The Neurobiology of the Self and of Self-Agency

The research on the neuroscience of the self has already created a vast literature and it quickly becomes apparent that there are a number of different fields of specialist research, which are not easy to integrate into a coherent picture. Each of these explores a particular area of neural circuitry in the human brain and the role that the chosen networks play in the sense of self and of self-agency. As yet, only a few researchers are exploring how these different developmental strands of self-experience and their underlying neurobiology can be integrated to begin to offer a more coherent overview. In one such review article, Uddin, Iacoboni, Lange, and Keenan (2007) described the differing neural networks that are involved in creating, supporting, and maintaining the self. They argued that the research evidence suggests that there are two main networks:

- A network composed of cortical midline structures (CMS), which includes the medial prefrontal cortex, the anterior cingulate cortex, and the precuneus. This network has been linked to self-processing and social cognition and overlaps with areas that comprise the “default network.” One of the defining characteristics of the default network is that the constituent areas show decreased activity during goal-related tasks but high metabolic activity when the mind is at rest or engaged in nonfocused activity such as autobiographical reminiscences, self-referential thought, or inner dialogue.
- A right-lateralized frontoparietal network that overlaps with mirror-neuron areas and that seems to be involved in self-recognition, self-awareness, and social understanding. This mirror neuron system (MNS) is active during goal-oriented actions and is central to the sense of embodied self, bridging the gap between the physical self and others through motor simulation mechanisms.

Uddin et al. (2007) highlighted the difficulties involved in teasing apart the relative contributions of the CMS and MNS to self- and other-representation and proposed a unifying model that integrates the body-based sense of self that develops through mirror neuron activity, with the more social and psychological aspects of the mental self that depend on CMS activity. (I discuss these integrative processes more fully later in this chapter.)

But this model does not fully spell out the fact that the CMS also depends on the subcortical midline systems described by Jaak Panksepp (1998), which, he suggested, underpin the basic sense of a core self. So the relationship between the CMS and this more fundamental subcortical aspect of midline activity also needs to be described.

In relation to the right-lateralized frontoparietal network, there are also two separate strands of research that need to be distinguished, one on the MNS and the other on aspects of the right orbitofrontal cortex described by Allan Schore and others. These different areas of research can be combined under three headings:

1. Mirror neuron research and the development of an embodied motor-intentional self
2. The research on cortical and subcortical midline structures and the development of a core emotional self
3. The right hemisphere and the development of a relational embodied self

It will be obvious from the wording of these three strands of research that there is considerable overlap between the aspects of the self that they explore, specifically the fact that embodied interpersonal interaction is the foundation of our sense of self and of self-agency. But Uddin et al. (2007), in their description of the differing functions of two main neural networks, suggested that the MNS is restricted to involvement in the earlier physical and social levels of agency, centering on motor simulation and imitation, including imitation of the facial movements involved in the expression of emotion (Carr, Iacoboni, Dubeau,
Mazzotta, & Lenzi, 2003; Sinigaglia, 2008; Wacker et al., 2003). This seems to accord with the views of mirror neuron researchers such as Gallese who suggested that “the shift from motor goals to intentions and abstract rules is beyond the functional properties of the MNS” (Gallese et al., 2009, p. 105). In contrast, the CMS and the right brain (especially the orbitofrontal cortex) seem to have a wider range of function, in that they are involved both in basic, embodied, emotional, and relational self-experience and, at higher cortical levels, with the higher intentional and representational levels of self and self-agency, which are expressed in words, not actions.

**Mirror Neuron Research**

Bodily imitation has been extensively explored by developmental researchers such as Andrew Meltzoff (2005) as the mechanism for recognizing the intentionality of others and using it to discover our own. The discovery of mirror neurons offers a firm neuroscientific foundation for the view that an infant’s self-agency is explored through physical action and through the direct physical mirroring of another’s motor intentionality. The crucial characteristic that defines mirror neurons is that the same neurons fire both when carrying out an action and when observing another performing an action.

Mirror neurons have different degrees of specificity, but they work together as a system to encode not just the observed actions per se, but the intention to perform those actions. So when mirror neurons fire, we know what we ourselves would intend if we performed that action and we therefore attribute the same intention to the person we observe. But Sinagaglia (2008) argued that the automatic mirror neuron understanding of the intention of an observed action is certainly not the same as mind reading, the intentional attributions concerning mental states, such as beliefs, desires, and intentions—the conscious reason for performing an action. Mirror neuron activity provides a direct matching of the others’ observed behavior to our own motor repertoire, a neurological mirroring process that functions automatically and does not require any conscious concept or inference. Sinagaglia pointed out the fact that mirror-based understanding specifically involves the immediate recognition of the goal-relatedness of the observed motor acts and this recognition depends on the fact that those acts are mapped onto the vocabulary of the observer’s own motor acts. (2008, p. 77)

He suggested, “The fact that mirror neurons cannot capture reasons, beliefs, desires, and intentions . . . is not, however, an argument against the possibility of their having a role in intentional attribution” (2008, p. 89). Mirror neurons are the means for action understanding, not mind understanding. In case any confusion remains in the mind of the reader, Rizzolatti and Sinagaglia spelled this out even more clearly:

In humans as in monkeys, the sight of acts performed by others produces an immediate activation of the motor areas deputed to the organization and execution of these acts, and through this activation it is possible to decipher the meaning of the “motor events” observed, i.e. to understand them in terms of goal-centred movements. This understanding is completely devoid of any reflexive, conceptual and/or linguistic mediation as it is based exclusively on the vocabulary of acts and the motor knowledge on which our capacity to act depends. (2008, p. 125)

A philosopher, Emma Borg (2007), has questioned this view of mirror neurons, suggesting that maybe what the mirror neurons do is activate intentionality itself rather than the specific form it takes. She argued that mirror neurons do not read the other person’s specific intention but merely identify that the other person was acting purposefully. In her view of mirror neurons, “if all they do is help determine which actions in the world count as intentional this still leaves it entirely open how one proceeds to attribute specific intentions to these actions” (Borg, 2007, p. 10). As Borg argued, picking up a cup can then lead to a number of subsequent actions, from lifting it to the mouth to drink to clearing it away.

However, Sinagaglia effectively questioned the underlying premises of Borg’s argument, showing that she has not understood the highly specific function of mirror neurons; she suggested that Borg seemed to be using the term intention to mean conscious motivation, the beliefs and desires from which the actions of adult humans do indeed largely originate. But the word intention can cover a spectrum, from the completely mindless automatic motor intentionality of an amoeba engulfing food to
the conscious highly symbolic expression of desire in romantic poetry. It is this confusion around the exact nature of intention that seems to give rise to some of the disagreements about the role of mirror neurons in intentionality.

Borg seemed to assume that human intentionality is always conscious. But many behaviors that appear to have conscious purposive intent are actually entirely nonconscious automatic action sequences, such as the dam building of beavers—but clearly still intentional in a motor sense. Daniel Dennett highlighted this distinction in his book _Darwin’s Dangerous Idea_, in which he suggested that highly complex animal behavior results from a “something as mindless and mechanical as an algorithm... a set of individually mindless steps succeeding each other without the help of any intelligent supervision” (1995, p. 59). However, the problem with Dennett’s model is the suggestion that these subroutines are hard-wired into each species’ brain as an algorithm, a set of instructions or a computational module in the animal’s mind, which has evolved through natural selection. This computational model implies some kind of centralized controlling module of information or set of instructions in the animal’s brain or central nervous system, but in Chapter 1, I have described the arguments given by Oyama, Hendriks-Jansen, Panksepp, and others that demonstrate the biological inconsistencies in that model.

Mirror neuron researchers do not propose a central set of instructions in the brain, but describe these motor action sequences as “intentional chains in which each motor act is facilitated by the previously executed one” (Fogassi et al., 2005, p. 665) and propose that these chains also provide the building blocks upon which the intentional understanding of another’s actions can be constructed given the appropriate contextual cues (Sinigaglia, 2008, p. 83). Rizzolatti and Sinigaglia expanded on this to explain that there are species-specific preferred action chains. For example, the action chains for grasping are more strongly linked in monkeys to putting food in the mouth than placing it elsewhere. They suggest that this bias in favor of certain action chains is genetically hard-wired in a species-specific way.

However, I would suggest that these biases are not necessarily hard-wired but are emergent, early developmental products of the infant’s interaction with caregivers and with the world around them. The infants of all species learn from a very young age that putting food into one’s mouth is far more enjoyable than placing it somewhere else. This view of mirror neuron phenomena as epigenetic, not innate, is also that of Ted Panksepp, whose work I discuss in the next section (Panksepp & Panksepp, 2008). These behaviors emerge from the interaction of subcortical, genetically programmed affective neural networks in the neocortex (the core-SELF described in the next section) with the stimuli provided by the species-typical environment, which together build the chain of automatic motor action sequences that is characteristic of each species, such as dam building in beavers.

Automatic behavior patterns in animals can therefore be understood as a result of genetic influence through the influence of subcortical affective neural networks. But mental imagery and thought are the result of much more complex interactions between brain, mind, and environment and in which genetic hardwiring plays virtually no part. These higher mental processes reflect the general information-processing activity of the human neocortex, as I discussed in Chapter 1.

There is one experiment conducted by Melzoff (2005) that does at first sight seem to undermine this argument that mirror neurons are the basis for motor or action understanding, not for understanding the conscious intention of the other person. In Melzoff’s experiment, there is a toy with a loop and another part with a hook. The infant observes the researcher, who moves as though to hang the loop on the hook, but drops it beside the hook instead, as though by mistake. Borg’s objection is that infants could not understand the intention of the adult if they had never seen the toy in use before and so could not have an understanding of what constitutes typical behavior with such objects. “Why would hanging the loop on the hook in this context count as ‘what’s most likely to come next’?” (Borg 2007, pp. 13–14). At first sight it does indeed look as though infants, when they hang the loop on the hook, have read the researcher’s mind, in that they do not copy the researcher’s action but appear to read the observer’s apparent conscious intention. Borg used this evidence in support of her argument that infants could not possibly read the specific intention of the adult but could identify that there is conscious intentionality behind the action.

But Sinigaglia suggested that the infant’s action of hanging the loop on the hook “depends on the selection of those action chains that are most compatible with the observed situation” (2008, p. 131). But why would hanging the loop on the hook be the preferred action sequence for the infant? Would, for example, the observation that one object frequently goes into another, such as food into a mouth, be sufficiently
similar to an action of hanging a loop on a hook to trigger the action chain? It seems to me that this is more compatible with the role of mirror neurons, whose activation is the mechanism by which the young of a species acquire a series of goal-directed action sequences, for example, by observing their parents' action sequences; this observation then activates the mirror neurons that are involved in the infant's own similar sequence of intention-action chains. Part of the species-typical environment is the behavior of the parent animal that stimulates and molds these automatic action sequences.

Gallese et al. extended this developmental approach to suggest that the infant's capacity to respond to a novel stimulus (such as the loop and hook) may have its origins in antenatal development, for example:

During pre-natal development specific connections may develop between the motor centers controlling mouth and hand goal-directed behaviors and brain regions that will become the recipients of visual input after birth. . . . Such connectivity could provide functional templates (e.g., specific spatiotemporal patterns of neural firing) to areas of the brain, that once reached by visual information, would be ready to specifically respond to the biological motion like hand or face gestures. (2009, p. 106)

For the infant who hangs the loop on the hook, the completion of the act has become structured in the secondary prefrontal and parietal areas of the infant's cortex as a relational motor dynamic, probably activated by the embodied similarity with previous satisfying actions of linking—such as clasping hands together, putting thumb in mouth, and other actions by which one object is connected with another, or one part of the body with another.

Mirror neuron researchers have found that there is another category of neurons in the premotor cortex, canonical neurons, which have properties linked to, but with some differences from those of mirror neurons. Gallese and Umiltà suggested that canonical neurons in the ventral premotor cortex of monkeys fired when the monkey, in the absence of any active movement, observed objects whose intrinsic features, such as size and shape, were strictly related to the type of action that the very same neurons motorically encoded. (2002, p. 37)

They suggested that these canonical neurons contribute to the relational basis for our understanding of objects in the world around, in that the objects whose observation triggers the neurons' response are analyzed in relational terms. Object observation . . . determines the activation of the motor programme that would be required, were the observer actively interacting with the object. Looking at objects means to unconsciously "simulate" a potential action. The object-representation is transiently integrated with the action-simulation (the ongoing simulation of the potential action). (Gallese & Umiltà, 2002, p. 37)

Gallese and Umiltà concluded that:

Objects are not merely identified and recognized by virtue of their physical "appearance" but in relation with the effects of the interaction with an agent. . . . [T]he object acquires a meaningful value by means of its dynamic relation with the agent of this action. (2002, p. 37)

In other words, they suggest that our meaningful experience of the world around us is rooted in the kinds of physical interactions we have with it and so with the experience of agency at the physical level. The key question, of course, is whether this action-based experience of agency can form the foundation for agency at the psychological level, through symbolism and abstract thought. I discuss this in the next chapter, but here I would highlight the role of mirror neurons in empathy. Gallese points out that there is a tight link between embodied simulation and our perception of the emotions of others, shown by their facial expressions. "When people observe pictures of emotional facial expressions, they show spontaneous unconscious and rapid electromyographic responses in the same facial muscles involved in the person's facial expression" (Gallese, 2007, p. 149). He indicates that this rapid and automatic activation of facial muscles is probably triggered by activation of the MNS. Gallese concludes:

Furthermore in an fMRI study, Carr, Iacoboni, Dubeau, Mazziotta and Lenzi (2003) showed that both observation and imitation of the facial expression of emotions activate the same
restricted group of brain structures, including the ventral premo-
tor cortex, the insula and the amygdala. The perception and pro-
duction of emotion-related facial expressions both impinge upon
common neural structures whose function could be characterized
as that of a mirror matching mechanism. (Gallese, 2007, p. 149)

This kind of automatic empathy, based on the activation of shared facial
expression, plays a crucial role in the experience of agency in social rela-
tionships, from infancy onwards.

The Research on Subcortical Midline Structures and the
Development of a Core Emotional Self

The model I shall draw on most extensively is that of Jaak Panksepp,
whose groundbreaking book Affective Neuroscience was published in
1998. There and in subsequent publications (Panksepp, 2008; Panksepp
& Northoff, 2009; Panksepp & Panksepp, 2000), he takes a biological
epigentic approach in which higher functions are identified as emer-
gent properties of the interaction of low-level core neural networks with
higher cognitive abilities. Panksepp repeatedly warned of the error of
assuming that genetic control determines the nature of the conscious
human mind. He stated: “Evolutionary psychologists have yet to reveal
a single higher human mind function that has clearly been molded by
genetic inheritance, not even the famous ‘language instinct’” (2008,
p. 414). His view accords with the epigenetic models of the develop-
mental biologists and psychologists, such as Susan Oyama and Annette
Karmiloff-Smith, that I described in Chapter 1.

But this does not mean that Panksepp in any way underestimates
the importance of biology in the development of the self. The key issue
is the neurological and developmental level at which genetic influence
predominates. Panksepp suggested that the most basic form of self is
biological and transspecies, consisting of genetically ingrained neural
networks that allow an organism to selectively and adaptively relate to
its environment. This proto-SELF consists of integrative processing and
sensitivity to an organism’s own internal bodily states and functions,
motor activity, and environmental stimuli and is present not just in
humans but in other mammals and even in early vertebrates. Damasio
also used the term proto-self to define “a coherent collection of neural
patterns which maps, moment by moment, the state of the physical
structure of the organism in its many dimensions” (1999, p. 154). But
Panksepp capitalizes SELF to make clear that he is referring to evolu-
tionarily determined specific midbrain neural networks, rather than to
concept or conscious experience of self. The networks for the proto-
SELF are those of the midbrain, such as the periaqueductal gray and
the deep layers of the superior colliculi. This subcortical midline system
5CMS) is in effect an autonomic-affective body schema, which activ-
ates “coherent action patterns with all the bodily and affective accom-
Panksepp pointed out that the deep layers of the superior colliculi may
well be the first evolutionary site for a bodily representation of the
self, in that they contain multimodal sensory systems and motor control
functions that can control simple orientation responses, such as the
eye movements an animal needs for rapid orientation during pursuit
(1998, p. 77). He also highlighted the role of the midbrain locomotor
region (Figure 3.1), which integrates neural networks that are essential
for setting up coherent action patterns (1998, p. 312). Panksepp’s view
is that these motor functions are more central to the SELF than are
somatosensory processes. It is action and motor coherence that allow an
organism to function in its environment. I would suggest that the proto-
SELF can therefore be considered as the neural network underpinning
the most fundamental motor expression of agency.

The proto-SELF provides the evolutionary substrate for the emer-
gence of the core-SELF, which includes specific and clearly defined
core emotional circuits concentrated in the medial mesencephalic
and diencephalic deep subcortical regions and shared by all mammals
(Figure 3.2). (The mesencephalon is the midbrain, including the areas
described in the previous paragraph. The diencephalon is the poste-
rior part of the forebrain that connects the midbrain with the cerebral
hemispheres, encloses the third ventricle, and contains the thalamus and
hypothalamus.)

Panksepp has offered a wealth of research to support his view that
these motivational and emotional systems of the core-SELF are those
of SEEKING, RAGE, LUST, CARE, PANIC, and PLAY (Panksepp,
1998; Panksepp & Panksepp, 2000). These are capitalized to mark the
fact that they refer, not to conscious emotional states of mind, but to
specific neurobiological circuits in the subcortical systems of all mam-
nalian brains. The core-SELF is the level at which primary-process
consciousness is possible, once the proto-SELF is linked to these
Forobrain
Diagram
of
the
midbrain.

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com,
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FIGURE 3.1

affective networks. This “affective consciousness” is the “relation of one’s body to the incentives in the environment as well as internally generated emotional arousals” (Panksepp & Northoff, 2009, p. 196), in other words, a primitive form of consciousness, which at this level is essentially affective.

The proto-SELF and the core-SELF together constitute the nomothetic SELF, the word nomothetic being used to make it clear that this is a universal neural substrate, shared across mammalian species, and not an individual subjective experience of self (the idiographic self, which I shall describe in a moment). Panksepp and Northoff highlighted the importance of agency in this nomothetic mammalian level of self:

Such a basic level of self may allow organisms to become spontaneously active organisms, able to relate intimately to the environment soon after birth. We envision the core-SELF to allow organisms to be active agents, as opposed to simply passive information-processing machines. (2009, p. 194)

One of the emotional/motivational systems of the core-SELF is that of the SEEKING system, which generates the seeking of resources essential to survival:

A system that provides a goad with no fixed goal for exploratory/investigatory activity. This system is capable of helping construct goal-directed behavior patterns based on the confluence of bodily

FIGURE 3.2
Diagram of diencephalous.
This system of the core-SELF could therefore be regarded as the emotional and motivational foundation of self-agency, a system that provides the drives and urges that direct an organism’s motor activity and by which it seeks to meet its needs.

The nomothetic SELF emerges not only from the activity of SCMS, but also from that of higher medial cortical levels, which facilitate affective cognitive integration, so yielding a fully developed nomothetic SELF. This process of integration is described by Panksepp as “self-related processing” (SRP), which allows stimuli from the environment to be related and linked to organismic needs by processing within SCMS. Panksepp and Northoff postulated that:

Core SRP operates automatically, is deeply affective, and is developmentally and epigenetically connected to sensory-motor and higher cognitive abilities. This core-SELF is mediated by SCMS, embedded in visceral and instinctual representations of the body that are well integrated with basic attentional, emotional and motivational functions that are apparently shared between humans, non-human mammals and, perhaps in a proto-SELF form, with other vertebrates. (2009, p. 194)

Self-related processing is thus an important part of the emotional experience of agency, because it allows external events to be linked to the organism’s felt emotional and motivational urges (Northoff & Panksepp, 2008).

The core-SELF and SRP provide the biological platform for the emergence of environmentally constructed subjective or idiosyncratic selves, “the reflective or cognitive self, which permits awareness as opposed to raw experience of phenomenal-affective contents” (Northoff & Panksepp, 2008, p. 195). It is these higher forms of self that are species-specific, require higher cognitive brain regions in the neocortex, and are probably largely confined to humans and some other animals (higher primates, elephants, and cetaceans). The idiosyncratic self in humans allows self-reflection and narrative processes and so underpins the sense of self-agency at the intentional and representational levels, which I discuss in more detail in Chapter 4. The idiosyncratic self emerges through individualized learning processes that result from each person’s unique developmental epigenetic cultural experiences. SRP provides the foundation for epigenetic emergence of these higher idiosyncratic forms of selfhood, integrating the core-SELF regions of the medial brain stem and medial frontal lobes with higher associative, more strongly cognitive regions of the brain such as lateral frontal and parietal cortices. Panksepp and Northoff (2009) pointed out that, once the idiosyncratic, reflective self has become established, it can modulate the core-SELF, so that there is a two-way influence between higher and lower forms of selfhood. This is an important consideration in relation to the possible neurobiological processes by which psychotherapy may help to establish and consolidate a patient’s secure sense of self and of self-agency.

The Right Hemisphere and the Development of a Relational Embodied Self

One of the strongest themes to emerge from studies of mother-infant relationships is that the infant’s earliest relational experiences directly affect the development of the brain; a healthy emotional environment allows key neuronal connections to flourish, while an adverse experience of relationships means that the growth of these pathways is stunted or inhibited to varying degrees.

In Chapter 2, I highlighted the fact that this interactive view, that interpersonal experience and intrapsychic development mutually influence each other, is at the core of what is meant by the concept of emergence in psychological development. Repeated patterns of interpersonal experience create and strengthen new neuronal pathways, enabling new mental, emotional, and relational capacities to emerge. These, in turn, stimulate new responses from the caregiver, which in turn stimulate the infant’s mind and brain. This point has been repeatedly emphasized not only by neurobiology researchers such as Allan Schore (1994, 2003a) and Daniel Siegel (1999), but also by clinicians who increasingly question the view that there are innate determinants of psychic life, as both psychoanalysis and analytical psychology propose. (Hogenson, 2004; Knox, 2003). There is no genetic blueprint guiding development, an issue that I summarized in the first chapter and a view supported by researchers such as Panksepp & Panksepp (2000), Deacon (1997), Hendriks-Jansen (1996), and Oyama (2000).
Allan Schore has explored the relational basis for the development of the brain, particularly the neuronal pathways involved in interpersonal experience and emotional regulation. His book *Affect Regulation and the Development of the Self* (Schore, 1994) was the first to pinpoint the role of right-brain interaction between mother and infant in facilitating affect regulation and a stable and secure sense of self. He suggested that the core of the self lies in patterns of affect regulation that integrate a sense of self across state transitions, thereby allowing for a continuity of inner experience. This highlights the importance of affect regulation in contributing to self-agency, our sense of being able to draw on and manage our own emotions for our own purposes and to express our conscious intentions, rather than being flooded by emotions that feel alien and out of control.

In recent articles, Schore argued that attachment theory has now moved from being primarily a theory of behavioral interaction between mother and infant to become one centered on affect and self-regulation, a view strongly supported by the observational studies of Beatrice Beebe and colleagues (discussed in Chapter 2). This shifts the focus of theory from external observed behavior to the internal world of felt experience, emotion, and relationship, the implicit relational knowledge the infant acquires from the first moments of life. Schore’s research shows that the self-other relationship is embedded in infant-caregiver, right hemisphere to right hemisphere, affective, attachment communications (Schore, 1994, 2001 2003a, 2003b, 2005, 2009). He pointed out that the emotion-processing human limbic system myelinates in the first year and a half (Kinney, Brody, Klonman, & Gilles, 1988) and the early maturing right hemisphere, which is deeply connected into the limbic system, is undergoing a growth spurt at this time, so attachment experiences specifically impact on limbic and cortical areas of the developing right cerebral hemisphere (Cozolino, 2002; Henry, 1993; Schore, 1994; Siegel, 1999).

These findings have important implications for our understanding of the development of self-agency and the crucial part that empathic maternal mirroring plays in this process. Neurobiological research on the mother-infant intersubjective dialogue indicates:

A number of functions located within the right hemisphere work together to aid monitoring of a baby. As well as emotion and face processing the right hemisphere is also specialized in auditory perception, the perception of motivation, attention, and tactile information (Houck & Todd, 2004, pp. 22–23)

...from infancy through all later stages of the life span, the right hemisphere is dominant for the development of our implicit relational knowing, the “nonconscious reception, expression, and communication of emotion and the cognitive and physiological components of emotional processing” (Schore, 2009, p. 6). In the previous chapter I described the research that shows that it is the turn-taking interactions and the experience of agency in the earliest relationships that form the foundation for this implicit relational knowing and for the subsequent development of self-agency.

Decety and Chaminade supported Schore’s view of the central role of the right hemisphere in relationship, writing that “self-awareness, empathy, identification with others, and more generally intersubjective processes, are largely dependent upon the right hemisphere resources, which are the first to develop” (2003, p. 591). More recently, Decety and Meyer stated:

Shared neural circuits, self-awareness, mental flexibility, and emotion regulation constitute the basic macrocomponents of empathy; these are mediated by specific neural systems, including aspects of the pre-frontal cortex, the anterior insula and frontoparietal networks. (2009, p. 14)

Decety and Meyer extended this exploration of the role of the right hemisphere to suggest that it not only underpins empathy but also the infant’s gradual discovery of his or her agency, and that the capacity to experience agency is also critical for empathy:

In a completely empathic experience, affective sharing must be modulated and monitored by the sense of whose feelings belong to whom (Decety & Jackson, 2004). Furthermore, self-awareness generally and agency in particular are crucial aspects in promoting a selfless regard for another, rather than a selfish desire to escape aversive arousal. (2009, p. 149)

So the mothers so poignantly described in the research by Beebe et al. (2010), discussed in Chapter 2, who could not bear their babies’ distress
because it aroused too much distress of their own, exactly reflect the situation described by Schore, Decety, and others. They were unable to show a selfless regard, to use their right brains to empathize with or mentalize about their babies. Their inability to relate empathically would, in turn, inhibit the infant’s developing right brain and so that child would also grow up with a diminished capacity for both empathy and agency, unless the parent is lucky enough to benefit from the kind of intervention so effectively offered to mothers by van den Boom (described in Chapter 2).

So what areas of the right brain are involved in the experience and attribution of agency? Decety and Meyer (2009) drew on neuroimaging studies to propose that the junction of the right inferior parietal cortex with the posterior temporal cortex (the temporoparietal junction) plays a critical role in the distinction between self-produced actions and actions generated by others. The temporoparietal junction is an association cortex that integrates input from the lateral and posterior thalamus, as well as visual, auditory, somesthetic and limbic areas. It has reciprocal connections to the prefrontal cortex and to the temporal lobes. Because of these anatomical characteristics, this region is a key neural locus for self-processing: it is involved in multisensory body-related information processing as well as in the processing of phenomenological and cognitive aspects of the self. (Decety & Meyer, 2009, p. 149)

Awareness of agency—that an action is self-generated—seems to depend on activation of the anterior insula bilaterally, whereas attributing an action to another person activates the right inferior parietal cortex, as shown by Farrer and Frith (2002), who conducted experiments in which participants were asked to use a joystick to drive a circle along a specific path. In one case, they knew they controlled the movement of the circle, so attributed the action to themselves, and the anterior insula was activated; in another case, they knew that the experimenter was actually in control, even though they themselves performed the same action with the joystick, and so they did not attribute the action to themselves. In this case the right inferior parietal cortex was activated. Interestingly, another experiment (Modinos, Ormel, & Aleman 2009) that involved reflecting on oneself or on another person seemed to activate the left occipital. But this experiment did not involve any action on the part of the participants, but only a process of conscious reflection on self and other. So this may not have activated the neural circuits directly concerned with the experience of agency, but rather those concerned with self-awareness, so the distinction between a sense of self (the Jamesian Me) and self-agency (the Jamesian I) may be reflected in these neurobiological findings.

But the experience of agency depends not only on the impact one has on the other, but also on the capacity to self-regulate one’s own emotional and bodily states. The psychological regulatory structures described by self psychology originate in the right hemispheric specialization in regulating stress and emotion-related processes (Sullivan & Dufresne, 2006). Indeed, the brain’s major self-regulatory systems are located in the orbital prefrontal areas of the right hemisphere (Bradshaw & Schore, 2007). Schore (1994) marshalled a wealth of evidence to support the view that the experience-dependent maturation of this affect regulatory system is thus directly related to the origin of the self and that the right hemisphere is specialized for generating self-awareness and self-recognition, and for the processing of “self-related material” (Miller et al., 2001).

Can These Three Models Be Integrated Into a Coherent Neurobiological Account of the Development of Self-Agency?

Each of these areas of research investigates a different aspect of self and of self-agency. Mirror neuron researchers study the role of motor simulation as the basis for a sense of embodied self. Panksepp and his colleagues examined the midline subcortical and cortical systems that create an emotional core SELF, while Allan Schore and colleagues placed the development of the right brain at the heart of the relational self from the first moments of life.

This brings me to the key question: To what extent do these networks become integrated during development, to contribute to a sense of self and of self-agency? There are, as yet, few articles that offer such integrative models, but there are some references to the issue of integration in some of the research I have already cited. For example, Biven and Panksepp (2007, p. 142) took up the point that I emphasized earlier in this chapter, that the mirror neuron-based intentional action chains, described by Fogassi et al. (2005), may not be hardwired (genetically
determined) but may be developmentally programmed by the midline 
subcortical systems—the SCMS described by Panksepp—that control
attentional and emotional arousal. This would be in keeping with the 
epigentic and emergent view of psychological development, for which I
described the detailed and overwhelming evidence in Chapter 1.

Once a connection between midline and mirror neuron networks 
has been established by such developmental processes, there is the possibility 
for the influence to be reciprocal. So not only can the SCMS entrain
mirror neuron intentional chains, the mirror neuron system can directly 
affect the CMS that activate the core-SELF emotional networks. The
fact that there are direct neural connections between these two systems 
is also described by Carr et al. (2003), whose research showed that both
observation and imitation of the facial expression of emotions activated
ventral premotor cortex (part of the MNS) and also the insula and the
amygdala (part of the limbic system). So the superior temporal and inferior
frontal cortices, which are critical areas for action representation,
are connected to the limbic system via the insula. Thus, the insula may
be a critical relay from the mirror neuron system to the SCMS, and so
from action representation to emotion.

Modinos et al. (2009) also highlighted the importance of the insula
in self-reflection and generally in self-referential processing, including
interoceptive awareness, and awareness of subjective feeling and
bodily arousal states. They suggested that insular activity could actually
be related to an emotional component that might be inherent to
self-processing; in other words, to the self being an emotional entity per
se, since emotion almost always involves consciously or unconsciously
evaluating an event as relevant to a person’s concerns or goals:

Taken together, this evidence supports the notion that the
insula is a supramodal structure, involved in a myriad of processes
closely related to facilitating a sense of self. Disturbances
in insula activity may result in social and emotional impairments
commonly observed in psychopathology, as recently suggested by
a study showing differential insula involvement in the failure to
maintain adequate social interactions by people with Borderline Personality Disorder. (Modinos et al., 2009, e4618)

These social and psychological aspects of the development of agency
may also depend on the activity of cortical midline and right brain
structures, such as the anterior cingulate and the orbitofrontal cortex.
Allan Schore (2001), in particular, has described in detail how early relational
experience with an empathic attuned caregiver allows the regulatory functions of the orbitofrontal cortex to impact on the limbic
and subcortical midline systems that govern the experience of emotion.
Schore regards the links between cortex, especially the right orbitofrontal
cortex, and subcortical systems as crucial:

In its critical period the orbitofrontal areas are synaptically connected
with other areas of the cerebral cortex, but they are also
forging contacts with subcortical areas. And so the orbitofrontal
cortex is a “convergence zone” where cortex and subcortex meet.
(2001, p. 224)

He highlights how vulnerable this system is to adverse relational experiences, in that early trauma or neglect induces excessive pruning of cortical-subcortical limbic-autonomic circuits. This severe growth impairment creates a developmental structural defect in limbic system organization. This has significant implications not only in terms of damage to the individual’s maturing stress coping systems, but also for
the development of self-agency, because, as I have indicated, self-agency
develops out of an active process of exploration, through processes such
as turn-taking, in relationship. At a neurobiological level, self-agency
can be thought of as an aspect of the SEEKING system of the core-
SELF and SCMS that Panksepp described. So if the cortical-subcortical
connections are severely impaired, relationships can no longer stimulate
the primordial motive systems to attach, which are located in subcortical
components of the limbic system.

These brainstem neuromodulatory and hypothalamic neuroendocrine systems that regulate the HPA axis are in a critical period
of growth pre- and postnatally, and they regulate the maturation of the later developing cerebral cortex. . . . severe attach-
ment problems with the caregiver negatively impact the postnatal development of these biogenic amine systems. (Schore, 2001, p.
207)

It is precisely this kind of damage to the attachment and SEEKING neural systems that may underpin some of the clinical phenomena,
which center on a profound inhibition of self-agency in relationships and which I describe in Part II.

The orbitofrontal cortex is not only where the cortex and subcortex meet, but also a convergence zone where the external and internal worlds meet, primarily through the relationship with the primary caregiver in infancy. So the role of the right brain and the development of the relational self is another central component of the integration of the three perspectives on the self that I am focusing on in this chapter. Schore emphasized that caregiver-induced trauma is qualitatively and quantitatively more potentially psychopathogenic than any other social or physical stressor because the immature infant’s brain is utterly dependent on the primary caregiver for stress regulation:

The stress regulating systems that integrate mind and body are a product of developing limbic-autonomic circuits (Rinaman, LeVitt, & Card, 2000), and because their maturation is experience dependent, during their critical period of organization they are vulnerable to relational trauma. (2001, p. 207)

When the caregiver fails to regulate the infant’s distress, this leads to a blunting of the stress response in the right (and not left) prefrontal cortex, and these interruptions of early cortical development specifically affect limbic association areas and social behavior (Talamini, Koch, Luiten, Koolhaas, & Korf, 1999). So, in human infancy, relational trauma interferes with the experience-dependent maturation of the brain’s coping systems, and therefore has a long-enduring negative impact on the trajectory of developmental processes, including that of self-agency. Clinical descriptions of the long-term impact of relational trauma on the development of self-agency follow in Part II.

In a comprehensive overview of the links between the three neural networks, in the article I cited at the start of this chapter, Uddin et al. (2007) proposed a unifying model that links the right brain, the MNS, and the CMS in representing the self. They supported Schore’s view of the importance of the right hemisphere for a sense of self, emphasizing “that a network of right frontoparietal structures is vital for generating self-awareness” (2007, p. 153), but also pointed out that these frontoparietal areas involved in self-recognition significantly overlap with areas that contain mirror neurons. They went on to 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. (Uddin et al., 2007, p. 154)

Uddin et al. went on to amplify this account of the CMS, by describing its role in maintaining social and psychological aspects of the self, which involve evaluative processes, such as self-referential judgments and self-appraisal. These CMS areas are also involved in other social tasks, such as processing social relationships, which require an understanding of others’ mental states, so, in effect, acting as a constant monitor of the self in a social context, a form of evaluative simulation comparable to the motor simulation of the MNS.

They pointed out that the existence of direct connections between the precuneus, which is a major node in the CMS, and the inferior parietal lobe, part of the MNS, suggests that this is one pathway by which the two networks may interact and coordinate their activity. There are also connections between the mesial frontal areas and the inferior frontal gyrus (Rizzolatti & Luppino, 2001). Uddin et al. concluded:

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. (2007, p. 156)

I discuss imagination more fully in Chapter 4, examining the part it plays in the developmental trajectory of self-agency from bodily action to emotional and mental expression. But to understand why imagination is so important from a neuroscientific and developmental perspective, I first need to introduce a fairly recent discovery in neuroscience, the default network, which Uddin et al. regarded as critically important to the processes by which the brain integrates memories, emotions, and self-experience.
The Default Network

The default network is a network of brain areas comprising the posterior cingulate and precuneus, anterior cingulate and medial prefrontal cortex, and temporoparietal junctions, which show more metabolic activity when the brain is at rest than during attention-demanding and goal-directed tasks, consuming 30% more calories for its weight than any other area of the brain (Raichle et al., 2001).

Buckner, Andrews-Hanna, and Schacter describe the multiple functions of the default network:

The default network is active when individuals are engaged in internally focused tasks including autobiographical memory retrieval, envisioning the future, and conceiving the perspectives of others. Probing the functional anatomy of the network in detail reveals that it is best understood as multiple interacting subsystems. The medial temporal lobe subsystem provides information from prior experiences in the form of memories and associations that are the building blocks of mental simulation. The medial prefrontal subsystem facilitates the flexible use of this information during the construction of self-relevant mental simulations. These two subsystems converge on important nodes of integration including the posterior cingulate cortex. (2008, p. 1)

Put together, these suggest that the default network might provide the brain with an inner rehearsal for considering future actions and choices. At first this was considered to be the mechanism for daydreaming but, in 2008, Michael Greicius found that there are resting state fluctuations in the default network—slow waves of neural activity that ripple through a coordinated fashion, linking its component brain areas into a coherent unit. The waves were up to 100 times slower than typical EEG brain-waves. These synchronized waves were found in both sedated humans and in early sleep, thus refuting the idea that they are only involved in conscious daydreaming (Greicius et al., 2008). Researchers now believe that the default network is central to the process of selectively storing and updating memories based on their importance from a personal perspective and their emotional quality. To prevent a backlog of unstored memories building up, the network is constantly communicating with the hippocampus and returns to its sorting process whenever the brain is not engaged in an active task.

Northoff and Panksepp also emphasized the importance of the default network in self-related processing (SRP), suggesting that high degrees of self-relatedness and emotional processing correspond to high resting-state neuronal activity, particularly in the subcortical and cortical midline regions, which are part of the default network:

The resting state is characterized by a predominance of interoceptive and affective processing with exteroceptive input remaining almost absent so that only the former, but not the latter, is related to current goal-orientation in self-related processing during the resting state. (2008, p. 262)

In the article referred to earlier, Uddin et al. (2007, p. 155) also pointed out that the CMS forms part of the default network and that it is likely that one function of the default network is to act as a constant monitor of
the self and its social relationships. Imagination is attracting increasing attention from neuroscience researchers and it is the activity of imagining that seems to integrate the different neural networks that contribute to the psychological expression of self-agency.

In the next chapter I examine the developmental and neurobiological processes that contribute to the developmental trajectory of self-agency, from its earliest expression through action to the mature experience of agency in mental processes such as imagination and symbolic thought.

In Chapter 3, one of the areas of research I described was the role that mirror neurons play in action understanding. In essence, it is through our own physical experience of agency that we intuitively understand the actions of other people, even though this understanding is not at all under conscious control. It might be called a kind of procedural knowledge, based on an instantaneous and automatic mapping of the other person's actions onto our own motor action sequences, which are activated when we see the other person's actions. This kind of direct mirroring also applies to emotional experiences, in that another person's facial expression of an emotion has been shown to activate the same neuronal pathways as those that fire when we experience the emotion ourselves (Rizzolatti & Sinaglia, 2008; Wicker et al., 2003). So this kind of direct neuronal mirroring of another's action or emotion seems to be one of the key neurobiological processes that underpins the experience of self-agency at the physical level, which depends on the highly contingent and unconscious, automatic response our own actions (including facial expressions) produce from the other person, right from the earliest moments of life (Meltzoff & Gopnik, 1993).

But human relationships are based on much more than automatic imitation and action understanding, or even the direct mirroring of emotional experience. Decety and Meyer have carefully differentiated imitation from empathy and have summarized the neuroscience of both of these, showing that both play an important role in the development of agency. They suggested that imitation is not a simple matching mechanism, but a complex construct involving a number of different processes, such as "perception-action coupling, visual attention, short-term
The field of mental health is in a tremendously exciting period of growth and conceptual reorganization. Independent findings from a variety of scientific endeavors are converging in an interdisciplinary view of the mind and mental well-being. An interpersonal neurobiology of human development enables us to understand that the structure and function of the mind and brain are shaped by experiences, especially those involving emotional relationships.

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