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The self and social cognition: the role of cortical midline structures and mirror neurons

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Recent evidence suggests that there are at least two large-scale neural networks that represent the self and others. Whereas frontoparietal mirror-neuron areas provide the basis for bridging the gap between the physical self and others through motor-simulation mechanisms, cortical midline structures engage in processing information about the self and others in more abstract, evaluative terms. This framework provides a basis for reconciling findings from two separate but related lines of research: self-related processing and social cognition. The neural systems of midline structures and mirror neurons show that self and other are two sides of the same coin, whether their physical interactions or their most internal mental processes are examined.

Introduction

The search for the neural correlates of self-related cognition has developed at an almost feverish pitch. In their attempts to isolate specific brain regions or networks, researchers have identified several strong candidates for creating, supporting and maintaining the self. In parallel, researchers in the domain of social-cognitive neuroscience have described several brain regions that support various aspects of social interaction and representation of others [1–4]. A network composed of cortical midline structures (CMS), including the medial prefrontal cortex, the anterior cingulate cortex and the precuneus (Box 1), has been associated with self-processing [5] and social cognition [6]. Moreover, a right-lateralized frontoparietal network that overlaps with mirror-neuron areas (Box 2) seems to be involved with self-recognition [2] and social understanding [7]. An outstanding question concerns how to tease apart the relative contributions of the mirror-neuron system (MNS) and CMS in self- and other-representation across different domains.

Here, we propose a unifying model that accounts for extant data on self and social cognition as supported by the MNS and CMS. We review evidence that suggests that a right-lateralized MNS is involved in understanding the multimodal embodied self (e.g. its face and its voice), whereas CMS seem to represent a less bodily grounded self as shaped by its social relationships. Interactions between these two systems are likely to be crucial to social functioning and might be compromised in conditions such as autism, where self-awareness and social cognition are impaired [3].

The right frontoparietal network and self

History and neuropsychology of self-recognition

A growing body of research suggests that a network of right frontoparietal structures is vital for generating self-awareness. The importance of the right hemisphere in terms of supporting the self was suggested by early researchers who presented pictures of the self-face to patients following split-brain surgery. Whereas Sperry found that the right hemisphere could recognize the self-face, Preilowski discovered that the right hemisphere provided a greater physiological reaction to the own-face compared with other faces and compared with left-hemisphere responses to the own-face [8]. Much progress has been made in the past 30 years, including the emergence of imaging techniques such as fMRI and transcranial magnetic stimulation (TMS). These techniques helped to reveal the special role that the right hemisphere has in self-representation and also highlighted the need for more precise definitions and constructs. Both conceptual and methodological issues account for much of the earlier incongruent evidence with regards to laterality of self-recognition (discussed in Refs [2,8]).

Patient data provide further evidence of a right frontoparietal bias for self-face and self-body processing. Mirror-sign, a condition in which patients misidentify their own face while retaining the ability to identify other faces, occurs following right frontoparietal damage [9]. Damage and clinically applied anesthesia to the right hemisphere results in anosognosia (denial that a limb is paralyzed) and asomotognosia (misidentification of one's own limb). Stimulation of right parietal regions results in autoscopic

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Box 1. The default-mode network

It has been well documented that certain areas of the brain (namely, the dorsal and ventral medial prefrontal cortex, precuneus and posterior lateral cortices) are characterized by high baseline metabolic activity at rest. These regions are thought to comprise a 'default mode' of brain function, as they exhibit decreases in activity during a variety of goal-directed behaviors. Various neuroimaging techniques (e.g. PET and fMRI) have confirmed the presence of this underlying default-mode network [33]. When subjects are explicitly engaged in attention-demanding goal-directed cognitive tasks, activity in this network is attenuated. Functional-connectivity analyses suggest that this default-mode network is inversely correlated with task-specific prefrontal activations [34]. Although the exact function of the tonic activity in the default-mode network is unknown, this activity has been linked to mental processes that have been termed 'task-unrelated imagery and thought' (TUITs) [35]. Such thoughts often take the form of autobiographical reminiscences, self-referential thought or inner speech. However, in some cases, increased activity, compared to rest in the default-mode network, has been documented during tasks of a social nature [26,36]. This suggests that both self-directed and socially oriented thoughts are implemented in the default-mode network.

Box 2. The mirror-neuron system

Mirror neurons were initially discovered in the macaque ventral premotor cortex [37]. These cells discharge during goal-oriented hand actions, such as grasping, tearing and holding. They also discharge during ingestive and communicative mouth actions, such as sucking and lip-smacking. The discharge of these cells typically occurs throughout the whole action and is not associated with the contraction of specific muscles. In addition, mirror neurons can fire during actions that are performed with different body parts. For instance, they can fire during grasping actions that are performed with the left hand, the right hand and even the mouth. However, mirror neurons often discriminate between different types of grips. Typically, mirror neurons that discharge during precision grips (i.e. the grasping of a small object that is performed with the opposition of the thumb and the index finger) do not fire during whole-hand grasps of larger objects, and vice versa [38]. Mirror neurons also discharge in association with visual and auditory stimuli. A mirror neuron that is active during the execution of a particular action will respond to the sight of similar actions. For instance, if a mirror neuron discharges during the execution of precision grips, it will also fire when the monkey observes somebody else grasping a small object with a precision grip [37,38]. The auditory stimuli that trigger the firing of mirror neurons are sounds that are associated with the actions coded by these neurons in motor terms. For instance, if a mirror neuron fires while the monkey breaks a peanut and while the monkey observes somebody else breaking a peanut, it will also fire if the monkey hears the sound of breaking a peanut [39]. The visual and auditory responses of mirror neurons are specific to these kinds of stimuli. This pattern of neuronal firing suggests that these neurons code agent-independent actions in rather abstract terms.

Thus far, there is evidence for mirror neurons in two anatomically connected cortical areas in the macaque brain: area F5 in the ventral premotor cortex and area PF/PFG in the rostral part of the inferior parietal lobule [38]. The human mirror-neuron system – revealed by a variety of fMRI [40], magnetoencephalography (MEG) [41], transcranial magnetic stimulation (TMS) [42] and EEG [43] studies – is analogously composed by two cortical areas in the inferior frontal cortex and in the rostral part of the inferior parietal lobule. In humans, the mirror-neuron system is strongly associated with imitative behavior [44] and social cognition [4].

delusions in which one feels outside of one's own body, or the experience that certain body parts extend or shrink. Data collected using TMS confirm these findings. TMS delivered to the right inferior parietal cortex disrupts the recognition of self-faces whereas TMS delivered to the left inferior parietal has no such influence [10]. Additional support for a localized network that enables self-awareness is derived from patients who, following a brain insult, experience either a loss of self-identity or an alteration of personality [11].

Neuroimaging of self-recognition

The self-face is the most obvious embodied representation of the self. Thus, it has been most commonly used in the attempt to operationalize the term 'self' and to investigate the brain correlates of self-awareness. When participants are presented with their own face, right frontal and right parietal networks are typically activated when compared with viewing other familiar faces [2,12–14]. Several versions of this paradigm have been used, including presenting participants with 'morphed' (i.e. combined) versions of the self-face (Figure 1). These different forms of face presentation reveal a consistent activation of the right frontoparietal network during self-face recognition [2]. In a series of recent studies, it has been shown that both the self-face and the self-body activate the right frontoparietal network [14–16]. Such activation also seems to include the self-voice, indicating that right-hemisphere activation might not be limited to the visual domain [17]. Although not all studies indicate a clear right-hemispheric bias [18], the data collected thus far indicate that self-recognition is mostly supported by right frontoparietal regions.

Three recent fMRI studies [2,13,14] on self-face recognition have suggested that the right frontoparietal areas that are associated with self-recognition overlap with areas that contain mirror neurons (Box 2; Figure 2). It has been proposed that these neurons can provide a link between self and other, enabling intersubjectivity through an intentional attunement mechanism that enables the understanding of the actions and associated mental states of others through the unreflective, automatic simulation of the actions and associated mental states of the self [19]. During self-recognition, mirror-neuron areas in the perceiving subject would process the perceived self (i.e. one's own face) using a similar simulation mechanism. Here, the perceived self is mapped onto the perceiving subject's motor repertoire. This mapping mechanism can produce an even better fit than the mapping of others onto self, thus resulting in increased 'resonance', which is reflected by higher fMRI activity [2]. Thus, frontoparietal mirror-neuron areas of the human brain can effectively function as bridges between self and other, by co-opting a system for recognizing the actions of others to support self-representation functions.

The simulation processes that are supported by the human mirror-neuron system go a long way towards explaining action and intention understanding. However, evidence for involvement of the MNS in more abstract forms of simulation and mentalizing is lacking. Instead, CMS structures seem to be more involved in internal aspects of representing self and others, where simple motor coding is insufficient.

Cortical midline structures and self

A comprehensive review of the debate concerning the definition of the term 'self' is beyond the scope of this

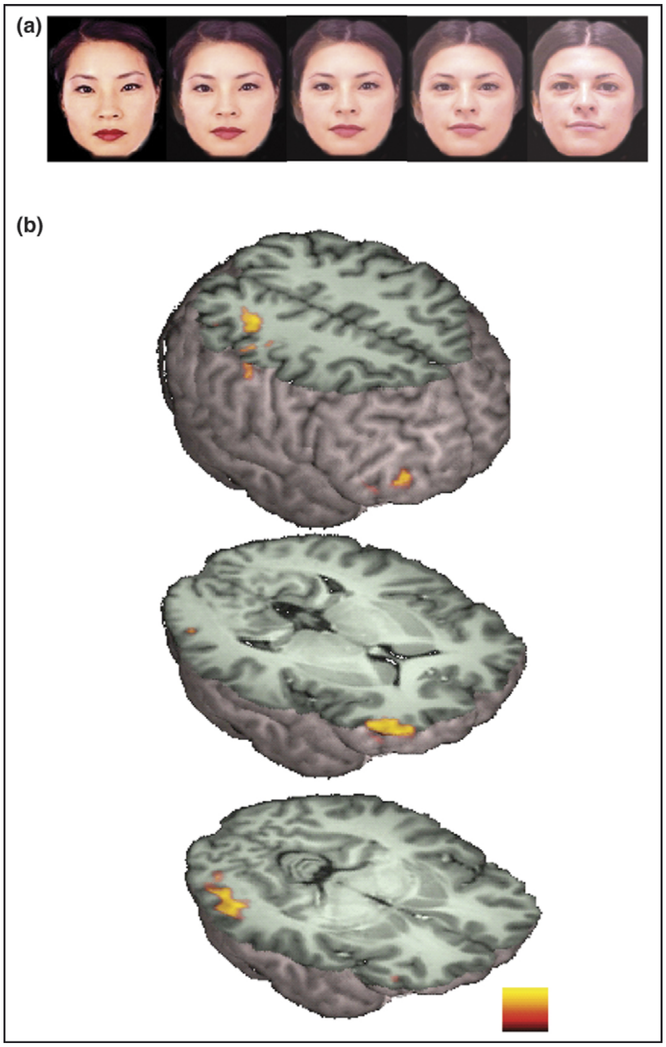

Figure 1. The neural basis of self-recognition. Humans are one of the only species capable of self-face recognition and, therefore, the self-face has been used as a measure of higher-order self-processing. **(a)** Typically, self-faces are contrasted with the faces of either familiar or unfamiliar faces. An adaptation of this method is to use 'morphs', in which faces are combined. Such use of morphs provides a more sensitive measure of self-recognition. **(b)** The presentation of these stimuli typically activates regions of the right frontoparietal network. Shown here are activation patterns from Uddin *et al.* [2] in which regions activated by fMRI were later disrupted using repetitive transcranial magnetic stimulation. (The actual morphs used in the study are not shown.)

discussion, but one common distinction in the literature is that between physical and mental aspects of the self [20]. While progress has been made towards understanding the neural basis of the physical self, parallel lines of research that have been inspired by social-psychological constructs have identified a network of brain regions that seem to support social and psychological aspects of the mental self. Interestingly, these networks seem to overlap with areas that comprise the 'default-mode network' (Box 1). The observation that cortical midline structures that are part of the default-mode network also tend to show increases in activity during tasks that require self-referential processing [21] has led some to suggest that this network might be a neural instantiation of the self [22]. Most studies that report such midline activations use tasks that are geared towards uncovering neural processes that are related to social or psychological aspects of the self, such as self-referential judgments [22], self-appraisal [23] and judgments of personality traits [24,25]. Perhaps not surprisingly, in addition to their purported role in various aspects of self-representation, cortical midline structures are also involved in the processing of social relationships [6,26] and recognizing personally familiar others [27]. Studies that show midline activations during understanding of social interactions between others [26] or ascribing social traits to others (impression formation) [1] typically require subjects to reference the mental state of others. Indeed, there is a large body of literature that implicates the medial prefrontal cortex in theory of mind or mental-state attribution [28]. Therefore, it seems that these midline structures might be involved more generally in representing both self and others in terms of their mental states or non-physical aspects. It is likely that one function of the so-called 'default network' is to act as a constant monitor of the self and its social relationships; thus, we see increases in activity in this network across a variety of paradigms where the social self is invoked, as well as when processing information about the mental states of others [29].

MNS and CMS: an integrated perspective on self and other

It has recently been proposed that internally oriented processes that focus on one's own or others' mental states rely on cortical midline structures, whereas externally focused processes based on one's own or others' visible features and actions rely on lateral frontoparietal networks [30]. We suggest here a similar distinction, which might further reconcile disparate findings with regard to the various proposed functions of cortical midline structures, while incorporating what is known about the role of the human mirror-neuron system in social cognition. Whereas there is mounting evidence that the right frontoparietal system is involved in representing the physical, embodied self (in addition to its role in understanding the actions of others), the cortical midline structures that comprise the default-mode network seem to be more

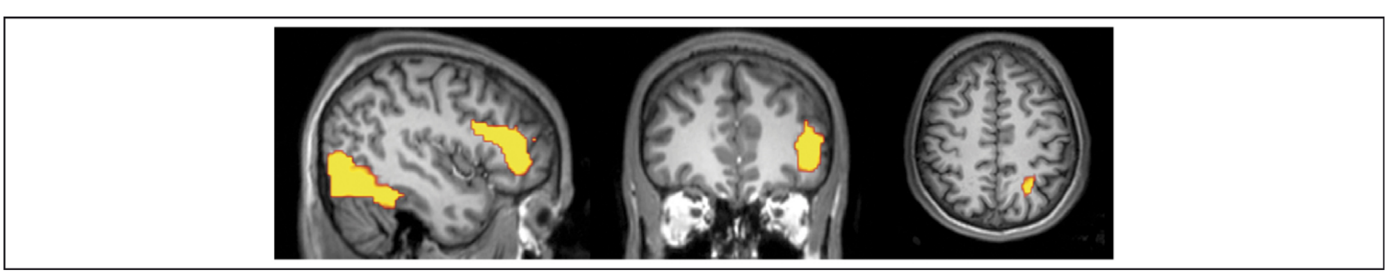

Figure 2. Overlap between areas involved in self-recognition and mirror-neuron areas. Self-recognition seems to engage mirror-neuron areas in the right hemisphere. Tasks of self-recognition [2,12] produce activations that significantly overlap with those from tasks that involve imitation and action observation [49]. Frontal and parietal areas of overlapping activity for the two tasks are shown.

involved in maintaining a self-representation in evaluative terms, which requires self-referential processing and understanding of others' mental states. We speculate that the CMS might support evaluative simulation in the same way that the MNS supports motor simulation. This distinction serves as a practical division of labor between two networks that are specialized for two related processes that are crucial to navigating the social world. The mirror-neuron system provides the essential physical other-to-self mapping that is necessary for comprehending physical actions of intentional agents, whereas cortical midline structures maintain and support processes that are related to understanding complex psychological aspects of others, such as attitudes, perhaps by simulation of one's own attitudes [29].

Because the MNS and CMS both seem to be involved in self–other representations, it seems only natural that they interact. The existence of direct connections between the precuneus (a major node of the CMS) and the inferior parietal lobule (the posterior component of the MNS) [24] suggests that this is one pathway by which such interactions might occur. Indeed, it has been suggested that, owing to its strong cortical and subcortical connections, the precuneus is likely to be involved in elaborating highly integrated and associative information, rather than directly processing external stimuli [31]. Additionally, there are direct connections between mesial frontal areas and the inferior frontal gyrus [32]. Thus, the anterior and posterior nodes of the CMS and MNS are in direct communication. Although the exact nature of the interactions between these two networks is unknown, it is likely that the direct connections between them facilitate integration of information that is necessary for maintaining self–other representations across multiple domains. One intermediate representational domain in which both neural systems might cooperate is the domain of imagination (Box 3).

Concluding remarks

Self- and other- representations are crucial to social functioning. Although most animals can distinguish, on some level, the self from others, such separation is more refined in the non-human primates that possess self-recognition, self-awareness and basic theory-of-mind skills. The right frontoparietal MNS and the CMS seem to support these abilities, albeit in different ways. Here, we propose that the MNS enables physical other-to-self mapping, whereas the CMS underscores mental state and evaluative simulation. Both processes are crucial to understanding other social beings. Although the distinctions are not fully understood, both neural systems contribute to the ability to move beyond simple motor imitation to more complex forms of social learning and understanding. By providing both the neural basis of the co-representation and the distinction of self and other, these two systems integrate with the brain as a whole to enable successful navigation of the social world. Priorities for future work include paradigms that are designed to understand precisely how and under what conditions these two networks interact. Studies of clinical populations in which social cognition is impaired, particularly autism, should help to illuminate how such network interactions might occur (Box 4).

Box 3. Imagining self and other

Imagination is an important mental function for social behavior. Rather than actually having to witness events that directly involve ourselves or others, we can mentally project these events and simulate outcomes.

In terms of self and other, imagining actions performed by the self or the other activates shared midline and frontoparietal structures [45]. This suggests that imagination is a common representational domain between CMS and MNS, as far as self–other relationships are concerned. Indeed, some of these regions seem concerned with a variety of imaginative processes that involve self and other, from feelings in socially relevant situations [46], to pain [47] and perspective taking [48].

Box 4. Questions for future research

- How do the cortical midline and mirror-neuron networks interact during typical social behaviors?
- To what extent can hypoactivity in these networks explain social-cognitive deficits in individuals who have childhood developmental disorders?
- How do the CMS and MNS structures interact to provide for a 'seamless' social experience?
- To what extent do these systems overlap in their functions in terms of social-cognitive processing?

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