The Role of the Right Temporoparietal Junction in the Control of Imitation

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Controlling neural representations of the self and other people is fundamental to social cognition. Brain imaging studies have implicated the right temporoparietal junction (rTPJ) in this ability, but causal evidence for its role is lacking. A debate is also ongoing regarding whether the control of, or switching between, self and other representations is a specialized or domain-general process: the rTPJ's well-established role in reorienting attention supports a domain-general process, but a role specific to social cognition has also been proposed. Neuronavigated repetitive transcranial magnetic stimulation was used to target the rTPJ (and a control mid-occipital site) during a task requiring participants to switch between representations of others' actions on both a social and a nonsocial level, by manipulating imitative and spatial compatibility simultaneously and independently. Both imitative and spatial compatibility effects were apparent on response times; however, the effect of imitative compatibility was significantly stronger, indicating less control of imitation, during stimulation of the rTPJ relative to the control site. This suggests that the rTPJ is involved in switching between self and other representations, and further, that this process may not be entirely domain general.

Keywords: imitative compatibility, self–other control, social cognition, TPJ, transcranial magnetic stimulation

Introduction

A fundamental aspect of social cognition is the ability to distinguish, and switch between, representations of the self and other people. For example, when taking another person's perspective, switching between "self" and "other" representations is required in order to inhibit the representation of one's own perspective and to enhance the representation of the other's perspective. Similarly, in theory-of-mind tasks, one needs to represent the beliefs, desires, or intentions of another person, rather than one's own beliefs, desires, and intentions. When empathizing with another person, the affective state that results from representation of the other's emotions must be distinguished from one's own (Singer and Lamm 2009), again requiring the ability to switch between representations of one's own and others' emotions. Finally, the control of imitation, a key aspect of social interaction (Chartrand and Bargh 1999), requires one to switch between motor representations activated by the observation of another's actions and self-generated motor representations (Brass et al. 2009).

Although these tasks involve different higher-level social cognitive processes, there is some evidence that a common lower-level process may contribute to all of them (Decety and Lamm 2007). This lower-level process may be the ability to control, or more specifically switch between, representations of the self and the other, whether these be representations of visual perspectives, mental states, emotions, or actions. In this framework, the requirement for the control of self and other representations occurs whenever the task requires the participant to excite one representation, while inhibiting the other. In this paper, we use the term "switching between" the 2 representations to refer to this process of exciting the self-representation and inhibiting the other-representation, or vice versa. In the case of theory-of-mind tasks, the 2 representations are of the mental states of the self and other, for example, in Young, Camprodon, et al.'s (2010) moral judgment task: I know the powder is sugar; but Grace believes it is toxic. I need to inhibit the representation of my mental state and to excite that of Grace's in order to carry out the task (in this example, the task requires me to assess her morality when putting the sugar labeled "toxic" into her friend's coffee). In the case of the control of imitation (e.g., Brass et al. 2001), the 2 representations are motor representations, for example: as a result of task instructions, I intend to lift my index finger, and activate the motor representation for index finger lifting; but the sight of someone else lifting their middle finger activates the motor representation for middle finger lifting. I need to inhibit the motor representation of the other person's action and to excite my self-generated motor representation in order to perform the task successfully. It can, therefore, be argued that the ability to switch between representations of self and other, whether these are mental representations in the case of theory of mind, motor representations in the case of imitation, or representations of visual perspective or emotions, helps to facilitate successful social cognition.

The neural basis of this ability to switch between representations of self and other has been investigated by searching for common neural correlates of these social cognitive tasks. A number of meta-analyses have demonstrated the recruitment of the right temporoparietal junction (rTPJ) in perspective-taking, theory of mind, and empathy (Decety and Sommerville 2003; Decety and Lamm 2007; van Overwalle 2009). The control of imitation has also been investigated extensively by Brass and colleagues (Brass et al. 2005, 2009; Spengler et al. 2009). Using functional magnetic resonance imaging (fMRI), these researchers found an increased response in the rTPJ, as well as in the medial prefrontal cortex, when participants have to control the tendency to imitate the actions of others.

However, since the majority of evidence summarized above has come from correlational brain imaging studies, there is relatively little causal evidence for the role of the TPJ in tasks that require switching between self and other representations. Lesion studies which investigate this question using higher-level social cognitive tasks provide mixed support. For example, Samson et al. (2004) demonstrated impaired theory-of-mind ability in 3 patients with left TPJ lesions. On the other hand, Spengler et al. (2010) did not find an overall deficit in the ability to control imitation in a group of patients with lesions to either the left or right

TPJ. However, they did find a correlation between the ability to control imitation and performance on measures of perspective-taking in this group, as well as trends toward correlations between the ability to control imitation and theory-of-mind performance. These results are consistent with the hypothesis that the TPJ supports a process common to all these tasks. Additionally, these 2 studies indicate, contrary to some meta-analyses of imaging data (e.g., Decety and Lamm 2007), that the left TPJ may be as important as the right for social cognition.

In healthy participants, brain stimulation techniques such as repetitive transcranial magnetic stimulation (rTMS) and transcranial direct current stimulation (tDCS) can demonstrate causal involvement of a brain area in a cognitive task. So far, the use of these techniques to investigate TPJ involvement in tasks that require switching between self and other representations has been limited to 3 studies. Two of these studies have found impairments in different aspects of theory-of-mind performance following rTMS to the rTPJ (Costa et al. 2008; Young, Camprodon, et al. 2010; however, the comparison questions in the study by Costa et al. did not control for the complexity of false-belief processing, see, e.g., Perner and Leekam 2008, and so the specificity of that effect is unclear). Another recent study, the first to consider other social cognitive processes, used tDCS to increase cortical excitability around the rTPJ. This resulted in an increased ability to switch between representations of the self and other in both perspective-taking and the control of imitation (Santiesteban et al. 2012). The first aim of the present study was therefore to build on that of Santiesteban et al. (2012) by using rTMS, a technique with greater spatial resolution than tDCS, to investigate the causal role of the rTPJ in switching between self and other representations.

A more fundamental problem concerns whether switching between self and other representations is a specialized or domain-general mechanism. For example, the rTPJ plays a well-documented role in reorienting attention, a domain-general ability (Corbetta and Shulman 2002). Therefore, it is unclear whether the ability to switch between representations of the self and other is a specialized mechanism for social cognition, or alternatively an example of domain-general attentional reorienting (Mitchell 2008). Part of the problem is that it is difficult to measure both social cognition and domain-general processing in the same task.

Two prominent fMRI experiments have attempted to investigate whether the involvement of the rTPJ in social cognition is specific or domain-general. Mitchell (2008; see also Rothmayr et al. 2011) found a considerable overlap between neural responses in the rTPJ to both social cognition (theory-of-mind stories) and domain-general processing (attentional reorienting following an invalid cue). In contrast, Scholz et al. (2009) claimed that the apparent overlap was due to low spatial resolution, and that distinct neural responses to these tasks can indeed be measured. However, these studies used different tasks to measure social cognition versus domain-general processing. Such tasks use very different stimuli and involve very different task demands. Thus, differential neural responses may reflect an aspect of the stimuli or task instructions, rather than differences in the underlying mechanism(s) of interest.

An alternative approach is to select a task in which both social and domain-general processing can be measured simultaneously, while stimuli and task instructions are held constant. Many tasks used in studies of theory of mind and perspective-taking present difficulties in this regard. Although the control

conditions are intended to control for domain-general processing, they often involve different stimuli, instructions, or questions (Scholz et al. 2009; Dumontheil et al. 2010), and may place differing demands on other processes, for example, working memory (Callejas et al. 2011). Young, Dodell-Feder, et al. (2010) sought to address these problems by using an fMRI design in which judgments of mental states were compared with that of physical properties (mental state contrast) for both unexpected and expected situations (salience contrast). The mental state contrast, but not the salience contrast, produced an increased response in the bilateral TPJ, emphasizing the involvement of the TPJ in mental state reasoning, and indicating that its involvement is not due to the greater salience of mental states. However, it could still be argued that the mental and physical stimuli differ on other dimensions, such as the presence of a protagonist. Therefore, the present study used a task that measures the control of imitation (Catmur and Heyes 2011; see also Brass et al. 2001; Bertenthal et al. 2006), in which the ability to control imitation can be measured simultaneously with the ability to control a nonsocial behavior: the tendency to respond in a spatially compatible location to that which is observed (Simon 1969). Crucially, both imitative and spatial response tendencies are measured in terms of response times (RTs) to task-irrelevant stimuli, and thus, the stimuli used and the task demands are the same for both the imitative and the spatial aspects of the task.

In this task, participants observe a hand at rest on a screen and are instructed to lift either the index or middle finger of their right hand in response to a colored cue. Imitative response tendencies (imitative compatibility effects) are measured by calculating the difference in RT to perform the task-relevant action in the presence of the image of an imitatively incompatible, versus an imitatively compatible, task-irrelevant action. For example, participants are slower to lift their index finger when the cue to lift is accompanied by the image of a lifting middle finger, compared with a lifting index finger. Spatial response tendencies (spatial compatibility effects) are measured by calculating the difference in RT to perform an action on the side of space that is spatially incompatible, versus spatially compatible, with that of the task-irrelevant action. For example, participants are slower to lift their index finger (a response on the left side of space) when the cue to lift is accompanied by an image of an action on the right, compared with the left, side of space.

Catmur and Heyes (2011) demonstrated that both imitative and spatial compatibility effects can be obtained in the same task by crossing the factors of imitative and spatial compatibility. Thus, on any given standard trial, the task-irrelevant action is either imitatively incompatible or imitatively compatible; and either spatially incompatible or compatible, resulting in 4 different trial types (Fig. 1A). Here, we used a modified version of Catmur and Heyes' (2011) task with the addition of baseline trials (Wiggett et al. 2013) in which the cue to lift is accompanied by a pixelated image of the resting task-irrelevant hand. The inclusion of these baseline trials can be considered an appropriate control task, as they produce the same temporal alerting effects as the task-irrelevant actions in standard trials and allow the measurement of baseline RTs without the influence of task-irrelevant actions. Such a control task is crucial in revealing whether rTPJ stimulation has an effect simply on one's ability to perform instructed finger lifts in the absence of compatible and incompatible task-irrelevant stimuli.

The size of the imitative compatibility effect is an inverse index of the ability to control the tendency to imitate. The
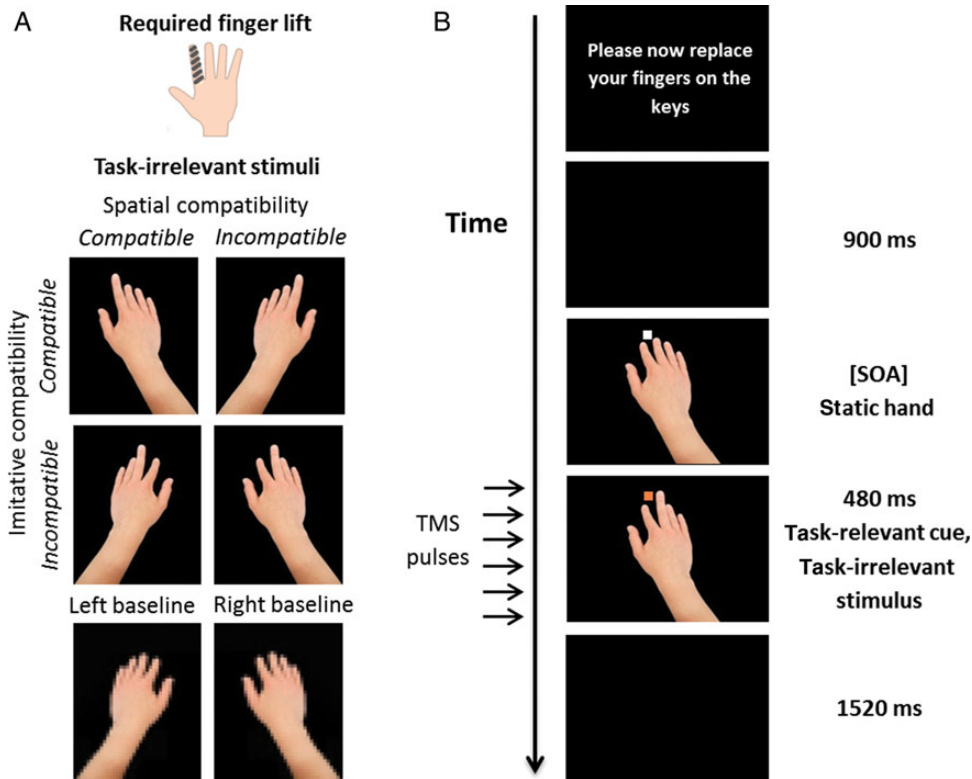
Figure 1. (*A*) Examples of task-irrelevant hand stimuli. Labels denote spatial and imitative compatibility of stimuli on the standard trials, illustrating the 2 × 2 design, and left- or right-hand stimuli on the baseline trials, and are with respect to the required finger lift shown (e.g., index finger lift; when a middle finger lift is required, levels of spatial and imitative compatibility are each reversed). Each hand stimulus shown was presented a total of 18 times during each stimulation condition. (*B*) One full trial in the experiment. Participants were first instructed to replace the index and middle fingers of their right hand on the "N" and "M" keys, respectively. After a brief interval (900 ms), the static hand and fixation square were presented (SOA: 1600, 2000, or 2400 ms), followed by the simultaneous onset of both the rTMS pulses (6 pulses at 10 Hz per trial) and the task-irrelevant stimulus, presented for 480 ms. Responses (finger lifts) were made according to the color of the task-relevant cue (orange or purple) presented with the task-irrelevant stimulus. For the response mapping for which orange = index finger lift, this trial is imitatively and spatially incompatible, whereas for the response mapping for which orange = middle finger lift, it is imitatively and spatially compatible.

observation of an action activates our own motor representation of that action, facilitating compatible and/or impeding incompatible actions (de Pellegrino et al. 1992; Brass et al. 2001). A large imitative compatibility effect, therefore, indicates a failure to inhibit the motor representation activated by the other's action and to excite the self-generated, task-relevant motor representation. Hence, this measure of the control of imitation has been extensively used to index the ability to switch between motor representations of the other and self (Brass et al. 2005, 2009; Spengler et al. 2009; Santiesteban et al. 2012).

In summary, the present study sought to investigate whether the rTPJ plays a causal role in the control of imitation; and, if so, whether it does so via a domain-general or specific mechanism. rTMS was applied to the rTPJ and a control mid-occipital (MO) site during performance of a task in which imitative and spatial response tendencies to task-irrelevant action stimuli were measured. rTPJ coordinates were selected based on previous fMRI studies of the control of imitation (Brass et al. 2005, 2009; Spengler et al. 2009), to maximize the chance of obtaining an effect of rTMS on this task. If the rTPJ is involved in the control of imitation, a greater imitative compatibility effect should be found during rTMS to rTPJ as it will impair participants' ability to control the tendency to imitate. If the rTPJ's role in this task is domain general, a greater spatial compatibility effect should also be found. It should be noted that, although we have optimized our stimulation site with respect to the task of interest,

that is, the control of imitation, a domain-general account of rTPJ function should predict that any increase in imitative compatibility is also found for spatial compatibility. In contrast, if rTMS to the rTPJ affects imitative but not spatial compatibility, this would suggest a more domain-specific mechanism.

Materials and Methods

Participants and Design
Sixteen healthy participants (5 males, 2 left-handed; mean age 26.2 years, standard deviation [SD] = 8.8) were recruited as they had previously acquired a structural T_1-weighted MRI scan and had no contraindications to TMS. Three further participants were excluded prior to data analysis as they made response errors on >15% of trials, but all received a small honorarium for taking part. Before the study, participants gave their written informed consent. The experimental procedures were approved by the local ethics committee and were carried out in accordance with the principles of the revised Helsinki Declaration (World Medical Associations General Assembly 2008).

A within-subjects design was employed, with each participant undergoing stimulation to both the rTPJ and MO control site. Both the site order (rTPJ or MO first) and mapping of cue color to index or middle finger responses were counterbalanced across participants.

Stimuli
All stimuli (Fig. 1*A*) were produced using Adobe Photoshop CS2 and presented in color on a black background (on a 19-in. LCD screen) via E-Prime2 (Psychology Software Tools, Sharpsburg, PA, USA). Task-

relevant stimuli (colored cues) consisted of squares (occupying 0.2° visual angle) colored orange or purple. A further white square of the same dimensions was used as a fixation point. Task-irrelevant stimuli were images of a female left or right hand subtending a visual angle of 6.5° horizontally and either 8.6° (static hand and pixelated control hand), 9.4° (index finger lift), or 9.2° (middle finger lift) vertically. Index and middle finger movements subtended an angle of 0.7° and 0.6°, respectively. Left-hand stimuli were a direct mirror along the vertical axis of right-hand stimuli. The immediate presentation of the movement stimulus (index or middle finger lift) after the static hand stimulus produced apparent motion of the finger; shown to be a robust method to elicit compatibility effects (Press et al. 2005). Both left- and right-hand stimuli were utilized to allow the manipulation of the spatial location of the observed finger movement, independent of its finger identity. The fixation point and task-relevant cues were presented equidistant from the index and middle fingertips of the static hand.

Procedure

Participants were seated approximately 100 cm from the screen, with their right arm (in the equivalent orientation to the hand stimuli) supported by a platform in front of them. All responses were made with the right hand via a computer keyboard. The experimental protocol consisted of a behavioral practice without TMS (12 trials), where participants were required to achieve 80% accuracy in order to move on to the main task. The main task then comprised 3 blocks of 36 trials for each stimulation site. Each block lasted approximately 4 min and each stimulation site was preceded by 10 practice trials with TMS. On these 10 trials, to ensure the participants were capable of performing the task during stimulation, they were required to achieve a mean RT equal to or faster than that achieved in their behavioral practice.

Each trial (Fig. 1B) began with the instruction "Please now replace your fingers on the keys." Once both "N" and "M" keys were pressed, the static hand and fixation square were presented for 1 of the 3 stimulus onset asynchronies (SOAs; 1600, 2000, or 2400 ms). These were subsequently replaced by the task-irrelevant stimulus along with an orange or purple square, presented for 480 ms. For half of the participants, an orange square indicated they should lift their index finger and a purple square indicated they should lift their middle finger from the "N" and "M" keys, respectively. The opposite pairing was assigned to the remainder of participants. An emphasis was placed on being both fast and accurate. During baseline trials, the static hand was replaced by a pixelated left or right hand in order not to elicit spatial and imitative compatibility effects, but matching the transient and alerting visual change in the standard trials (Wiggett et al. 2013). rTMS (6 pulses at 10 Hz) was delivered simultaneously with the onset of the cue and movement/pixelated hand and was triggered via the parallel port of the stimulus presentation computer.

Task-irrelevant movement stimuli were manipulated in a 2 × 2 (imitative compatibility: compatible, incompatible × spatial compatibility: compatible, incompatible) design (Fig. 1A), resulting in 4 standard trial types. The left- and right-hand baseline stimuli comprised a further 2 trial types. A fully factorial combination of the 6 trial types, SOA and task-relevant cue color, resulted in a total of 36 possible trials, which were presented in a randomized order to make up one full block. Three blocks were presented per stimulation site, thus each of the 6 trial types was presented 18 times per site.

TMS Navigation and Protocol

Prior to the experiment, structural MRI scans were manually registered to the standard MNI-152 template in the Brainsight2 neuronavigation system (Rogue Research, Montreal, Canada) and stimulation targets set using predefined MNI coordinates (rTPJ = 54, −47, 26; MO = 0, −95, 26). rTPJ coordinates are the average of the peak coordinates found by Brass et al. (2005, 2009) and Spengler et al. (2009) when investigating the control of imitation. Appropriate trajectories of stimulation were set for each individual, and landmarks were set on the surface reconstruction of the participant's head.

On arrival, each participant's resting motor threshold (rMT) was identified, defined as the lowest intensity of stimulation required to elicit motor evoked potentials (MEPs) of at least 50 μv in the first dorsal interosseous muscle in the right hand, on 3 of 5 trials. MEPs were recorded using surface skin electrodes and the Brain Vision software (Brain Products, Gilching, Germany).

The participant's head was then registered in the neuronavigation system using an infrared camera and participant tracker. During the main task, rTMS (6 pulses at 10 Hz per trial) was delivered using a figure-of-eight coil and a Magstim Rapid2 stimulator (The Magstim Company, Whitland, UK) at 110% of each participant's rMT. The location of the coil with respect to the target site was monitored online, allowing precise coil location to be maintained throughout the experiment. The TMS coil was replaced and re-calibrated between stimulation conditions, or if the stimulator indicated overheating of the coil.

Results

RTs and errors for finger lifts in each trial were recorded. Trials where RT deviated significantly (±2.5 SD) from the participant's mean RT, or if rTMS trains were not delivered (in instances where the coil overheated; 1.5% of trials), were discarded. Trials where inaccurate finger lifts were performed were also discarded from the RT analysis. The Mean RT and number of errors were calculated for each of the 6 trial types for both TMS sites. RTs for the standard trial types were subsequently transformed into compatibility effects (incompatible RTs−compatible RTs) for display purposes. As each trial within the experiment is either imitatively compatible or incompatible as well as either spatially compatible or incompatible (see Fig. 1A), all analyses run and presented take into account both imitative and spatial compatibility.

Response Time Data

RTs during both spatially and imitatively compatible trials, as predicted, were faster than those during the respective incompatible trials (Table 1). Baseline trials elicited broadly similar RTs regardless of stimulation site and whether a left- or right-hand stimulus was presented.

A 3-way, repeated-measures analysis of variance (ANOVA) was performed on the RT data from the standard trials. The within-subjects factors were the site of stimulation (rTPJ and MO), spatial compatibility (compatible and incompatible), and imitative compatibility (compatible and incompatible). There was a significant main effect of spatial compatibility, whereby responses were faster on trials where task-irrelevant stimuli were spatially compatible with the required finger lift (mean ± standard error of the mean [SEM]; 437 ± 14 ms) compared with incompatible (500 ± 15 ms), $F_{1,15} = 65.53$, $P < 0.001$, $\eta^2 = 0.81$. There was also a significant main effect of imitative compatibility, whereby responses were faster on trials where task-irrelevant

Table 1

Mean ± SEM RT (ms) and percentage errors for each trial type during rTPJ and MO stimulation conditions

Trial type	rTPJ		MO	
	RT	Percent error	RT	Percent error
SCIC	425.9 ± 12.8	2.5 ± 1.0	431.2 ± 14.7	2.0 ± 1.3
SCII	447.2 ± 11.5	2.7 ± 0.8	444.5 ± 15.9	3.2 ± 0.9
SIIC	488.7 ± 12.9	10.1 ± 1.8	500.8 ± 15.7	8.9 ± 2.3
SIII	506.6 ± 15.4	13.8 ± 2.6	502.1 ± 16.1	15.7 ± 3.6
Left baseline	469.9 ± 11.7	4.4 ± 1.4	467.8 ± 14.0	3.6 ± 2.0
Right baseline	469.9 ± 12.1	5.1 ± 1.2	474.1 ± 14.4	3.6 ± 1.3

SCIC: spatially compatible, imitatively compatible; SCII: spatially compatible, imitatively incompatible; SIIC: spatially incompatible, imitatively compatible; SIII: spatially incompatible, imitatively incompatible.
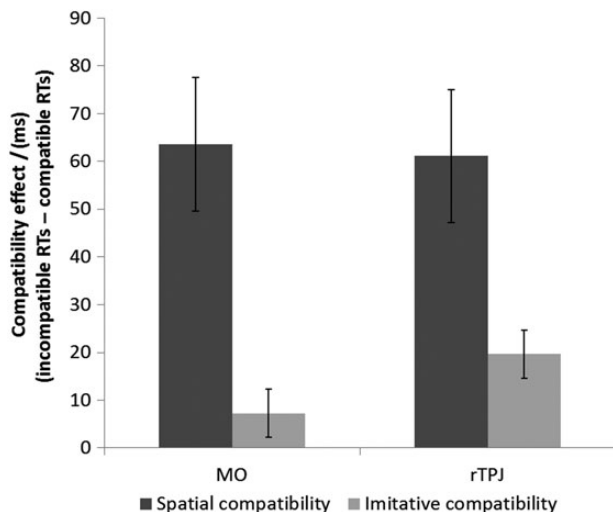
Figure 2. Spatial and imitative compatibility effects (incompatible RTs−compatible RTs) for both rTPJ and MO stimulation conditions. Error bars represent the SEM.

stimuli were imitatively compatible with the required finger lift (462 ± 14 ms) compared with incompatible (470 ± 15 ms), $F_{1,15} = 11.44$, $P = 0.004$, $\eta^2 = 0.43$.

Crucially, there was a significant interaction of site by imitative compatibility; $F_{1,15} = 5.10$, $P = 0.039$, $\eta^2 = 0.25$ and no significant interaction of site by spatial compatibility; $F_{1,15} < 1$, $P = 0.647$, $\eta^2 = 0.01$. No other main effects or interactions reached significance (all $P > 0.05$). Figure 2 shows the spatial compatibility and imitative compatibility effects for both rTPJ and MO stimulation sites, indicating a similar spatial compatibility effect across both stimulation sites, but a larger imitative compatibility effect during stimulation to the rTPJ than the control MO site. Therefore, rTMS to the rTPJ impaired participants' ability to control the tendency to imitate, but not their ability to control spatial response tendencies.

To ensure that the above results could not be due to whether a task-irrelevant left or right hand was presented, a 2-way, repeated-measures ANOVA (site × hand) was carried out on the RT data for the baseline trials. The within-subject factors were the site of stimulation and the hand presented (left or right). This revealed no significant main effects or interactions (all $P > 0.05$) and thus confirmed no difference in RTs across the 2 stimulation sites or the left–right-hand manipulation of task-irrelevant stimuli.

Error Data

Participants made more errors during compatible than incompatible trials (Table 1). A 3-way, repeated-measures ANOVA (site × spatial compatibility × imitative compatibility) on response errors confirmed the presence of a spatial compatibility effect; $F_{1,15} = 24.28$, $P < 0.001$, $\eta^2 = 0.62$, and an imitative compatibility effect that was close to significance; $F_{1,15} = 4.01$, $P = 0.064$, $\eta^2 = 0.21$. No significant interaction was found between either site and spatial compatibility; $F_{1,15} < 1$, $P = 0.786$ or site and imitative compatibility; $F_{1,15} < 1$, $P = 0.400$, unlike that observed in the RT data. No other main effects or interactions were observed (all $P > 0.05$) and a 2-way ANOVA (site × hand) on error rates for baseline trials revealed no significant main effects or interactions. These analyses, as well as the ceiling effects apparent in participants' response

accuracy whereby few errors were made (<7% overall error rate), meant error data were not pursued in further analyses. However, they do confirm that the compatibility effects found in the RT data were not a result of a speed/accuracy trade-off.

Discussion

This study demonstrated an increased imitative compatibility, but not spatial compatibility, effect during rTPJ stimulation. Relative to control site stimulation, disruptive rTMS over rTPJ coordinates previously implicated in the control of imitation led to a decrease in its function and thus, in the ability to control the tendency to imitate. The ability to control the tendency to respond in a spatially compatible location, however, was not affected by rTPJ stimulation. Thus, these data suggest that the rTPJ's role in switching between self and other representations may be domain specific. They also suggest that previous effects of rTMS and tDCS over the rTPJ on social cognitive tasks may indeed have resulted from interference with (Costa et al. 2008; Young, Camprodon, et al. 2010) and enhancement of (Santiesteban et al. 2012) the ability to control, or switch between, self and other representations, rather than a more domain-general process.

Although the rTPJ has been argued to be fundamental for both social and nonsocial tasks, the present data indicate that its involvement may be dissociated between the two. This provides evidence against previous claims that the rTPJ is not selective for social cognition (Mitchell 2008) and, therefore, adds to the ongoing theoretical discussions and increasing interest in the functioning of the "social brain" (Blakemore et al. 2004; Insel and Fernald 2004; Adolphs 2009; Blakemore 2012; Dunbar 2012).

If this area within the rTPJ does indeed show domain specificity for social cognition, it might be disputed whether the accuracy with which the navigation system can track the TMS coil is sufficient to enable the stimulation of identical regions for each participant and thus, to stimulate coordinates that are distinct from those argued to be involved in nonsocial functions. However, since in the present study, rTMS to these specific coordinates (previously shown to respond during the control of imitation) modulated only the imitative compatibility effect, it is unlikely that spatial resolution is a major limitation of the present study. It should be noted that, under the alternative account, whereby the involvement of the rTPJ in social cognition is due to domain-general processes, we should have found modulation of the (domain-general) tendency to respond in spatially compatible locations, as well as of the (domain-specific) tendency to respond with imitatively compatible actions, even when stimulating over coordinates optimized for social cognition.

It appears from the present data that the region of the rTPJ targeted in the current study may be specifically social in function. Nevertheless, as the nonsocial aspect of the task was not designed as a measure of attention, it does not necessarily follow that this region of the rTPJ is discrete from that critical to attentional reorienting (Scholz et al. 2009); but these data are supportive of that possibility.

So far, we have considered that imitative and spatial compatibility effects can be distinguished by the dimension of domain specificity (social vs. nonsocial). However, one possible alternative explanation of these results that should be considered is

whether the 2 types of compatibility effect can be distinguished on any other dimension. A possible dimension of interest is the selectivity of the mappings between stimuli and responses, and thus of the mappings between representations of the other and self.

At the imitative level, the representation of the other's action can be mapped onto one's own representation of that action at a high level of selectivity. For example, the sight of an index finger lifting will activate motor representations specific to index finger lifting in the observer. At the spatial level, however, the sight of a movement on the left side of space will activate far less selective motor representations for any response on the left side of space. Perhaps, therefore, the rTPJ's involvement in switching between self and other representations is most prominent when more selective switching is required to inhibit one representation and to excite the other. In the present study, this would be at the imitative level, which could explain the effect of rTPJ stimulation on imitative, but not spatial, compatibility. Relatedly, patients with extinction—an attentional deficit commonly attributed to TPJ damage (de Haan et al. 2012) —demonstrate worse performance when a more selective attentional focus is required (Baylis et al. 1993; Vuilleumier and Rafal 2000). Therefore, an alternative explanation for the present results is that the TPJ may be involved in controlling competing representations (regardless of modality) when there is a high degree of overlap between these representations, and thus, greater selectivity is required to inhibit one representation and to excite another.

If the above suggestion is correct, it should be possible to find examples of switching between self and other representations that are not affected by TMS to rTPJ. One promising avenue for future research is to investigate effector compatibility. This occurs when participants are faster to perform an action with the same effector as that which they observe, regardless of whether the observed effector is performing the same action or not (Leighton and Heyes 2010; Cook and Bird 2011). The sight of an effector such as a hand will activate motor representations for many hand actions, and thus, the motor representation(s) activated by the sight of the effector will be less specific than that activated by the sight of a finger movement. The present experiment was not designed to test whether effector compatibility is modulated by rTPJ stimulation, but the fact that the baseline trials showed no interaction between observed hand (i.e., effector) and stimulation site is certainly supportive. Another relevant finding is that prosocial priming affects imitative, but not effector, compatibility (Cook and Bird 2011), indicating that the 2 types of compatibility effect can be modulated in different ways.

A further consideration for future research is investigation in to the possible lateralization of the functions of the TPJ. There is currently some causal evidence for the involvement of the left TPJ in social cognition (Samson et al. 2004; Spengler et al. 2010); however, it is not yet clear whether left and right TPJ perform the same or different social cognitive processes.

In conclusion, the present study provides causal evidence for the role of the rTPJ in social cognition, in particular in the control of imitation. It further suggests that the type of processing performed by this part of the rTPJ is not entirely domain general. However, questions remain as to whether this area is specialized for social cognition per se, or instead whether its involvement in the control of imitation can be explained by any other dimension on which imitative and spatial compatibility effects can be distinguished.

Notes

Conflict of Interest: None declared.

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