., 2016; Ross & Olson, 2010; Zahn et al., 2007). In the present meta-analysis there was a higher level of convergent activation for ToM in the anterior MTG/STG, but the location of this difference moves around across prior studies. Importantly though, the differences are small compared to the large degree of overlap. In the present study, the difference between ToM and SCN was overlapping with a much larger left ATL cluster which was activated consistently across both domains (also see Beauchamp, 2015; Deen et al., 2015 for comparisons of social perception with language and voice perception).

This overall pattern is consistent with the *graded semantic hub* account (Bajada et al., 2019; Binney et al., 2012; Rice, Hoffman, et al., 2015), which characterises the bilateral ATL as a unified

representational space, all of which is engaged by the encoding and retrieval of semantic information of any kind. The centre of this hub exists over the ventrolateral ATL and its engagement in semantic processing is largely invariant to stimulus factors (e.g., modality). Towards the edges of this space, however, there are gradual shifts in semantic function such that regions on the periphery are more sensitive to certain types of semantic features (for a computational exploration of this general hypothesis, see Plaut, 2002). Why exactly ToM tasks would engage the dorsolateral ATL more than general semantic tasks is unclear. One possibility is that the meaning conveyed by typical ToM stimuli (i.e., the state of mind of an actor in absence of explicit descriptors) is not directly observable and, therefore must be inferred to a greater extent than in a typical semantic task. This may rely heavily on verbally-mediated semantic information, which has been shown to engage these parts of the ATL more (Binder et al., 2009; Rice, Hoffman, et al., 2015; Visser & Lambon Ralph, 2011). Another possibility is that it reflects a proximity to and strong connectivity with the limbic system (via the uncinate fasciculus; (Bajada et al., 2017; Binney et al., 2012; Papinutto et al., 2016) and a role of this ATL region in processing semantic features related to emotion (Olson et al., 2007; Rice, Hoffman, et al., 2015; Vigliocco et al., 2014). In the present study, there was no evidence of ventrolateral ATL involvement in ToM or semantic processing. This can be explained by the fact that most of the studies included used fMRI, and conventional forms of this technique are unable to detect blood-oxygen level-dependent (BOLD) signal in these parts of the ATL (Devlin et al., 2000). ATL-optimised distortion-corrected fMRI studies, on the other hand, detect robust ventral ATL activation during both semantic and ToM tasks (Balgova et al., 2022; Binney et al., 2010; Castelli et al., 2000; Devlin et al., 2000; Sharp et al., 2004). This methodological factor may be particularly important for understanding the lack of left ATL activation for nonverbal stimuli, as prior studies have shown this is almost entirely limited to ventral and ventromedial ATL structures which suffer the most from signal dropout. (Rice, Lambon Ralph, et al., 2015; Visser, Embleton, et al., 2010).

There were also differences in the extent to which the right ATL was engaged, with a greater proportion of the right anterior MTG involved in ToM. Moreover, the involvement of the right ATL

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

4.4. The Temporo-Parietal Junction

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

been implicated in integration and storage of conceptual knowledge by some authors (Binder et al., 2009; Kuhnke et al., 2020) and attributed with a more domain-general role by others (e.g., the multi-sensory buffering of spatio-temporally extended representations; Humphreys, Lambon Ralph, et al., (2021; Humphreys & Tibon, (2022)). The left MTG/STS appears to be involved in processes that constrain semantic retrieval and which could also be engaged during ToM (Diveica et al., 2021). The right TPJ does not appear to be engaged by semantic processing which is consistent with claims that it has a selective role in social and moral processing (Numssen et al., 2020; Saxe & Kanwisher, 2003; Saxe & Wexler, 2005; Young et al., 2010). However, the present study cannot rule out involvement in other cognitive domains.

4.5. Concluding remarks and future directions

In conclusion, we observed considerable overlap between the cortical networks engaged by semantic tasks and theory of mind tasks. We propose that this reflects shared underlying processes and, further, that ToM relies in part on processes related to semantic cognition (Binney & Ramsey, 2020). Alternatively, this overlap could, on closer inspection, turn out to reflect tightly yet separately packed cognitive functions that only dissociate when investigated at higher spatial resolutions or at the level of individual participants. Further research is needed to explore these alternatives. Furthermore, inferences afforded by functional neuroimaging data are merely correlational and, therefore, the field needs to increasingly turn to patient models such as stroke, temporal lobe epilepsy, and frontotemporal dementia (Kumfor, Hazelton, et al., 2017; Kumfor, Honan, et al., 2017; Rankin, 2020, 2021), and non-invasive techniques like transcranial magnetic stimulation, to directly probe whether certain brain regions are necessary for both social *and* semantic cognition.

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CRediT Author Statement

Eva Balgova: conceptualisation, methodology, data curation, investigation, formal analysis, visualisation, writing- original draft, writing- review and editing.

Veronica Diveica: conceptualisation, methodology, data curation, investigation, funding acquisition, writing- review and editing

Rebecca L. Jackson: conceptualisation, methodology, data curation, investigation, funding acquisition, writing- review and editing

Richard J. Binney: conceptualisation, methodology, funding acquisition, supervision, project administration, writing- original draft, writing- review and editing

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