

# Chapter 13

## The Emergent Self: How Distributed Neural Networks Support Self-Representation

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The self has been broadly conceptualized and divided into two main aspects—the mental/psychological and the physical/embodied self—with two different brain networks, the default mode network (DMN) and the mirror neuron system (MNS) implicated as its neural foundations. As the self-face is the most identifiable marker of the physical aspect of the self, it has been the subject of extensive study at the behavioral and neural level. Recent functional magnetic resonance imaging (fMRI) studies of self-face recognition have consistently found right frontoparietal areas associated with identification of the self-face. These areas appear to broadly overlap the human MNS. Mirror neurons are active when someone performs an action and when they observe that same action being performed. This neural simulation of motor acts and related representations creates an agent-independent link between actor and observer. In fact accumulating evidence suggests that simulation processes are used in a multitude of cognitions that constitute the self including autobiographical memory and prospection, perspective taking, understanding other's actions and mental states, and embodied self-representation. Equally, components of the DMN - particularly the medial prefrontal cortex and the posterior cingulate cortex - have been implicated in representing aspects of the mental self, including autobiographical memory and self-knowledge. Thus interactions of the DMN and MNS may subserve the integration of self-relevant traits within the context of autobiographical memory as well as future action goals—positioning the self as a “center of gravity” of one's private and social behavior.

### Scope and Limitations of Current Review

One major and useful distinction that has guided much research on the neural representation of the self is that between the physical and psychological aspects of the self (Gillihan and Farah 2005). Physical aspects of the self are typically examined in studies of self-face recognition, body recognition, agency, and perspective taking. Psychological aspects of the self tend to be operationalized

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with studies examining autobiographical memory and self-knowledge in the form of personality traits. This conceptual distinction bears out in neuroimaging work, which suggests that physical or embodied self-related processes and psychological or evaluative self-related processes rely on distinct yet interacting large-scale brain networks (Lieberman 2007; Molnar-Szakacs and Arzy 2009; Uddin et al. 2007).

In the current work, we review how recent advances in the study of large-scale human brain networks have contributed to our understanding of self-related cognition and representation. We will follow the useful distinction of physical versus psychological aspects of the self in this chapter by limiting its scope to illustrative studies on these two areas. We begin by discussing seminal theories on the self to provide a historical context. We give working definitions and descriptions of terminology relevant to our discussion of the self and the brain. Next, we describe the mirror neuron system (MNS) and the default mode network (DMN), two brain systems thought to subservise complementary aspects of self-representation. We then discuss paradigms that have been used to operationalize the study of the self, within the domains of self-face recognition and self-trait recognition—the most commonly examined physical and psychological aspects, respectively. We conclude with a discussion of autobiographical memory and propose a means by which an emergent self arises from complex interactions among seemingly disparate representations.

## Historical and Contemporary Definitions of Self

A central feature of human experience is our sense of self that persists across space and time. Understanding the essence of this experience has challenged scholars for many centuries. What is the self? The term itself is difficult to define and has led some of the most influential thinkers in psychology to theorize about the self. William James wrote in *The Principles of Psychology* that the self is not a single primordial entity (James 1983). This early conceptualization of multiple aspects of the self set the stage for later work examining these different facets. Ulric Neisser, a social psychologist, suggests that people have access to five different kinds of self-knowledge, which may develop during different periods: (1) the ecological self, perceived with respect to the physical environment; (2) the interpersonal self, depending on emotional and other species-specific forms of communication; (3) the temporally extended self, based on memory and anticipation, implying a representation of self; (4) the private self, reflecting knowledge that our conscious experiences are exclusively our own; and (5) the conceptual self, based on sociocultural experience (Neisser 1995). His claim is that the self is not some special part of a person or brain, but rather a whole person considered from a particular point of view. For example, the ecological self is the individual considered as an agent in the environment, and the interpersonal self is that individual engaging in face-to-face contact with others. Key to this theory is that perception of oneself in these different ways is the first and most fundamental form of self-knowledge and self-awareness. This definition of self in terms of one's existence in the world shifts focus from an inward-looking view based on private experience to an outward-looking view of the self as ecologically and socially situated (Neisser 1993).

Dennett (1991) relates a language-based approach to the self, referring to the self as the center of narrative gravity. According to this view, humans, with our unique capacity for language, spin narratives that are the essence of ourselves: “Our fundamental tactic of self-protection, self-control, and self-definition is...telling stories, and more particularly concocting and controlling the story we tell others—and ourselves—about who we are.” This center of narrative gravity posited as the self is analogous to a center of gravity in the physical sense—a simplified, single point of origin.

Expanding on the idea of a narrative self, Shaun Gallagher (2000) delineates a distinction called the “minimal” self versus the “narrative” self. Here, the “minimal” self is referred to as the self devoid

of temporal extension, a consciousness of oneself as an immediate subject of experience, depending on brain processes and an ecologically embedded body. The “narrative” self, on the other hand, involves personal identity and continuity across time and is a self-image constituted with a past and future in stories that we and others tell about ourselves.

Marc Jeannerod, on the other hand, grounds the self in the body and, more specifically, the motor system. He holds the view that a key component of self-recognition in humans is recognizing oneself as the owner of a body and the agent of actions. These sensations of agency and ownership arise from congruence of proprioceptive feedback and sensory signals from body parts, and central signals that contribute to the generation of movements. He claims that the sense of agency provides a way for the self to build an identity independent of the external world (Jeannerod 2003).

An extreme view put forth by the philosopher Thomas Metzinger is that there are no such things as selves. Metzinger (2003) claims that nobody ever has or had a self and that all that exists are conscious self-models. He states, “the phenomenal self is not a thing, but a process—and the subjective experience of being someone emerges if a conscious information-processing system operates under a transparent self-model.” This conscious self-model of human beings is a way of allowing an organism to conceive of itself as a whole and thus causally interact intelligently with its environment.

The last 20 years have seen enormous advances in our understanding of the human brain, and this has allowed cognitive neuroscientists and neuropsychologists to begin the study of linking the “self” to its neural substrates. Acquisition of much of this new knowledge has been facilitated by developments in brain imaging technology including methods that (1) measure neuronal firing patterns at the scalp (using electroencephalography, EEG); (2) measure the decay of an injected radioactive isotope, generally glucose which is taken up by active neurons in the brain, reflecting regional metabolic activity (using positron emission tomography, PET); (3) measure the changing levels of deoxygenated blood in response to neuronal firing patterns throughout the whole brain (using functional magnetic resonance imaging, fMRI); and (4) measure motor evoked potentials caused by electromagnetic induction from a rapidly changing magnetic field that leads to depolarization in the neurons of the brain (using transcranial magnetic stimulation, TMS). Researchers are using these methods to ask which brain regions and systems are critical to self-awareness and other forms of self-related processing, usually by focusing on one particular aspect of the self, such as visual self-recognition, to uncover the neural basis of that particular process.

## Large-Scale Brain Networks and Methods in Cognitive Neuroscience

Recent years have witnessed a paradigm shift in cognitive neuroscience (Aminoff et al. 2009). Whereas early functional brain imaging work focused primarily on localization of function, revealing activation in specific brain regions during performance of cognitive tasks, interest has recently shifted toward developing a deeper understanding of intrinsic brain connectivity and the architecture of brain networks that influences cognitive and affective information processing. A network, generally, is any set of objects that interact or share some relationship with one another (Wig et al. 2011). We are familiar with networks in our daily lives in the form of the World Wide Web. A brain network consists of individual brain regions (or nodes) that interact via structural and/or functional connections. A brain network can be defined based on structural connectivity as measured in the human brain with diffusion tensor imaging (DTI), or functional connectivity as typically measured by fMRI (Bressler and Menon 2010). Conceptualizing the brain in terminology used to characterize large-scale networks has proven to have a great deal of explanatory value; thus many cognitive neuroscientists have adopted this way of thinking about brain function and cognitive processes.

Two networks that have been linked to social cognition and therefore deeply implicated in the study of the self in particular—the human mirror neuron system and the default mode network—are described in detail in the following sections.

## The Neural Networks

### *The Mirror Neuron System in Humans*

For the authors of this chapter, one of the most exciting recent developments to emerge from cognitive neuroscience, with the potential to impact significantly both our conceptualization and our understanding of the self, is the discovery of the so-called human mirror neuron system (MNS) (Rizzolatti and Sinigaglia 2010). In essence, the MNS allows us to understand and predict the behavior of others, by engaging the neural regions required to produce such behavior ourselves. That is, when we see *another's hand* grasping an object, we activate the regions of *our brain* that control grasping; when we hear sounds associated with *someone else's action*, we activate the appropriate movement regions of *our brain*; and by extension, when we observe the *emotional states of others*, we can feel the same emotion in empathy (Carr et al. 2003; Gazzola et al. 2006; Molnar-Szakacs et al. 2006). It has thus been suggested that “mirror neurons are a kind of ‘neural wi-fi’ that monitors what is happening in other people. This system tracks their emotions, what movements they’re making, what they intend, and it activates, in our brains, precisely the same brain areas as are active in the other person. This puts us on the same wavelength and it does it automatically, instantaneously and unconsciously” (Goleman 2006).

Since the discovery of the MNS, the brain can no longer be considered as an independent input–output, perception–action machine—it is deeply, intrinsically connected with our bodies and, most intriguingly, with our understanding of the actions of other individuals (Cattaneo et al. 2011). Such a conceptual shift offers a helpful new framework for our understanding of the self as well, which of course is also hard to conceptualize as an independent entity, as we are each of us intrinsically connected with our physical environment as well as with those around us.

In the macaque monkey brain, neurons with mirror properties have been recorded using single-unit electrode recordings in both area F5 of the premotor cortex and in parietal area PF (Rizzolatti and Craighero 2004). These visuomotor neurons discharge both during the performance of an action and during the observation of another individual performing a similar action (di Pellegrino et al. 1992; Gallese et al. 1996; Rizzolatti et al. 1996a, b). Parietal mirror neurons have the special property of coding motor acts as belonging to an action sequence, predicting the intended goal of a complex action (Fogassi et al. 2005). In addition, it has been shown that a subset of mirror neurons are able to represent actions even when the final part of the action is unseen (Umiltà et al. 2001) or from hearing sounds associated with particular actions (Kohler et al. 2002). Thus, area F5 of the ventral premotor cortex and area PF of the inferior parietal lobule in the macaque brain form a frontoparietal mirror neuron system critical to action understanding and intention attribution (Fogassi et al. 2005; Rizzolatti and Craighero 2004; Rizzolatti et al. 2001).

Soon after the discovery of mirror neurons in the monkey brain, neuroimaging using PET (Grafton et al. 1996; Rizzolatti et al. 1996a, b) and TMS studies (Fadiga et al. 1995) demonstrated a network with similar functional properties in the human brain. Fadiga and colleagues (1995) provided an elegant demonstration of the matching neural representation in humans for actions observed and those performed by the self. In their study, magnetic stimulation was delivered to the scalp above the motor cortex, the source of motor commands for action, (1) while participants were observing an experimenter perform various hand actions in front of them or (2) during control conditions including arm movement observation, object observation, and dimming detection, while motor evoked

potentials (MEPs) were recorded from hand muscles. MEPs serve as a quantifiable index of activity within the motor cortex. Results showed that during hand action observation, but not in the other conditions, there was an increase in the amplitude of the MEPs in the *same* hand muscles that are used when the observed action is actually performed by the observer (Fadiga et al. 1995). This increase in MEPs resulting from observing a hand action reflects a facilitation or priming of the motor cortex—an increased potential for action—due to “inner imitation” of the hand action that was observed. Subsequent work then confirmed and extended these findings (Borroni and Baldissera 2008; Gangitano et al. 2001; Montagna et al. 2005; Strafella and Paus 2000), leading researchers to conclude that in humans there is a neural system, resembling the one described in the monkey, matching observed actions and executed actions.

During development and into adulthood, we acquire the basis of language and our culture, including a multitude of motor skills—like how to play sports and use everyday objects—through imitation, by reproducing observed behaviors (Greenfield 2006). It is very likely that most of these functions have, at their bases, a simulation mechanism (Iacoboni 2009; Pineda 2008; Rizzolatti and Craighero 2004). Simulation, or inner imitation, refers to the fact that the same neural resources are recruited while one observes *and* while one executes an action, allowing the brain to link the perceptions of an observer to the actions of an agent at the neural level. Furthermore, the fact that the same neural networks are activated within the brains of all individuals who participate in an interaction—the observer(s) *and* the agent(s)—allows for shared representations to be established among individuals, giving rise to a mutual understanding of the interaction.

Imitation is a ubiquitous human behavior composed of both an observation and an execution phase, making it an ideal paradigm for the study of neural activity associated with observation–execution matching in the human brain. fMRI was used to localize the brain regions matching observed action to executed action using an imitation paradigm. Basing their predictions on neural firing rates in the monkey (Gallese et al. 1996), Iacoboni and colleagues (1999) hypothesized that areas of the human brain that show mirror properties would show an increase of brain activity in the same area during action observation *and* during action execution, and action execution would lead to approximately double the increase in activity as action execution contains an overt motor response. In turn, imitation, which contains both an observation and execution component, would lead to the greatest increase in neural activity. This study found two cortical areas of the human brain that showed this predicted pattern of activity, the posterior inferior frontal gyrus (IFG) and the rostral sector of the inferior parietal lobule (IPL) (Iacoboni et al. 1999).

A wealth of additional studies have shown that mirror resonance mechanisms are involved in action perception and performance, meaning that the same neural network subserves the understanding of actions we observe, as in planning and executing our own movements (Aziz-Zadeh et al. 2006; Binkofski et al. 1999; Buccino et al. 2004; Chong et al. 2008; Fadiga et al. 1995; Grafton et al. 1996; Grezes et al. 2003; Iacoboni et al. 1999, 2005; Johnson-Frey et al. 2003; Koski et al. 2002; Molnar-Szakacs et al. 2005a; Nishitani and Hari 2000; Oberman et al. 2005; Rizzolatti et al. 1996a, b; Woodruff and Maaske 2010). The presence of an MNS in the human brain is also corroborated by the fact that its main neuroanatomical nodes—inferior frontal gyrus (IFG) and premotor cortex (PMC) anteriorly and inferior parietal lobule (IPL) posteriorly—are considered homologous to the areas forming the MNS in the monkey (Amunts et al. 1999; Mazziotta et al. 2001; Petrides and Pandya 1997; Rizzolatti and Matelli 2003; Tomaiuolo et al. 1999; VonBonin and Bailey 1947; VonEconomo and Koskinas 1925). Taken together, results of these studies imply that perception and action are inseparable, both in our daily behavior, as well as within the neural networks supporting them in our brain. In fact, it appears that the MNS may have further evolved to subservise more sophisticated functions in humans that are only rudimentarily present or even completely absent in monkeys, such as imitation, recognition of intransitive and symbolic gestures, language, intention understanding, and, of immediate interest to this chapter, self-representation. Based on the property of mirror neurons to internally simulate actions performed by others, it has been proposed that the

MNS may provide the link between the physical representation of the self as related to the physical image of others. Thus, the inner mirroring of other's actions and emotions, as supported by the human MNS, allows us to see the self, reflected in others.

### *The Default Mode Network*

Another brain network that has been most consistently linked to self-related processing is the so-called default mode network (DMN). The repeated observation that the ventral medial prefrontal cortex (VMPFC), posterior cingulate cortex (PCC), lateral parietal cortices, and medial temporal lobes paradoxically exhibit high levels of activity during resting baseline and decreases in activity during externally oriented cognitive tasks led to the initial characterization of these regions as belonging to a "default mode network" (Esposito et al. 2006; Fransson 2006; Gusnard et al. 2001; McKiernan et al. 2003; Raichle et al. 2001). This network has also been referred to as the "task-negative network" (Fox et al. 2005), or the "cortical midline structures" (Northoff et al. 2006), and was originally proposed as a system for evaluating "information broadly arising in the external and internal milieu" (Raichle et al. 2001). The network has since been posited to underlie a variety of functions, many of them social cognitive in nature. The DMN has been linked to episodic memory (Greicius and Menon 2004) and memory consolidation (Miall and Robertson 2006) in some studies and social (Iacoboni et al. 2004; Uddin et al. 2005) or self-related processes (Buckner and Carroll 2007; Gusnard et al. 2001; Wicker et al. 2003) in others. Recent theories posit that this network is critical for self-projection, or thinking about the future (Buckner and Carroll 2007). It is also notable that the network resembles that which is activated during theory of mind or mentalizing tasks where participants are asked to consider the mental viewpoint of another, as well as tasks requiring moral social evaluations (Harrison et al. 2008). Still other studies associate default mode function with more general processes such as stimulus-independent (Mason et al. 2007) or task-unrelated thought (McKiernan et al. 2006).

It is difficult to envision one comprehensive theory explaining the DMN's ability to support such a diverse array of cognitive functions and be associated with such a wide range of psychiatric and neurological disturbances. One common thread that can be seen, however, is that the functions attributed to the DMN are all in some sense self-related and in particular involve the representation of the psychological aspects of the self and its relationship to the external world. At present, the authors take the view that the DMN may be involved in maintaining a self-representation in evaluative terms, which requires both self-referential processing and understanding of others' mental states. We further speculate that the DMN might support evaluative simulation in the same way that the MNS supports motor simulation (Uddin et al. 2007).

Aberrations in activity of the DMN have been linked to cognitive deficits in a number of clinical conditions that are related to disturbances of the self. To date, abnormalities in the DMN have been demonstrated in individuals with autism spectrum disorders (Kennedy et al. 2006), Alzheimer's disease (Greicius et al. 2004), and schizophrenia (Liang et al. 2006). These disorders all manifest as altered psychological self-related cognition in the realms of social, memory, and self-monitoring processes.

Interestingly, recent theories related to different aspects of self-representation, as well as to conditions which involve a disturbance of self-related processing, often invoke explanations that are based either in deficits of the DMN, the human MNS, or both. For example, theories of *how we understand other minds* have implicated both the DMN (Spreng et al. 2009) and the MNS (Gallese and Goldman 1998); theories about *moral thinking* have been linked to both the DMN (Harrison et al. 2008) and the MNS (Molnar-Szakacs 2011); and the DMN and the MNS have both been implicated in theories of *physical self-representation* (Molnar-Szakacs and Arzy 2009;

Uddin et al. 2007). In the realm of psychiatric or neurological disturbances, both the DMN (Cherkassky et al. 2006; Kennedy et al. 2006) and the MNS (Dapretto et al. 2006; Molnar-Szakacs et al. 2009) have been implicated in *autism spectrum disorders*, and aberrant DMN connectivity (Garrity et al. 2007) and MNS dysfunction have been suggested in *schizophrenia* (Iacoboni and Dapretto 2006). Taken together, this evidence from both the healthy and the atypical brain suggests that these two neural systems—the human MNS and the DMN—are functionally connected and are together profoundly implicated in self-related cognition.

## Operationalizing the Self

### *Physical Self-recognition*

A key component of the self is embodiment, and that part of the body that functions as the most unique identifier is the face. Thus, the self-face is a critical component of self-identity. Cole (1999) describes cases of individuals with various problems affecting visual face perception and the effects of these disorders on their sense of selfhood. He discusses a case of a congenitally blind patient who, though unable to extract visual information from faces, still understood the importance of face-to-face contact in social communication: "... in order to interact and talk with people you present your face to them. It's not just a place your voice comes out of, it allows contact with others." A patient who became completely blind later in life reflects on a loss of identity resulting from his blindness: "To what extent is the loss of the image of the face connected with loss of the image of the self?" A patient with Möbius syndrome, which renders the subject unable to move any of the muscles of facial expression, relates the feeling of "living entirely in [his] head" due to his inability to engage in social emotional interactions. Patients with Bell's palsy and autism are also discussed in light of their problems with emotional facial expression and subsequent issues with self-representation (Cole 1999). A particularly interesting case of aberrant self-recognition is that referred to as "mirror sign." Phillips and Howard (1996) describe a patient who exhibited some global cognitive impairment and was unable to recognize herself in a mirror. The patient had no insight into her condition. The authors classify the phenomenon as a delusion of self-misidentification on the basis of a normal CT scan (Phillips and Howard 1996). Others have reported on this strange phenomenon as well, some emphasizing right hemispheric dysfunction as being an underlying common thread (Breen et al. 2001). Thus, as these examples highlight, the self-face plays a seminal role in our physical, psychological, and social identity throughout the lifespan.

As early as 1889, Preyer used mirrors to assess the development of the self-concept, noting that "the behavior of the child toward his image in the glass shows unmistakably the gradual growth of the consciousness of self out of a condition in which objective and subjective changes are not yet distinguished from each other" (Preyer 1889). It has been demonstrated that infants around 2 years of age begin to show behavior indicative of self-recognition in front of a mirror (Amsterdam 1972). Early observations led Gallup to conclude that self-recognition is predicated on a sense of identity—that this capacity is indicative of an underlying self-concept (Gallup 1977). While these studies were among the first to systematically use mirrors to test hypotheses regarding self-awareness and self-concept, the use of mirrors to this end has also been reported by Charles Darwin (Darwin 1877). While the purported relationship between self-recognition and other forms of self-awareness has been discussed and evaluated for a long time, the ability to mirror-self-recognize has only been demonstrated in humans, chimpanzees (Gallup 1970; Povinelli and Gallup 1997), orangutans (Lethmate and Ducker 1973), elephants (Plotnik et al. 2006), the bottlenose dolphin (Reiss and Marino 2001), and for the first time in a nonmammalian species, the magpie (Prior et al. 2008).

We, as well as others, have shown that self-face recognition abilities rely on a frontoparietal network in the right hemisphere (Platek et al. 2006; Sugiura et al. 2005; Uddin et al. 2005). In particular, in our own work, we observed that the pattern of signal increases observed in the right inferior frontal gyrus (IFG) and right inferior parietal lobule (IPL) were related to the amount of self-face presented in morphed stimuli. In other words, the greater amount of “self” present in the stimulus, the greater the activation in right frontoparietal areas that overlap with the human MNS (Uddin et al. 2005). We proposed that mirror areas may be more active for stimuli containing more “self” because their role is to establish communication between individuals via a simulation mechanism that maps actions of others onto one’s own motor repertoire, thereby making others “like me” (Meltzoff and Brooks 2001). Thus, when one sees one’s own image, these mirror areas are more strongly activated because of the ease with which one can map oneself onto one’s own motor system. This mapping produces the best match or correspondence, reflected in activity of the mirror neuron system, primarily in the right hemisphere (Uddin et al. 2005). Interestingly, we have also observed similar brain activation patterns distinguishing the self-voice from other voices, suggesting that the right hemisphere MNS may contribute to multimodal abstract self-representation (Kaplan et al. 2008). We have also used image-guided repetitive transcranial magnetic stimulation (rTMS) to create a “virtual lesion” over the parietal component of this self-recognition network to test whether the region is necessary for discriminating self-faces from other familiar faces. We showed that 1-Hz rTMS to the right IPL selectively disrupted performance on a self–other discrimination task, whereas applying 1-Hz rTMS to the left IPL had no effect. Thus it appears that activity in the right IPL is essential to the task, providing causal evidence for a relationship between the right IPL and self-face recognition (Uddin et al. 2006). Another recent rTMS study has also corroborated the finding of right hemisphere dominance for self-face recognition (Heinisch et al. 2011).

While recent neuroimaging reports have shown that several additional brain regions may contribute to self-face processing, a review of these studies highlights the common finding of right frontal and parietal activations accompanying self-face viewing, especially when compared to other familiar faces (Devue and Bredart 2011). Interestingly, a meta-analysis of studies of self-face recognition found that in addition to right frontoparietal regions which overlap the human MNS, the right precuneus is a region that is also associated with this task (Platek et al. 2008). This finding is particularly relevant to our hypothesis that the human MNS and the DMN give rise to an integrated self-representation—given the fact that the precuneus is often linked with the DMN. While useful for the purposes of study and discourse, the lines we have drawn between physical and psychological self-representation may not be as relevant in functional terms. Based on their recent review of the literature, Devue and Bredart conclude that it remains difficult to determine which specific cognitive operation is reflected by each recruited brain area and, thus, suggest that goals for future research should include understanding the precise cognitive operations induced by perception of the self-face in order to better determine the functional significance of brain activations in specific regions (Devue and Bredart 2011).

### *Self-trait Recognition*

Unlike self-face recognition, which recruits autobiographical representations through specific visual processing invoking memory retrieval processes (Fink et al. 1996; Keenan et al. 2001), personality-trait words likely access a representation of the self predominantly through linguistic aspects of the self-schema (Faust et al. 2004; Molnar-Szakacs et al. 2005b; Moran et al. 2006). Self-schemata are cognitive representations of the self derived from past social interactions and experiences that promote elaboration and organization of stored information and may be used to guide behavior (Markus 1977). As traits are incorporated into the self-schema, subsequent

memory for these trait words is increased (Rogers et al. 1977). For example, memory for previously presented trait adjectives (e.g., happy) was better if they had been processed with reference to the self (e.g., “does happy describe you?”) than if they had been processed only for their general meaning (e.g., “does happy mean the same as optimistic?”), a phenomenon labeled the self-reference effect (Symons and Johnson 1997).

There have been two major competing explanations for the self-reference memory effect. The first view is that the self is a cognitive structure that possesses special mnemonic abilities, leading to the privileged status of material processed in relation to self. The contrasting view is that no distinct structure or neural process is dedicated to self-referential processing, and the memory enhancement that accompanies self-referential processing can be interpreted as a standard depth-of-processing effect. That is, because we know a lot of information about ourselves, we encode additional information about the self more deeply. In turn, this elaborative encoding enhances the memory for self-relevant information. Functional imaging studies have identified multiple regions that are responsive to various aspects of self-relevant processing. For example, within the category of self-related linguistic stimuli, regions of the left prefrontal cortex are involved in semantic encoding. But are there neural structures that are selective for self-relevant information?

Kelley and colleagues (2002) designed an fMRI study to look precisely at this question—whether knowledge about the self is unique in terms of its functional anatomic representation within the human brain. Participants were imaged while making judgments about trait adjectives under three experimental conditions—self-relevance, other-relevance, or case judgment (upper- versus lowercase letters). The authors found that while the semantic processing component found across all conditions activated left prefrontal regions, the self-trials were distinctive for their selective activity in areas of the medial prefrontal cortex (MPFC), suggesting that this region might be involved in processing self-referential linguistic information (Kelley et al. 2002).

The special role of the MPFC in processing self-related material has now been demonstrated in a variety of neuroimaging studies. For example, dorsomedial prefrontal cortex (DMPFC) activation was observed during evaluation of self-referential statements (e.g., “I like Leipzig: yes/no”) compared with memory retrieval trials (Zysset et al. 2002). In an fMRI study using self-descriptive positive and negative words, it was found that processing related to the self recruited the right DMPFC and posterior cingulate cortex (PCC) specifically during self-referential evaluation irrespective of the valence of the presented words (Fossati et al. 2003). A subsequent study by the same group found that the correct recognition of self-related positive and negative words reactivated the right DMPFC. Activity in this region was driven by the self-negative words, indicating that self-characteristic negative stimuli may facilitate retrieval of the self-schema (Fossati et al. 2004). Indeed, in addition to the MPFC, neuroimaging studies suggest a role for the PCC and the adjacent precuneus in integrating self-referential stimuli. For example, activation in the PCC and precuneus was observed when subjects had to indicate whether a word or statement was self-descriptive or not (Fossati et al. 2003; Johnson et al. 2002; Kircher et al. 2000). Similarly, reflection on one’s own personality traits was associated with activation in the precuneus and MPFC when compared with reflection on traits of the Danish queen (Kjaer et al. 2002).

A wealth of other functional brain imaging studies have revealed activations in this set of cortical midline structures—the VMPFC, the DMPFC, the posterior cingulate, and the precuneus—that form part of the DMN when people reflect on their psychological characteristics (Crain et al. 1999; D’Argembeau et al. 2005; Fossati et al. 2003; Johnson et al. 2002; Kelley et al. 2002; Kjaer et al. 2002; Lou et al. 2004; Mitchell et al. 2005; Moran et al. 2006; van Buuren et al. 2010; Whitfield-Gabrieli et al. 2010). In fact, the DMN structures are recruited when reflecting both on one’s own characteristics as well as those of others (Amodio and Frith 2006; Jenkins et al. 2008). Jenkins and colleagues (2008) proposed that the reason for this was that individuals automatically refer to their own mental states when considering those of a similar other, and used the repetition suppression paradigm in fMRI to investigate this hypothesis. In support of their hypothesis, they found that ventral medial

prefrontal cortex (VMPFC) response was suppressed when self-reflections followed either an initial reflection about self or a judgment of a similar, but not a dissimilar, other (Jenkins et al. 2008). Recently, Sugiura and colleagues (2008) used fMRI to investigate face-specific and domain-general neural responses to self, familiar and unfamiliar faces, and proper names. In addition to finding networks that respond to self-faces (as described above), they also found higher activation for the self and familiar other, compared to the unfamiliar other, in the medial cortical structures during face *and* name recognition (Sugiura et al. 2008). These data show that cortical midline structures respond to both self and familiar others' images *and* names, suggesting a domain-general role for the DMN in self-related cognitions. These results suggest that we use the self as a point of reference, even when thinking about the mind of another person; however, these brain structures do appear to be more engaged when referring to the self (see Northoff et al. (2006) for a meta-analysis). Taken together, these data suggest an important role for midline structures—including the VMPFC, DMPFC, PCC, and precuneus—that form part of the DMN in processing self-relevant information.

### ***Autobiographical Memory***

Self-reference and self-relevance—whether by visual self-face recognition or through the enhanced memory for trait adjectives that are part of the self-schema—invoke autobiographical memory processes (Molnar-Szakacs and Arzy 2009). Memory is vital to the survival of the “self” as we use our memory for past events to predict the future in a cogitation called “mental time travel” (for reviews, see Schacter et al. 2007, 2008). Accordingly, it has been found that patients with amnesia are markedly impaired relative to matched control subjects not only in retrieving past events but also at imagining new experiences. In fact, a particular aspect of this deficit in thinking about the future is an impairment in predicting events about one's *personal* future rather than public or world events (Hassabis et al. 2007).

Recent neuroimaging studies have started to investigate the neural networks subserving self-projection in time (Addis et al. 2007; Arzy et al. 2008; Buckner and Carroll 2007; Szpunar et al. 2007). For example, Arzy and colleagues used a paradigm that involved participants making self-projections to both past and future and found that self-location in time recruits a distributed neural network—including anterior temporal, occipitotemporal, and temporoparietal regions—that partly overlaps the DMN (Arzy et al. 2008). The authors also found an effect of “self” in the behavioral data whereby participants responded significantly faster to personal (self-relevant) events than to world (non-self-relevant) events. In terms of brain regions, the above results show an overlap with the regions recruited during other self-relevant tasks, such as visuospatial perspective taking and spatial self-location (Arzy et al. 2006; Blanke et al. 2005; Vogeley and Fink 2003).

The finding that DMN structures were recruited when reflecting on one's own image, traits, past, and future confirms the important role of these brain structures in processing self-relevant information and maintaining a sense of self that is continuous through time. D'Argembeau and colleagues also found that the degree of activity within this network varied significantly according to the target of reflection. More specifically, reflecting on the self in the present elicited greater activity in the ventral and dorsal MPFC and PCC compared to reflecting on the self in the past or reflecting on an intimate other (D'Argembeau et al. 2008). In fact, it has been proposed that not only does activity in MPFC track with self-referential processing but it also contributes to the encoding of self-relevant memories (Macrae et al. 2004). Thus, structures of the DMN may be important in indexing the degree to which a psychological trait corresponds to the self-schema or a physical image represents the self. The more strongly a stimulus is related to the self, the more activity it will elicit in DMN structures (Molnar-Szakacs and Arzy 2009; Moran et al. 2006; Northoff et al. 2006; Schmitz and Johnson 2007; Uddin et al. 2007).

## The Emergent Self: Conclusions and Future Directions

The distinction drawn in this chapter between functions of the DMN and MNS serves merely as a practical division of labor for purposes of discourse between two networks that subserve related and interacting processes which are crucial to giving rise to a cohesive sense of self that is continuous through time (Molnar-Szakacs and Arzy 2009; Uddin et al. 2007). While the MNS provides the physical other-to-self mapping that is necessary for comprehending physical actions of intentional agents, the DMN maintains and supports processes that are related to understanding psychological states of others by reflecting on one's own attitudes (Jenkins et al. 2008; Mitchell et al. 2005). In a broad sense, these neural networks allow us to know about our own mind *and* others' minds, as well as to adopt a point of view that is different from our current experience of the world. Through the constant functional interaction of these networks, the "self" is able to make inferences about what is going on inside other people—their intentions, feelings, and thoughts—allowing us to thrive in our social world.

Questions for future work include understanding the precise conditions under which these two systems interact with each other and how this seamless interaction contributes to social cognition. Developments in the tools of research, such as diffusion tensor imaging (Jbabdi et al. 2007) which provides information about the structural connectivity of the human brain, and developments in computing, such as functional connectivity modeling (Friston et al. 2003) which provides estimates of information flow between structures, will continue to be an active area of research and integration. Just as the brain's networks integrate information within and among them, researchers must integrate information from many different approaches, techniques, and sources to be able to answer the eternal question of what is the "self" (Aminoff et al. 2009).

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