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Hemispheric Specialization within the Superior Anterior Temporal Cortex for Social and Nonsocial Concepts

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Abstract

■ Studies of semantic dementia, imaging, and repetitive TMS have suggested that the bilateral anterior temporal lobes (ATLs) underpin a modality-invariant representational hub within the semantic system. Questions remain, however, regarding functional specialization across a variety of knowledge domains within the ATL region. We investigated direct evidence for the functional relevance of the superior ATL in processing social concepts. Using converging evidence from noninvasive brain stimulation and neuropsychology, we demonstrate graded differentiation of right and left superior anterior temporal areas in social cognition. Whereas the left superior ATL is necessary for processing both social and nonsocial abstract concepts, social conceptual processing predominates in the right superior ATL. This graded hemispheric specialization is mirrored in the patient results. Our data shed new light on the classic debate about hemispheric differences in semantic and social cognition. These results are considered in the context of models of semantic representation and the emerging data on connectivity for left and right ATL regions. ■

INTRODUCTION

Human behavior occurs in social contexts. Human neuroscience needs to understand which brain regions support social behavior and how they function. Multiple lines of evidence suggest that the anterior temporal lobes (ATLs) are part of the network supporting semantic (Lambon Ralph, 2013) and social cognition (Zahn et al., 2007; Amodio & Frith, 2006; Moll, Zahn, de Oliveira-Souza, Krueger, & Grafman, 2005).

The role of the ATL in semantic cognition has been supported by patient investigations (Patterson, Nestor, & Rogers, 2007; Snowden, Goulding, & Neary, 1989), neuroimaging studies (Visser, Embleton, Jefferies, Parker, & Lambon Ralph, 2010; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996), and neurostimulation studies (Pobric, Jefferies, & Lambon Ralph, 2007, 2010; Lambon Ralph, Pobric, & Jefferies, 2009). Neuropsychological evidence comes from patients with semantic dementia (SD), who have bilateral atrophy and hypometabolism in the ATLs. In addition to a generalized yet selective semantic impairment, right ATL (rATL) neurodegeneration has been associated with impairments of social behavior (Chan et al., 2009), such as lack of empathy (Rankin et al., 2006), socially inappropriate behavior (Zahn et al., 2009), and theory of mind tasks (Irish, Hodges, & Piguet, 2014), although with careful assessment, similar neuropsychiatric features are observed in cases with predominantly left ATL (lATL) atrophy, only less frequently (Chan et al., 2009).

Studies of patients with SD have given rise to the "hub-and-spoke" hypothesis in which the ATLs are a key node in the semantic network where different inputs converge to form modality-invariant conceptual representations (Lambon Ralph, Sage, Jones, & Mayberry, 2010; Patterson et al., 2007; Rogers & McClelland, 2004). Given that SD is a neurodegenerative condition, there is always the possibility that semantic dysfunction follows from pathology extending beyond the ATL, and it is this more subtle, widespread damage that is the cause of the patients' semantic impairment (Martin, 2007). In addition, because SD is characterized by bilateral atrophy, albeit sometimes very asymmetric in the early phase, it is not possible to investigate the contribution of lATL and rATL in isolation. Given these facts, the contributions of the ATL to semantic processing cannot be uniquely defined on the basis of this neuropsychological evidence alone.

Neuroimaging studies of semantic cognition have highlighted the role of the left hemisphere in the comprehension and production of spoken language (Wise, 2003). Furthermore, the importance of left anterior temporal cortex for language processing and semantic memory has been highlighted with PET (Devlin et al., 2000; Vandenberghe et al., 1996), intracranial recordings (Halgren, Baudena, Heit, Clarke, & Marinkovic, 1994), and MEG (Marinkovic et al., 2003). Bilateral ATL activations have been observed in semantic tasks for words (Binney, Embleton, Jefferies, Parke, & Lambon Ralph, 2010; Zahn et al., 2007), sounds, spoken names, and pictures (Visser & Lambon Ralph, 2011; Sharp, Scott, & Wise, 2004). The neuroimaging literature of social cognition has reported a right hemispheric bias for social stimuli (Skipper, Ross, & Olson, 2011; Zahn et al., 2007). Zahn and colleagues (2007) have suggested that the right superior ATL (sATL) selectively represents social

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concepts. When participants were making semantic judgments about social concepts (e.g., "honor–brave") versus animal function concepts (e.g., "trainable–ridden"), right sATL regions were activated. This was independently corroborated in a recent study (Skipper et al., 2011)—although the peak activations were found in the lATL rather than rATL region in another study (Ross & Olson, 2010), calling into question the strength of ATL laterality for social conceptual processing. In addition, ATL activations have been reported for other high-level social verbal and nonverbal tasks: moral judgments (Moll et al., 2005), social versus nonsocial gestures (Straube, Green, Jansen, Chatterjee, & Kircher, 2010), social attribution stimuli such as Heider and Simmel animations (Ross & Olson, 2010), and socioemotional stories (Ferstl & von Cramon, 2002). This consistency of ATL activations to high-level social tasks irrespective of the modality of the task (verbal or nonverbal) has led to its inclusion in the "social brain network" (Frith & Frith, 2012; Amodio & Frith, 2006).

It is clear that diverse social stimuli and tasks evoke activations in the ATLs. However, the precise role of the ATLs in the network remains controversial (Simmons, Reddish, Bellgowan, & Martin, 2010). By combining neurostimulation with patient investigation, we addressed three key limitations in the literature: (1) Most patients with neurodegeneration show widespread damage that is not only confined to subregions of the ATL unilaterally; (2) fMRI does not provide causal evidence for the necessity of activated regions in the task of interest; and (3) to our knowledge, no study has directly compared processing of social concepts in left and right sATL.

First, we established the necessary role of sATL in processing social versus nonsocial abstract concepts via TMS. We predicted that, if the rATL is involved in processing social concepts, as observed in patients with rATL neurodegeneration, then repetitive transcranial magnetic stimulation (rTMS) should generate a greater effect on social than nonsocial concepts. If the lATL or rATL is implicated in general semantic processing, but not general cognition (as per patients with SD), then stimulation should impact on performance with both social and nonsocial abstract concepts but not on difficulty-matched nonsemantic tasks. In the neuropsychological part of the study, we predicted the lATL case would be impaired on processing both social and nonsocial concepts, in keeping with general degradation of semantic knowledge observed in patients with SD. On the basis of previous patient (Zahn et al., 2009) and neuroimaging evidence (Skipper et al., 2011; Zahn et al., 2007), we predicted that the rATL case would exhibit a greater impairment on processing social versus nonsocial concepts.

METHODS

To establish a necessary role of the ATLs in representing semantic knowledge of social and nonsocial concepts, we investigated convergent evidence from TMS and neuropsychology. TMS is a well-established, noninvasive technique that induces electrical activation in the underlying cortex. A long train of low-frequency stimulation temporarily suppresses neural processing and disrupts behavioral tasks that rely on that cortical region (Walsh & Cowey, 2000). Cortical sites for TMS were left and right sATL and the occipital pole as a control site. Sites were identified in each individual participant through coregistration with their MRI scan. In a semantic synonym judgment task, participants were required to pick which of two concepts (e.g., "honest" vs. "eager") is more closely related to the probe ("sincere"). Our control task was a difficulty-matched, number magnitude judgment assessment. Performance was assessed before and after TMS stimulation. In the neuropsychological part of the study, we used a semantic discrimination task, which probed knowledge of social and animal function concepts in two rare cases of focal neurodegeneration of the lATL and rATL, respectively.

Design

A 3 × 3 × 2 repeated-measures design was used, with site (right sATL vs. left sATL vs. occipital pole), task (nonsocial synonym judgment vs. social synonym judgment vs. magnitude judgment), and TMS (no TMS vs. rTMS stimulation) as the three within-participant factors. The study utilized rTMS, using the "virtual lesion" method in which the train of rTMS is delivered offline (without a concurrent behavioral task), and then behavioral performance is probed during the temporary refractory period and compared with performance on the same task outside this refractory window.

Participants

Twelve right-handed participants took part in the experiment (seven women; mean age = 25.8 years, *SD* = 3.8 years). All participants were strongly right-handed, with a laterality quotient above 75 (mean = 88.33, *SD* = 6.24) on the Edinburgh Handedness Inventory (Oldfield, 1971) and had normal or corrected-to-normal vision. All participants provided written consent for participation after being screened for adverse effects of TMS. The experiment was approved by the local ethics committee.

Stimuli

One hundred sixty concept trials were used in the synonym judgment task, and 80 number trials were used in the number judgment task. Each trial contained three concepts: a probe concept (e.g., "sincere"), a target choice (e.g., "honest"), and an unrelated foil (e.g., "eager"). All words within a triad were matched for frequency (mean = 28.49, *SD* = 11.23; Kučera & Francis, 1967) and imageability (mean = 275.71, *SD* = 43.72; Bird, Franklin, & Howard, 2001). All triads were divided into social and nonsocial trials based on ratings from independent evaluators. Item ratings were obtained for 450 words by asking 40 undergraduate students (8 men and 32 women) whose ages ranged from 18 to 32 (mean = 25) years to rate the words based on how social they are. Students were given a 7-point scale (1 = *very nonsocial* to 7 = *very social*) and asked to indicate the rating of each word. Students were given examples of possible ratings for words not included in the set. From that set, we created 80 social and 80 nonsocial trials. For nonsocial trial, the mean rating was 2.34, with *SD* = 0.60 and range = 1.73–2.94. For social trial, the mean rating was 5.77, with *SD* = 0.79 and range = 5.02–6.56. Consequently, social and nonsocial trials were matched on psycholinguistic variables as well as behavioral measures: RTs and accuracy in pilot experiments. The format for the number task was the same as for the synonym judgment task: A three-digit probe number was presented at the top of the screen, and underneath, 2 three-digit number choices were given. Participants were required to pick which of the two numbers was closest in value to the probe. The pilot studies revealed that making magnitude judgments about three-digit numbers was the best behavioral match (in terms of RTs and accuracy) for our synonym task.

Task and Procedure

A PC running E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA) allowed the presentation of stimuli and recording of the responses. In a single experimental session, participants performed a synonym judgment task and a number magnitude judgment task. In a semantic synonym judgment task, participants were required to pick which of two words (e.g., "honest" vs. "eager") is more closely related to the probe ("sincere"). The probe is presented at the top of the screen, and the two word options are presented underneath. The participants indicated their choice by using both hands for pressing a single key (M or Z). Half of the targets were associated with each key, so they used each hand for 50% of the answers. The occurrence of target location was randomized for each participant and each session. The experiment began with a practice block of 10 trials for each stimulus set. Experimental trials were presented in a random order in two blocks (80 synonyms and 40 numbers). After 10 min of offline rTMS, another two blocks (80 synonyms and 40 numbers) followed. This yielded 240 trials per experimental session. The blocks were randomized across participants. Stimuli were presented until the response was given (maximum duration = 3000 msec) and followed by a blank screen (duration = 500 msec). Computer key presses were recorded using a computer keyboard that was placed in front of each participant. Response latencies were recorded by the computer, and the accuracy was checked in the analyses.

TMS

A MagStim Rapid2 (Magstim Co., Whitland, UK) stimulator with two external boosters was used (maximum output = approx. 2.2 T). Magnetic stimulation was applied using a 50-mm figure-of-eight coil.

Selection of TMS Site

The structural T1-weighted MRI scans were coregistered with the participant's scalp using MRIreg (www.mccauslandcenter.sc.edu/mricro/mricron/index.html). Immediately before the TMS session, scalp coordinates were measured using an Ascension Minibird (www.ascension-tech.com) magnetic tracking system. The right Montreal Neurological Institute coordinates for the sATL (53, 8, −13) were obtained by averaging peak coordinates from previous fMRI studies associating the right sATL with knowledge of social concepts (Zahn et al., 2007: 51, 15, −12; (Zahn et al., 2009: 54, 0, −3) and peak coordinates of resting state glucose hypometabolism from a study of social concepts in frontotemporal lobar degeneration (FTLD; 54, 9, −24: Zahn et al., 2009). The coordinates for the left sATL corresponded to the homologue region (−53, 8, −13). A middle occipital stimulation site (Oz) was also employed as a site to control for possible nonspecific TMS effects.

Stimulation Parameters

Individual active motor threshold was determined for every participant. rTMS was delivered offline for 10 min at 1 Hz (600 sec at 120% motor threshold level) applied to the right sATL, left sATL, and Oz. The coil was securely held by experimenter, centered over the site to be stimulated. The average stimulation intensity during rTMS was 64% of the machine output.

NEUROPSYCHOLOGICAL INVESTIGATION

Patients

Two female (age = 60 and 61 years at the time of testing, education = 13 and 14 years) right-handed patients with FTLD according to Lund–Manchester Consensus criteria (Neary et al., 1998) were selected from a larger case series because they exhibited the rare picture of predominant atrophy of the lATL versus rATL, respectively. The Lund–Manchester Consensus criteria were previously shown to correlate highly with postmortem neuropathological diagnoses (Snowden et al., 2011). The study was approved by the South Manchester NHS Research Ethics Committee, and the patients gave written informed consent. In addition to extensive background neuropsychological testing, a neurological examination, and an extensive neuropsychiatric interview with their caregivers, they received the social concept discrimination task (Zahn et al., 2009). Both patients showed features of SD as classified by a senior neuropsychiatrist (R. Z.) and senior neuropsychologist (M. A. L. R.), but the rATL case presented primarily with behavioral features. Data for healthy older adults are taken from published test norms and, for the same test, from Zahn et al. (2009).

Materials and Procedure

The semantic task consisted of two carefully matched conditions to compare concepts describing social behavior (i.e., social concepts) and concepts describing nonsocial behavior or properties of animals (i.e., animal function concepts) of equal familiarity and descriptiveness (see previous description in Zahn et al., 2009). A prime word describing a concept (e.g., "adventurous") was presented at the top of a screen, and participants had to decide which of two concepts underneath was more related in meaning to the prime concept at the top. Target (e.g., "courage") and distracter (e.g., "controlled") concepts were chosen from the same category as the prime concepts (e.g., animal function concept prime: "trainable," target: "ridden," distracter: "bites") and had been used in our previous fMRI studies (Ross & Olson, 2010; Zahn et al., 2007). Seventy-three items with 80% response agreement in aged controls were presented randomly (25 positive social concept triads, 24 negative social concept triads, and 24 animal function concept triads).

RESULTS

RT Analyses

The RTs for all participants and all conditions were submitted to a repeated-measures ANOVA with three within-participant factors: Task (nonsocial synonym judgment, social synonym judgment, and magnitude judgment), Site (right sATL, left sATL, and Oz), and TMS (no TMS vs. rTMS). We removed 16 items from the synonym task (11 nonsocial and 5 social) and two items from the number task that yielded over 50% errors in the no-TMS condition. This resulted in removal of 7.9% of items. The main effects of Task, Site, and TMS were not significant. We observed a significant interaction between Task and TMS ($F = 36.108$, $df = 2, 22$, $p < .001$). We also report a significant interaction between Task and Site ($F = 4.196$, $df = 2, 22$, $p = .029$). Crucially, we observed a significant three-way interaction between Task, Site, and TMS ($F = 5.259$, $df = 4, 44$, $p = .001$). To explore the three-way interaction further, we split the original analysis by task and carried out three repeated-measures ANOVA with two within-participant factors Site (right sATL, left sATL, and Oz) and TMS (no TMS vs. rTMS). For the nonsocial task, main effects of Site and TMS were not significant. However, we observed a significant interaction between Site and TMS ($F = 7.279$, $df = 2, 22$, $p = .004$). For the social task, we observed a main effect of TMS ($F = 14.994$, $df = 1, 11$, $p = .003$) and a significant interaction between TMS and Site ($F = 6.005$, $df = 2, 22$, $p = .008$). For the number task, we only observed a main effect of the TMS ($F = 10.698$, $df = 1, 11$, $p = .007$). Planned t tests on the RTs were used to compare performance in rATL and lATL for social and nonsocial concepts. After controlling for false discovery rate (Benjamini & Hochberg, 1995), there was a difference for social and nonsocial concepts between rATL and lATL. The rATL was more involved in processing social than nonsocial concepts, with a significant TMS effect for social concepts, $t(11) = 3.713$, $p < .01$, but not for nonsocial concepts, $t(11) = 1.67$, $p > .05$, whereas the lATL was involved in both social and nonsocial concepts ($t(11) = 3.63$, $p < .004$, and $t(11) = 2.285$, $p < .05$, respectively; see Figure 1A).

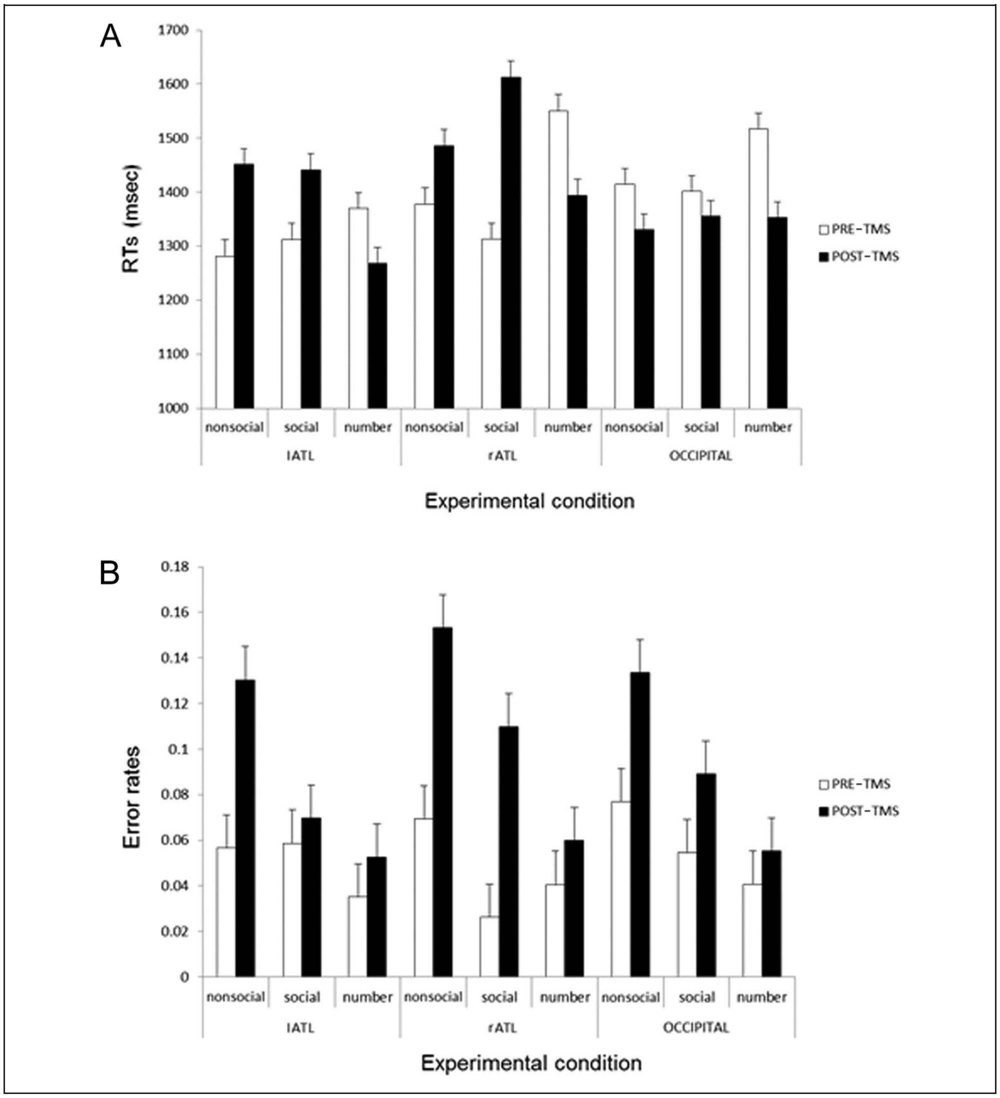
Error Analyses

The error rate was examined in a repeated-measures ANOVA with Task (synonym judgment, number judgment), Site (right sATL, left sATL, and Oz), and TMS (no TMS vs. rTMS) as factors. There was a main effect of Task ($F = 6.341$, $df = 2, 22$, $p = .007$) as well as a main effect of TMS ($F = 20.982$, $df = 1, 11$, $p = .001$). We also observed a significant interaction between Task and TMS ($F = 6.613$, $df = 2, 22$, $p = .011$). All other main effects or interactions were not significant ($p > .1$). To explore the task-and-TMS interaction further, we split the original analysis by task and carried out three repeated-measures ANOVA with two within-participant factors Site (right sATL, left sATL, and Oz) and TMS (no TMS vs. rTMS). For the nonsocial task, the main effect of TMS was significant ($F = 14.88$, $df = 1, 11$, $p = .003$). All other main effects or interactions were not significant ($p > .1$). For the social task, we observed the main effect of TMS ($F = 15.604$, $df = 1, 11$, $p = .002$), whereas the main effect of Site and Site x-TMS interaction were not significant ($p > .1$). For the number task, all main effects or interactions were not significant ($p > .1$; see Figure 1B).

Neuropsychological Results

Neuropsychological data were analyzed using an established method for directly comparing two single cases with each other (C_CTC; Crawford, Garthwaite, & Wood, 2010). We report one-tailed p values (lower performance on social concepts relative to animal function concepts in patients with rATL damage compared with patients with no damage to this region). We also compared the performance of patients with the control group by using an established method for individual patient-based analysis (Singlims: Crawford & Garthwaite, 2002). Both the rATL and lATL cases were impaired relative to the controls on social and nonsocial concepts (all $t(29)$s $>$ 2.35, all ps $< .013$, one-tailed). However, the difference in impairment between social and nonsocial concepts

Figure 1. Effect of rTMS on synonym judgment and magnitude judgment tasks for RTs (A) and error rates (B). Each bar represents the mean decision time alongside the corresponding standard error adjusted for within-participant comparisons (Loftus & Masson, 1994) for each condition. Occipital = occipital pole.



was significantly larger for the rATL case than for the lATL case, $t(29) = 3.0$, $p < .005$ (see Figure 2).

The similarities between our TMS data and neuropsychological investigation can be observed in Figure 3.

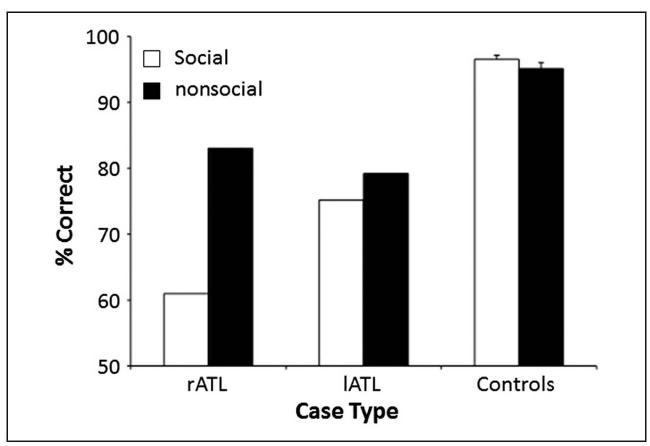


Figure 2. Overall performance of the lATL patient and rATL patient compared with the control group on social and nonsocial concepts. Error bars indicate *SEM* on the control group ($n = 30$) performance.

DISCUSSION

In this study, we were able to ascertain differential contributions of left and right sATL regions to social cognition and general semantic processing. The left sATL region was implicated in both social and nonsocial concepts. In contrast, the right sATL made a greater contribution to social than nonsocial concepts. Our results are in agreement with the central role of the ATL in representing conceptual knowledge (Lambon Ralph, 2013; Patterson et al., 2007; Spitsyna, Warren, Scott, Turkheimer, & Wise, 2006; Bozeat, Lambon Ralph, Patterson, Garrard, & Hodges, 2000) and the importance of the right temporal lobe for social cognitive impairments in rATL neurodegeneration (Chan et al., 2009; Liu et al., 2004).

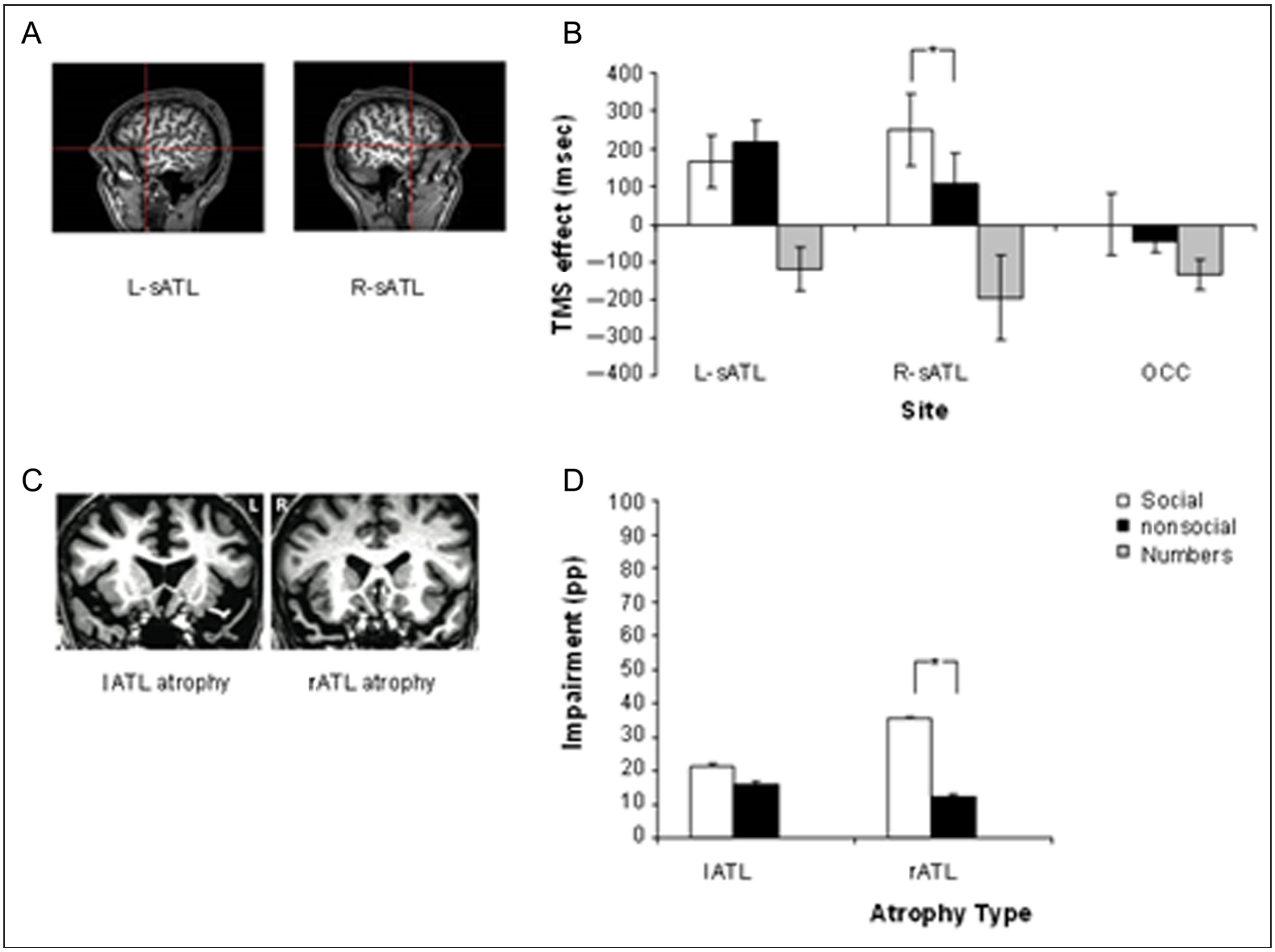


Figure 3. Stimulation sites, TMS results, lesion sites, and patient performance data on social and nonsocial concept task conditions. (A) ATL regions that were disrupted with TMS, shown for one participant. (B) The TMS effect on semantic judgments of social and nonsocial concepts and magnitude judgment of numbers. Each bar represents the TMS effect as RT change caused by TMS. Error bars indicate *SEM* adjusted to reflect the between-condition variance used in repeated-measure designs (Loftus & Masson, 1994). (C) MRI images for patients with lATL- and rATL-predominant SD. (D) Overall impairment in percentage points (% correct control − % correct patient) of the lATL patient and rATL patient compared with the control group on social and nonsocial concepts. Error bars indicate *SEM* on the control group (n = 30) performance. L-sATL = left sATL; R-sATL = right sATL; OCC = occipital pole; LATL atrophy = patient with predominantly lATL atrophy; RATL atrophy = patient with predominantly rATL atrophy. Asterisk denotes significantly slower RTs after rTMS than at baseline. Asterisk denotes significantly worse performance on a task.

In a review of the role of superior temporal areas (STS), Hein and Knight (2008) proposed that the same brain region can support different cognitive functions determined by a task-dependent network of connections. Indeed, this hypothesis has been formally explored previously for the ATLs and semantic processing, using computational models (Schapiro, McClelland, Welbourne, Rogers, & Lambon Ralph, 2013; Lambon Ralph, McClelland, Patterson, Galton, & Hodges, 2001). Most relevant to the current findings, Lambon Ralph et al. (2001) demonstrated that a bilateral ATL semantic system exhibits a left-sided sensitivity to language (speech production) as a consequence of greater connectivity of the lATL to left-hemisphere language centers. Following the same line of argument, the differential involvement of left and right sATL regions in social and nonsocial conceptual processing could be explained by the specific pattern of connections between the ATL regions with the rest of the brain. Indeed, Skipper et al. (2011) have already proposed that a greater role for the right temporal region in social processing might reflect a right-sided pattern of connectivity to social-processing regions.

These proposals are consistent with the emerging story from recent white matter connectivity studies. Specifically, the temporal pole has dense connections with fusiform gyrus, limbic structures, and pFC (Pascual et al., 2014; Gloor, 1997). These brain areas are involved in linguistic, social, and emotional processing as well as decision-making (Simmons et al., 2010; Gloor, 1997). In an in vivo probabilistic tractography study, Binney, Parker, and Lambon Ralph (2012) showed that there is strong intratemporal lobe ATL white matter connectivity, conducive to the information integration required for the extraction of modality-invariant, general semantic representations. Furthermore, there are more regionally specific connectivity patterns to nontemporal lobe areas. Relevant to the formation of social concepts, the sATL and temporal pole are connected to the frontal lobe and OFC via the uncinate fasciculus (UF), a bidirectional white matter pathway. In a recent study, Catani and colleagues (2013) used tractography to show that damage to UF correlated with deficits in semantic processing in patients with primary progressive aphasia. It is quite possible, therefore, that the sATL-rTMS effect on social concepts observed in this study reflects either the convergence and representation of socially relevant information at the sATL site and/or the perturbation of information transmission between ATL and orbitofrontal regions (Quentin, Chanes, Migliaccio, Valabrègue, & Valero-Cabré, 2013; Neubert, Mars, Buch, Olivier, & Rushworth, 2010).

The graded, differential roles of lATL and rATL in social and general concepts may well result from the pattern of connectivity. As noted above, the role of sATL in social concepts (left and right) probably reflects its connectivity between temporal cortex and OFC (Pascual et al., 2014; Catani et al., 2013; Binney et al., 2012; Moran, Mufson, & Mesulam, 1987). After previous proposals and computational demonstrations (Lambon Ralph et al., 2001), the graded functional differences between left and right probably reflect (i) a right > left bias in UF density (Highley, Walker, Esiri, Crow, & Harrison, 2002)—which will encourage a rightward division of labor for social conceptual processing—and (ii) greater left-sided language connectivity (both "dorsal" arcuate fasciculus and "ventral" medial longitudinal fasciculus/extreme capsule complex language pathways are left hemisphere biased; Parker et al., 2005).

The bilateral ATLs play a crucial role in semantic memory (Lambon Ralph et al., 2009; Patterson et al., 2007). It is undisputed that the left hemisphere has a central role in the comprehension and production of spoken language (Wise, 2003). Furthermore, imaging studies show that abstract nouns produce greater activation almost exclusively in the left hemisphere in superior temporal and inferior frontal cortex (Binder, Desai, Graves, & Conant, 2009; Spitsyna et al., 2006; Sabsevitz, Medler, Seidenberg, & Binder, 2005). This finding has been confirmed by neurostimulation (Hoffman, Jefferies, & Lambon Ralph, 2010) and patient studies (Hoffman, Pobric, & Lambon Ralph, 2012). Moreover, patients with lATL neurodegeneration also exhibit behavioral problems such as behavioral rigidity, disinhibition, apathy, and obsessional behavior as well as mood changes such as depression (Chan et al., 2009). However, these problems are often masked and underreported given the predominant language problems associated with lATL neurodegeneration. Although the left UF connects lATL with pFC, it has been shown that direct stimulation of the left uncinate does not result in general language impairments (Duffau, Gatignol, Moritz-Gasser, & Mandonnet, 2009). Therefore, one possibility is that the lATL is specialized for verbal semantic processing because language representations are left lateralized: For example, using a connectionist model, Lambon Ralph et al. (2001) accounted for left–right asymmetries in picture naming in terms of stronger connections between lATL and speech output processes in the left hemisphere.

Extending this hypothesis, it is possible that the right temporal lobe might make a greater contribution to social semantic processing if the socially relevant information that interacts with semantic representations comes more strongly from right than left posterior regions or if the preferential left-hemisphere language connectivity induces a division of labor across the ATLs such that the rATL defaults to social processing because of connections to right prefrontal and orbitofrontal regions. This is in accordance with a recent meta-analysis of functional imaging studies of conceptual knowledge, which argues for a graded version of the hub-and-spoke account, whereby the representation of conceptual knowledge is supported by bilateral yet graded connectivity between the ATLs and modality-specific sensory, motor, and limbic cortices (Rice, Lambon Ralph, & Hoffman, 2015).

Although we used SD as a test case for patient performance, these results have broader implications and are consistent with social processing deficits in other neurological and psychiatric syndromes. Specifically, it is well established that individuals with psychopathy have marked difficulties in processing abstract concepts (Kiehl et al., 2004). Subsequently, in an fMRI study, decreased rATL activations were reported when psychopaths were making lexical decisions about abstract concepts. In addition, in this group, ATLs are characterized by structural abnormalities such as reduced gray matter volume, including weaker connections from rATL to orbitofrontal regions (Craig et al., 2009).

As well as giving insights about the role of lATL and rATL regions in social and general semantic concepts, the current results provide a new perspective on the rich set of clinical results. Detailed studies of left and right temporal lobes, FTLD (SD) cases have tended to emphasize the fact that left-sided cases have a predominantly language-focussed presentation; and the right-sided patients, a social deficit (Chan et al., 2009; Zahn et al., 2009; Rosen et al., 2005; Miller, Darby, Benson, Cummings, & Miller, 1997). Consistent with the results from the current study and implications of the white matter neuroanatomy reviewed above, Hornberger, Geng, and Hodges (2011) found that patients with SD had decreased fractional anisotropy values in the left and right UF, compared with the healthy controls. Yet, only in patients with rATL neurodegeneration did decreased fractional anisotropy values correlate with behavioral symptoms. The clinical literature does not support, however, an absolute dissociation between general versus social conceptual representations in lATL versus rATL regions, respectively. Indeed, in a more formal assessment of neuropsychiatric symptoms, Chan et al. (2009) found that both patients with predominantly left- and right-sided ATL were reported to have social and behavioral impairments to different degrees. Our study validates these clinical studies (Chan et al., 2009; Zahn et al., 2009) by combining approaches from classical neuropsychology and cognitive neuroscience; we demonstrate graded hemispheric specialization of ATL regions to social cognition and general semantic knowledge.

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