Neuroscience and Biobehavioral Reviews 42 (2014) 298–302

Contents lists available at ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

Task-relevance dependent gradients in medial prefrontal and temporoparietal cortices suggest solutions to paradoxes concerning self/other control

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ARTICLE INFO

Article history:
Received 17 October 2013
Received in revised form 4 February 2014
Accepted 13 February 2014

Keywords:
Self/other control
Cognitive control
Temporoparietal junction
Medial prefrontal cortex
Imitation
Perspective taking

ABSTRACT

Contrary to the prevailing view, Nicolle and colleagues (2012) recently demonstrated that dorsal and ventral regions of the medial prefrontal cortex (mPFC) and temporoparietal cortex (TPC) do not distinguish between action values relating to the self and to another individual; rather, these regions differentiate whether an action is currently relevant or irrelevant to the task at hand. This finding suggests solutions to paradoxes in social cognition. The first paradox concerns self/other control: With some experimental tasks TPC activity is associated with the promotion of self over other representations; in different tasks the association is with other over self (Santiesteban et al., 2012a). The second paradox concerns the control of imitation: MPFC has been associated with both the facilitation and inhibition of imitation. Considering task-relevance (i.e. whether the participant's task is to respond according to their own action values or to respond as if they were another individual) suggests possible solutions to these paradoxes.

Contents

1. Task-relevance dependent gradients in mPFC and TPC?

Activity in the medial prefrontal cortex (mPFC) has long been associated with representing the self and other individuals (for meta-analyses see Denny et al., 2012; Gilbert et al., 2006; Van der Meer et al., 2010; Mitchell, 2009a; Northoff et al., 2006; Van Overwalle, 2009; Qin and Northoff, 2011; Wagner et al., 2012). The prevailing view of the mPFC is that ventral areas are associated with representations of the self (Kelley et al., 2002; Van der Meer et al., 2010; Denny et al., 2012), including the subjective value of one's own actions (Behrens et al., 2008; Boorman et al., 2009; Knutson et al., 2005; Plassmann et al., 2007), whereas dorsal regions have been implicated in representing others (Behrens et al., 2008; Frith and Frith, 1999, 2006; Hampton et al., 2008; Saxe, 2006). It has therefore been suggested that a spatial gradient exists within mPFC such that ventral areas are associated with self-processing and progressively more dorsal activation is increasingly associated with other-related judgments (Denny et al., 2012).

A recent paper by Nicolle and colleagues (2012) challenges this view, arguing that the gradient within mPFC is organised according to task-relevance, and does not depend on whether the self, or another, is represented. On each trial of their task, participants chose between receiving a small monetary reward following a short delay or a larger reward following a longer delay. In the 'Self condition' participants made the choice for themselves (believing that at the end of the experiment one of their choices would be ran-

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http://dx.doi.org/10.1016/j.neubiorev.2014.02.007
0149-7634/

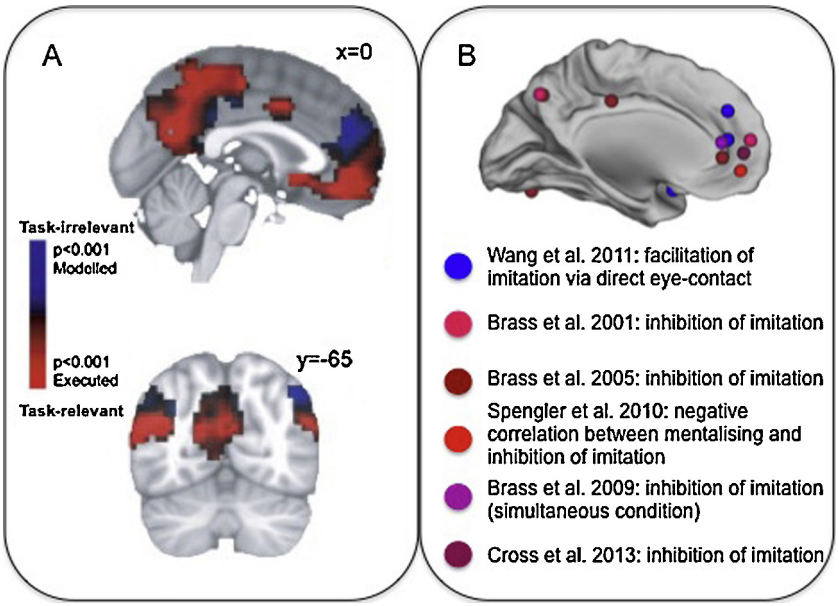

Fig. 1. (A) Activation map from Nicolle et al. (2012). More ventral regions (red) of mPFC and TPC were associated with task-relevant representations: that is activity correlated with self preferences when judgements were made for the self, but with other preferences when judgements were made for the other. Activity in more dorsal regions (blue) correlated with the preferences relating to the task-irrelevant recipient (i.e. the partner's preferences in the Self condition and their own preferences in the Other condition). Figure reproduced with permission from Neuron. (**B**) Peak voxels for fMRI studies relating to the facilitation of imitation (blue) and the inhibition of imitation (red). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

domly selected for them to take home). In the 'Other condition' participants chose on behalf of a partner whose preferences they had learned earlier. Pre-screening ensured that participants were paired with partners who had differing value preferences (i.e. a participant with a preference for larger rewards later in time would be paired with an individual with a preference for smaller, earlier rewards). Based on previous studies Nicolle and colleagues reasoned that, on each trial, the participant would, (a) note whether they should make the choice for themselves or on behalf of their partner, (b) temporally discount each of the choices according to their own preference when in the Self condition or their partner's preference when in the Other condition, and (c) choose the option with the highest value. For example, in a trial from the Other condition the participant may see "Choice A: £10 today", and "Choice B: £30 in 5 months"; calculate that their partner's subjective valuation of these options would be £10 for Choice A and £5 for Choice B; and subsequently select option A on behalf of their partner. Nicolle and colleagues further hypothesised that participants also conduct this same procedure for the recipient (self or other) who is not the subject of the current trial. Thus, in our example the participant would also calculate which option they would have chosen if they had been given the opportunity (e.g. "Choice A is worth £10 to me and Choice B is worth £25, so I would have chosen B").

If the location of activity in mPFC follows the commonly-accepted self-other organisation, self trials should be associated with ventral activation and other trials with dorsal activation. If activation is determined by task-relevance, then activity in mPFC should be independent of whether self or other preference is modelled, and instead be determined by which recipient was task-relevant on any particular trial. Results overwhelming supported the task-relevance model (Fig. 1A); activity in ventral regions correlated with self preferences when judgements were made for the self, but with other preferences when judgements were made for the other. Activity in dorsal regions correlated with the preferences that were calculated for the recipient for whom participants were not making the choice (i.e. the partner's preferences in the Self condition and their own preferences in the Other condition). Thus Nicolle and colleagues found novel evidence for task-relevance-dependent organisation in mPFC, with activity in ventral regions representing preferences relevant to the current task and dorsal regions representing task-irrelevant preferences which were nonetheless modelled. Interestingly, and of relevance to the rest of this article, the temporoparietal cortex (TPC) showed the same pattern of activity as the mPFC. The ventral–dorsal distribution of activity was determined by task-relevance, rather than whether the preferences of the self, or of the other, were represented.

2. MPFC and TPC involvement in the control of automatic imitation and self/other representations

The findings reported by Nicolle and colleagues have important implications for an area of growing neuroscientific interest: the control of automatic imitation. Automatic imitation – a tendency to copy observed actions even when they are not relevant to the task at hand (Heyes, 2011) – has received increasing interest since the discovery of mirror neurons (Di Pellegrino et al., 1992), which are thought to be integral to this behaviour (Catmur et al., 2009). Automatic imitation (also known as mimicry) is intricately linked with social interaction. Being imitated increases altruistic behaviour (Van Baaren et al., 2004) and positive social attitudes such as rapport (Chartrand and Bargh, 1999) and trust (Bailenson and Yee, 2005). In turn, positive social attitudes promote imitation (Cook and Bird, 2011, 2012; Hogeveen and Obhi, 2012; Lakin and Chartrand, 2003; Leighton et al., 2010). Thus, imitation is bi-directionally associated with social attitude and the expression of imitation is modulated depending on the social context.

A growing body of studies implicates the mPFC and TPC in the facilitation and inhibition of automatic imitation. Following from observations that individuals with mPFC lesions exhibit heightened levels of involuntary imitation (Brass et al., 2003; Lhermitte, 1986; Spengler et al., 2010a), Brass, Spengler and colleagues used fMRI to show that activity in the mPFC and a ventral region of the TPC called the temporoparietal junction (TPJ) is associated with the inhibition of imitative responses (Brass et al., 2001, 2005, 2009; Spengler et al., 2009a, 2009b, 2010b). Recent work by Cross and

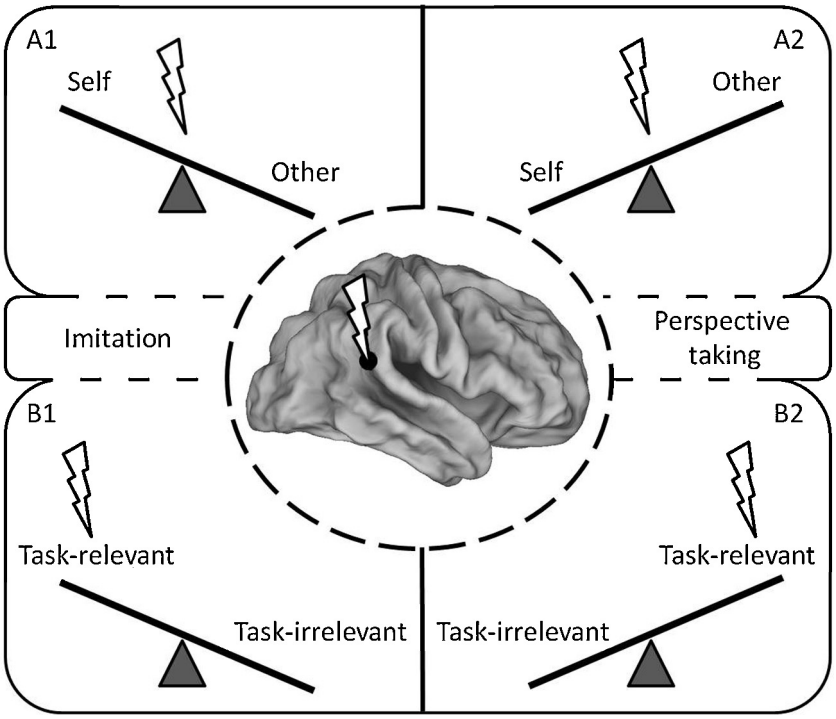

Fig. 2. Cartoon of the hypothetical effects of tDCS on self/other control. (A) Santiesteban and colleagues showed that applying tDCS (lightning bolt cartoon) to enhance activity in TPJ promoted self over other representations in an imitation task (A1) and promoted other over self representations in a perspective taking task (A2). Such results may be due to facilitatory effects of tDCS on switching between self and other representations (as illustrated by the position of the lightning bolt). (B) In the imitation task (B1) the task-relevant action always pertained to the self representation, whereas in the perspective taking task (B2) the task-relevant action always pertained to the representation of the other. Thus an alternative hypothesis for the obtained results is that tDCS facilitated task-relevant representations.

colleagues (2013) provides further support for a key role for mPFC in the inhibition of imitation. Hamilton and colleagues (Wang et al., 2011a, 2011b) used a combination of fMRI connectivity data and behavioural analyses to demonstrate that mPFC plays an important role in the facilitation of imitation by direct eye contact, possibly via connections between mPFC and visual regions associated with action processing (i.e. the superior temporal sulcus). Thus, in some experimental situations mPFC and TPC are implicated in the facilitation of imitation, whereas in others they are implicated in its inhibition.

One account of this apparent paradox is that both imitation facilitation and inhibition require switching between representations of the self and of the other. More specifically, imitation facilitation involves the up-regulation of representations of the other and down-regulation of self representations, whereas the converse is required for the inhibition of imitation. Thus it has been argued that mPFC and TPC play a key role in self/other switching. Preliminary evidence showed that autistic individuals who had difficulties distinguishing their own mental state from the mental state of another agent also showed poor inhibition of imitation (Spengler et al., 2010c). Furthermore, mPFC activity during a mentalising task – which was hypothesised to involve switching between self and other representations – was related to the ability to inhibit imitation, whereby mPFC was less active in participants who had greater problems inhibiting imitation (Fig. 1B). More direct evidence for this proposal was obtained by Santiesteban and colleagues (2012b), who found that imitation inhibition training, which is hypothesised to improve self/other switching, enhanced the ability to take the visual perspective of another agent. Recent evidence has shown that application of direct current to excite the TPC results in a reduced tendency to imitate and an enhanced ability to take another person's visual perspective (Santiesteban et al., 2012a).

This most recent finding deserves further attention. Santiesteban and colleagues (2012a) used transcranial direct current stimulation (tDCS) and a number of behavioural tasks to investigate the role of the TPJ (ventral TPC) in self/other switching. In one task participants were asked to perform a finger movement whilst observing either the same or a different finger movement. Experimental trials required participants to inhibit imitation by enhancing self-representations of action and inhibiting representation of the other's action. Three groups were tested; an anodal group, for which the cortical excitability of TPJ was enhanced; a cathodal group, for which the excitability of TPJ was decreased; and a sham (control) group. Compared to the sham and cathodal groups, the anodal group exhibited reduced imitation. Thus enhancing TPJ excitability promoted self representations relative to other representations (Fig. 2A1).

In another task employed by Santiesteban and colleagues, participants were required to adopt the perspective of a "director" who gave them instructions to move one object within an array of objects. Participants viewed the array from the front whereas directors were situated behind the array with an occluded view of some objects, thus there was conflict between the director's and the participant's perspective. Optimal performance demanded enhancement of the other and inhibition of the self perspective. Intriguingly, anodal stimulation to TPJ also improved performance on this task; the anodal group was better able to take the director's perspective than the cathodal and the sham groups. Thus in this situation enhancing TPJ excitability promoted other representations relative to self representations (Fig. 2A2). In agreement with the results of Santiesteban and colleagues, Costa et al. (2008) used transcranial magnetic stimulation to disrupt (rather than facilitate) activity in the same part of ventral TPC and found that the ability to infer the mental states of others was impaired in a task in which participants were specifically instructed to infer the other's belief. Similarly, Sowden and Catmur (2013) recently demonstrated that disrupting TPJ activity using repetitive TMS led to a decreased ability to control the tendency to imitate.

In sum, existing studies suggest that mPFC and TPC play important roles in the modulation of imitation – facilitating imitation in some contexts and inhibiting imitation in others. The authors of these studies conclude that mPFC and TPC play key roles in switching between representations of the self and of the other, and that the ability to switch between representations impacts on one's propensity to imitate.

3. Implications of task-relevance gradients for the control of automatic imitation and self/other representations

Nicolle and colleagues' agent-independent task-relevance gradients in the mPFC and TPC offer an appealing explanation for the paradoxical task-specific effects of exciting TPJ (Santiesteban et al., 2012a). Models of the effects of brain stimulation (Herwig et al., 2003) suggest that Santiesteban and colleagues excited a ventral region of the TPC corresponding to Talairach coordinates 63, −45, 24 (*x*, *y*, *z*; Koessler et al., 2009; Fig. 2(central panel)). Under Nicolle and colleagues' framework one would expect this ventral stimulation to selectively enhance representations of task-relevant actions, but not to affect any task-irrelevant actions which may be modelled, but not executed. This should occur irrespective of whether the task-relevant action relates to the self or the other. In the imitation task employed by Santiesteban and colleagues, the task-relevant action always pertained to the self and the task-irrelevant action to the other (participants were instructed to ignore the other hand when it moved). Thus enhancing TPJ excitability may have enhanced self (relevant) over other (irrelevant) representations (Fig. 2B1). In the perspective taking task the task-relevant action always pertained to the other whereas the task-irrelevant action pertained to the self (participants were instructed to respond according to the director's perspective). Therefore enhancing TPJ excitability may have enhanced other (relevant) over self (irrelevant) representations (Fig. 2B2). Thus, considering whether the self or the other is the task-relevant dimension suggests an alternative hypothesis: Exciting TPJ promotes representations of currently instructed courses of action (such as taking the director's perspective) over those that are modelled but task-irrelevant (e.g. one's own perspective) irrespective of whether they are related to the self or to another individual. Similar task-set dependent findings would be hypothesised to result from tDCS application to mPFC.

The hypothesis that enhancing TPJ excitability facilitates processing relating to the instructed task feeds into an existing debate over the role of the TPJ in domain-general attentional processes (Mitchell, 2008) versus specific socio-cognitive processes such as representing others' mental states (Saxe and Kanwisher, 2003; Saxe and Powell, 2006; Saxe and Wexler, 2005). The view that the ventral part of TPC, which encompasses the TPJ, is concerned with task-relevant information but not whether that information concerns the self or other is consistent with the argument that the TPJ plays a domain-general role in maintaining attention on the instructed task (Mitchell, 2008). Further support for this comes from a number of studies which have demonstrated an association between TPJ activity and reorienting to task relevant stimuli following distraction (Astafiev et al., 2003, 2006; Corbetta and Shulman, 2002; Corbetta et al., 1993, 2000, 2005; Kincade et al., 2005; Serences et al., 2005).

The task-relevancy framework also suggests a novel empirical hypothesis for the imitation control literature. Fig. 1B shows that peak voxels associated with the *inhibition* of imitation fall within regions which Nicolle and colleagues identified as representing task-relevant actions. Peak voxels associated with the *facilitation* of imitation fall within regions identified as representing task-irrelevant actions. Given the paucity of relevant fMRI studies (in particular relating to the facilitation of imitation) caution is required when drawing conclusions. However, the combination of these two literatures does produce a testable hypothesis: imitation facilitation may be underpinned by an enhancement of the representation of task-irrelevant relative to task-relevant representations, whereas imitation inhibition may be underpinned by enhanced representations of task-relevant relative to task-irrelevant representations.

Thus far it has been argued that the task-relevance framework developed by Nicolle and colleagues can usefully be applied to studies of perspective-taking and control of imitation via the common requirement for task-relevant control of representations of the self and the other. At present, the extent to which the framework can be applied to other socio-cognitive tasks that also require self/other representation is an open question. For certain tasks the relevance of the value-based preference task used by Nicole and colleagues is clear. For example, when participants are asked to make personality judgements about the self or a similar individual (e.g. Mitchell et al., 2006), they must make judgements about the relative value of certain actions (e.g. going to a party versus reading a book alone) in order to make a personality trait judgement (e.g. extraversion/introversion). Thus both types of task depend on value estimations. However, a potentially important difference between the paradigm employed by Nicolle and colleagues and those often employed in studies of self/other representation concerns the ambiguity of the representation of the other. Nicolle and colleagues trained participants such that, from the on-screen stimuli, partner's preferences could be calculated quickly, and with minimal ambiguity, using the same reasoning one would use to calculate one's own preferences. Many existing paradigms require the participant to reflect upon unfamiliar others or inanimate shapes; the answers are ambiguous, often there is no single correct answer. Future studies are required for a better understanding of the cortical organisation of ambiguous task-relevant and – irrelevant self and other representations. Indeed an existing theory of mPFC organisation posits that vmPFC may be primarily associated with stimulus-driven processes such as computing the value of stimuli relevant to a current judgement, whereas dmPFC may support more reflective processes such as those employed in selecting higher level social and affective meanings (Olsson and Ochsner, 2008). In line with this it has been argued that the dmPFC is more strongly associated with social inferences based on minimal information relative to unambiguous social inferences which are linked to vmPFC activity (Jenkins and Mitchell, 2010; Mitchell, 2009b).

4. Summary

In conclusion, this article argues that the task-relevance framework developed by Nicolle and colleagues may provide solutions to paradoxes concerning perspective-taking and the control of imitation via the common requirement for task-relevant control of representations of the self and other. Preliminary evidence that the control of imitation is atypical in adults with autism spectrum conditions (Cook and Bird, 2012) and that imitation control and perspective taking continue to develop throughout adolescence (Cook and Bird, 2011; Dumontheil et al., 2010, 2012) suggests important implications of such research for developmental and psychiatric populations. The extension of Nicolle and colleagues' findings to the imitation and self/other control literatures is speculative at present and requires validation; however, the merging of these research fields promises to be an interesting avenue of investigation.

Acknowledgments

JC is supported by an AXA postdoctoral fellowship. JC would like to thank S Fallows, R Brewer, G Bird, C Press and R Cook for comments on earlier drafts.

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