

Understanding the self: a cultural neuroscience approach

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Abstract: The self has been addressed extensively by philosophers and psychologists from different cultures. Recent cognitive neuroscience studies have uncovered neural substrates underlying the processing of different aspects of the self. As social psychologists have shown evidence for differences in self-construal styles between Western and East Asian cultures, recent transcultural neuroimaging research sought to find potential neural mechanisms mediating cultural specific self-related processing. The findings of transcultural neuroimaging research help to understand the culture-dependent nature of the self and its underlying neural substrates. This also sheds light on how to conceptualize the self in psychological and philosophical terms.

Keywords: culture; neuroimaging; self; medial prefrontal cortex

Introduction

Understanding the self has been one of the most salient problems throughout the history of philosophy and psychology (Gallagher, 2000; Northoff, 2004; Zhu and Han, 2008). For example, William James distinguished between a physical self, a mental self, and a spiritual self. These distinctions seem to reappear in recent self-concepts discussed in neuroscience. Damasio (1999) and Panksepp (1998; 2003) suggest a “proto-self” in the sensory and motor domains, respectively, which resembles James’s description of the physical self. Similarly,

what has been described as the “minimal self” (Gallagher, 2000) or “core or mental self” (Damasio, 1999) might correspond more or less to James’ concept of mental self. Finally, Damasio’s (1999) “autobiographical self” and Gallagher’s (2000) “narrative self” strongly rely on linking past, present, and future events with some resemblances to James’ spiritual self.

The distinct self-concepts differ in the class of stimuli and their specific material or content reflecting what is called different domains. The “proto-self” refers to the domain of the body whereas the “autobiographical self” reflects the domain of memory. Other self-concepts like the emotional self (Fossati et al., 2003), the spatial self (Vogeley and Fink, 2003), the facial self (Keenan and Nelson, 2001), the verbal or interpreting self (Turk et al., 2003), and the social self (Frith and Frith, 1999, 2003) refer to further domains. Recent neuroimaging research of neural correlates of self

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highlights the role of cortical midline structures (CMS) in self-related processing (Northoff and Bermpohl, 2004; Northoff et al., 2006). Most of the imaging studies implicitly presuppose a concept of the self as self-consciousness or self-awareness (see Gusnard et al., 2001; McKiernan et al., 2006). Various tasks applied in these studies required subjects to make explicit reference to some aspects of themselves and to consciously access and monitor representational content about one's self, that is, conducting self-referential processing. Self-referential processing consists of consciousness or awareness of the self and is supposed to involve higher-order cognitive function, out of which the self emerges at the pinnacle of the psychological and neural hierarchy. At the philosophical level, such higher-order view of self-referential processing corresponds to predominantly cognitive and higher-order accounts of the self. The characterization of the self as higher-order cognitive function is however not compatible with the alleged domain-independence of the self. Our recent meta-analysis showed that self-related processing remains domain-independent, that is, occurring across various domains, be it verbal, facial, spatial, or even sensorimotor, each time recruiting the CMS (Northoff et al., 2006). If so, the self cannot be characterized as higher-order cognitive functions because then one would expect no occurrence of the self in the lower-order domain of sensorimotor functions.

What, however, is self-related processing? We assume that self-related processing provides a special code, format, or mode by means of which sensory, emotional, or cognitive stimuli become oriented toward and associated with the respective person. This may be tested empirically by investigating the relationship between self-relatedness and sensory processing. We would postulate that the latter is guided implicitly by the former. What does this imply for the concept of the self? If self-related processing is indeed a special kind of format or code, self-related processing should be implicated in all kinds of processing in a very basic sense rather than emerging as higher-order cognitive or meta-cognitive function at the pinnacle. If this is true, self-relatedness codes, formats, and consecutively

determines the mode in which all incoming stimuli, be they extero- or interoceptive, are processed by our brain. Though we can seemingly not escape from self-relatedness, we are apparently at least able to modulate our reactivity toward it by means of cognitive modulation. Cognitive modulation allows us to distance ourselves from our own self by, for example, self-awareness or self-consciousness where one takes an observing or analytical perspective (rather than an experiential one) on one's self. Self-relatedness can then no longer be regarded as the output of some higher-order cognitive function but rather the input to the latter that aims to control and modulate it. In this case, self-relatedness is no longer higher-order function among others like working memory, attention, etc., but rather a very basic function that predisposes and determines higher-order functions.

This characterization of self-relatedness as basic formatting and organizing functions entails the following empirical predictions. First, one would expect close relationship between self-related processing and social processing, since self-relatedness should then modulate and impact all incoming stimuli from the social environment. Second, one would expect neural overlap between self and other with both no longer mutually exclusive and contradicting each other with regard to their neural correlates. Third, self-related processing as basic and formatting function should occur in an implicit and automatic mode. Indeed, these features of self-related processing have been well observed in recent transcultural neuroimaging research.

Because the self of each individual develops in a specific sociocultural context, it may undergo strong modulations of social contexts and cultural values and formulate a particular style to adjust the way to efficiently interact with other individuals in social environments. Indeed, social and cultural psychologists have shown ample evidence for cultural difference in the self and self-related processing (Markus and Kitayama, 1991; Zhu and Han, 2008). The findings of social and cultural psychology raise further interesting questions of whether neural representation of the self and neural substrates of self-related processing are

shaped by socio-cultural contexts. Moreover, as the self can be divided into different domains, one would further expect to observe cultural influence on neural substrates linked to different domains of the self such as high-level self-trait processing and low-level self-face recognition in an implicit and automatic fashion. Research along this line has stimulated the emergence of cultural neuroscience (Chiao and Ambady, 2007; Han and Northoff, 2008).

In this paper, we first review neuroimaging findings regarding the neural substrates underlying different domains of the self. We then present recent transcultural neuroimaging studies that have shown preliminary evidence for cultural influences on neural mechanisms of self-related processing. We finally discuss how the neuroimaging observations help us to conceptualize the self in psychological and philosophical terms.

Neural correlates of self-related processing

Neuroanatomy of self-relatedness and social processing

The last decade has witnessed an increasing number of functional neuroimaging studies focusing on self-related processing or self-referential processing (Phan et al., 2004; Craik et al., 1999; Kelley et al., 2002; Turk et al., 2003; Northoff and Bermpohl, 2004). A recent meta-analysis of imaging studies on the self demonstrated an involvement of medial cortical regions in self-related tasks across different domains (motor, emotional, memory, verbal, spatial, facial, and social) (see Northoff et al., 2006). Results from neuroimaging studies indicate that the more anterior medial prefrontal cortex (MPFC) is implicated in the self function and consists of Brodmann areas (BAs) 9 and 10 (medial regions), 24, 25, and 32, with 11 and 14 in the medial orbital cortex. In addition, the more posterior (caudal) regions are also involved in the self function, specifically the posterior cingulate (PCC), precuneus, and retrosplenial regions. The more anterior dorsal regions, in particular the dorsal MPFC (DMPFC), have been activated in many

studies on the self, which include a strong evaluative or judgmental component (e.g., Zysset et al., 2002; Johnson et al., 2002), while the more rostral, ventral regions have been activated in studies that had a self-reflection component (e.g., Seger et al., 2004; Kelley et al., 2002; Lieberman et al., 2004). Finally, the more posterior central midline structures have typically been activated in tasks involving autobiographical memory (e.g., Fink et al., 1996; Piefke et al., 2003). The relationship between the anterior and posterior CMS has also been investigated in a recent PET–TMS study (Lou et al., 2004). Analysis of functional connectivity revealed a significant interaction between the DMPFC, the posterior cingulate, precuneus, as well as other regions (lateral prefrontal, inferior parietal, and middle temporal).

In parallel to the impressive development in the functional neuroanatomy of self-related processing, neuroimaging studies of the processing of social stimuli also developed extensively. The cognitive and emotional processes involved in response to social stimuli have been coined “social cognition,” which includes (among others) knowledge about the self, perceptions of others, and interpersonal motivations. More recently, investigation of the functional neuroanatomy of social cognition has become one of the main streams in social psychology and gave birth to a new interdisciplinary field of social cognitive neuroscience (Ochsner and Lieberman, 2001). The central premise here is that dedicated brain systems have developed to process social stimuli, parallel to the dedicated neurophysiological processes underlying inherently social behaviors such as grooming and cooperation (e.g., Caldji et al., 1998; Rilling et al., 2002). In neuroimaging studies, social cognition has recently been associated with activity in brain regions, such as the MPFC and the anterior cingulate cortex (ACC), the temporo-parietal junction, the superior temporal sulcus, and the temporal poles (Amodio and Frith, 2006).

Converging findings implicate MPFC involvement in both social cognition and self-related processing and provide strong empirical support to our view presented above. If social salience is processed by the MPFC and reflects the relation

between others and oneself, the MPFC should be activated by the processing of oneself and others. This has indeed been the case; MPFC structures have been activated when subjects formed impressions about people as opposed to objects (Mitchell et al., 2005a, b) or observed social interactions between others (Iacoboni et al., 2004; Han et al., 2005). The neuroanatomical convergence of self-relatedness and social cognition is not limited to the MPFC, but can be seen in additional brain regions that have been associated with social cognition and with the self function, like the PCC. The PCC activates with social as compared to more visceral emotions (Britton et al., 2006), but also with self-generated emotions (Damasio et al., 2000), in response to listening to autobiographical scripts (Fink et al., 1996). In addition, studies that have investigated self-referential processing through autobiographical memory (Cabeza et al., 2004), self-association tasks (Phan et al., 2004), and self-related judgments (Johnson et al., 2002; Kelley et al., 2002) have also implicated both the PCC and MPFC. The differential role of rostral versus caudal structures, in determining self-relatedness, remains to be established.

“Self” and “other”

Our conceptualization of self-relatedness offers a different perspective on the question of “self” versus “other.” Traditionally, “self” and “other” were viewed as distinct categories and thus often contrasted in functional neuroimaging research. We however propose that the “other” person is perceived, by the self-relatedness function, on a continuum from self to nonself. Here, the “self” is the extreme end of a spectrum of self-relatedness, and the “other” is on the same continuum but not to the same degree. It is likely tagged as “like-self but not-self,” and thus these two concepts are “tagged” by the same brain regions. The ability to identify conspecifics as “like-self but not-self” allows the organism to define relative relatedness of group members, predict behaviors, develop empathy, share resources, and navigate in complex social environments. In fact, this ability to create an internal “map” of self-relatedness likely

offered a selective advantage during evolution, particularly for species with complex social organizations, and thus became highly complex and evolved in humans.

Imaging studies indeed report an overlap between the processing of the self and others, especially in the DMPFC and ventral MPFC (VMPFC) (Schmitz et al., 2004; Platek et al., 2004; Seger et al., 2004; Beer et al., 2006). However, neural dissociation between the self and others has been observed within the same regions, as well as in other lateral prefrontal, parietal, and temporal cortical regions (Craig, 2002; Kelley et al., 2002; Platek et al., 2004; Seger et al., 2004; Schmitz et al., 2004; Ochsner et al., 2005). How can one reconcile such discrepancy? The key issue here might be the degree of self-relatedness of the other person; the more the other is identified as self-related, the greater the similarity between VMPFC/DMPFC responses to the self and other. Mitchell et al. (2005a, b) who found that the more the similar subjects rated others’ faces to their own, the greater the activation observed in the VMPFC, suggesting that the VMPFC is engaged in viewing others in terms of one’s own self, thus providing support to the simulation theory (see also Mitchell et al., 2006). These empirical data support our notion of a common, self-related processing, underlying both self and other on a self–nonself continuum rather than a self–nonself dichotomy. Conceptually, the distinction between the self and other is not primarily relevant to our brains’ processing, which instead may represent and code a “more primary intersubjectivity” (see also Iacoboni, 2006) in terms of self-likeness.

Self-related processing as implicit and automatic

We assume that self-related information processing does not typically occur on an explicit and consciously aware level, even though it may be rich in affective consciousness (Panksepp, 2007). Instead, it can be either cognitively preconscious or unconscious and thus implicit, but accompanied by experienced shifts in affective feeling states that are prepropositional and hence hard to put into words.

The concept of an automatic self (Koole et al., 2001) has been suggested and characterized by operating automatically at an implicit, cognitively nonreflective level, yielding automaticity in self-evaluation without deliberative thought, often in situations with decreased cognitive control, and commonly associated with positive emotions. Lieberman et al. (2004) further proposed an X-system for the processing of intuition-based implicit and automatic self-knowledge and a C-system for the processing of evidence-based, nonautomatic, conscious self-knowledge. They also showed evidence that the X-system is associated with the VMPFC, nucleus accumbens, and amygdala whereas the C-system is linked to the lateral prefrontal cortex, hippocampus, and posterior parietal cortex.

How are the “implicit and affective forms of selfhood” (we assume these are the nomothetic aspects of the self) and the various “explicit and cognitive forms of selfhood” (the idiographic aspects) related to each other in neurobiological terms? Some studies reported activation (and increased functional connectivity) in anterior and posterior CMS during self-related tasks with low cognitive load (Kjaer et al., 2002; Lou et al., 2004). Conversely, deactivation (and low functional connectivity) in CMS has been observed in tasks with high cognitive load and low degrees of self-relatedness (Gusnard et al., 2001; Kelley et al., 2002). The implicit and explicit aspect of self-related processing may be integrated through the interaction between subcortical and cortical midline regions (Panksepp and Northoff, 2009). Subcortical regions may determine the basic self-relatedness of the organism by coding the relation between different stimuli: interoceptive, exteroceptive, motor, and emotional. This relation is expressed in affective and valuative terms. The resulting “sense of relatedness” may then be further elaborated in cortical midline regions in cognitive and temporal terms. Higher-order cognitive abilities like attention, impulse control, working memory, executive functions, etc., may allow a representation of the “sense of relatedness” on a cognitive or high mental level independent of any actual stimulus. This allows an organism to distinguish one’s “sense of

relatedness” from others’ “sense of relatedness” and thus from the environment, resulting in what we above called the “sense of distinction.”

Cortical midline regions may also regulate the subcortically established “sense of relatedness” temporally. Recent studies in humans indicate that the CMS are involved in both anticipating future events and recollecting past events (Schacter and Addis, 2007). Furthermore, self-relatedness induced delayed signal changes more in CMS than in subcortical structures (Schneidera et al., 2008). Thus, it is likely that CMS may be crucially involved in temporally extending the subcortically processed here-and-now immediacy of self-relatedness. By delaying or anticipating neural activity and dissociating it from the presence of the actual stimulus, CMS may put the already established self-relatedness into a wider temporal context when compared to subcortical regions where it seems to be tied to the actual presence of internal or external stimuli and state-control functions (e.g., basic homeostatic and emotional states).

Cultural influence on neural substrates of self-related processing

Cultural difference in self-referential processing: overlap between the self and close others

Unlike the Western philosophy that often discusses the unique dispositions to define the self or self–other distinctions, East Asian philosophy puts strong emphasis on human connections with each other in social contexts and believes that the highest achievement of a person is the identification of the individual with the universe (Zhu and Han, 2008). The difference in philosophical thinking of the self has influenced greatly the formation of psychological concept of the self. For instance, the Western cultures result in an independent view of the self with a bounded structure that emphasizes unique dispositions or traits of the self that keep invariant across different social contexts, whereas the East Asian cultures produce an interdependent view of the

self with a variable structure that stresses the fundamental connections between the self and others and between the self and social contexts (Markus and Kitayama, 1991). Does such cultural influence extend to the neural substrates underlying the processing of self-related information?

To address this issue, we (Zhu et al., 2007) scanned two cultural groups (i.e., English-speaking Westerners and monolingual Chinese subjects) while they performed trait judgment tasks regarding self and a close other (i.e., mother). Cultural universal neural activity related to the self-referential processing was localized to the MPFC and the anterior ACC by contrasting trait judgment of the self and trait judgment of a public person in both cultural groups. An interesting finding of this work is that, relative to trait judgment of the public person, trait judgment of one's mother also activated the MPFC in Chinese subjects, providing evidence for shared neural structure for representation of both the self and a close other. However, Western subjects did not show increased activation in any brain areas in the contrast of mother-judgment compared to other-judgment. The findings provide the first piece of neuroimaging evidence for cultural difference in the neural structure of the self. Specifically, Chinese individuals use the MPFC to represent both the self and the mother whereas Westerners use the MPFC to represent exclusively the self. Zhu et al.'s (2007) work contrasts with Heatherton et al.'s (2006) observation that MPFC activity failed to differentiate between the self and a close other (i.e., the best friend) in North Americans. However, as there has been no research that compared Chinese self and the best friend, it is unknown whether the neural structure of the Chinese self extends to the degree to include other close persons besides mother.

Cultural values differ between two cultural groups as well as among individuals in a specific cultural group. For example, in one cultural group, some individuals show greater extent of adherence to individualism and independent self whereas others show greater extent of adherence to collectivism and interdependent self (Chiu and Hong, 2006). Can the magnitude of neural activity in the brain area related to self-referential

processing predict individuals' difference in self-construal styles? Chiao et al. (2009) recently scanned Caucasian Americans and Japanese in tasks requiring judgments of general trait descriptions or contextual self descriptions. Moreover, they assessed individuals' degree of endorsement of independent and interdependent self-construals using Self-Construal Scale (Singelis, 1994). While Chiao et al. did not observe significant interaction between cultural groups and different judgment tasks in modulation of MPFC activity, they found positive correlation between MPFC activity differentiating contextual and general trait judgments and the degree of interdependent self-construal style. The results provide further evidence for the influence of cultural values on individuals' neural substrates underlying self-reflective thinking.

While these neuroimaging studies suggest that Western/East Asian cultures result in variation of the contents of the self and the underlying neural activity, other cultural beliefs may strongly modulate the way of thinking of the self. For example, Christianity advocates denial of self or self-transcendence in order to highlight human contingency and dependence on God (Burns, 2003; Ching, 1984). Moreover, Christianity emphasizes judgment of the self from God's perspective rather than from one's own perspective. Since the VMPFC plays a key role in coding self-relatedness of stimuli (Moran et al., 2006; Northoff et al., 2006), Han et al. (2008) predicted that Christian beliefs weaken the process of coding self-relatedness of stimuli and thus induce decreased activity in VMPFC. In addition, taking others' perspective during self-judgment may activate the brain area that is involved in theory-of-mind such as DMPFC. To test these hypotheses, Han et al. (2008) scanned both Chinese nonreligious and Christian subjects in trait judgment tasks associated with self and others. The Christian subjects had been attached to the local faith communities for 1–7 years when participated in the study. While the fMRI results from nonreligious subjects replicated previous findings by showing increased activation in VMPFC during self-judgment relative to other-judgment, a different pattern of the brain imaging

results was observed in Christian subjects. Both ROI and random effect analyses did not show significant activation in the VMPFC when Christian subjects made judgment regarding the self as compared to others. However, there was evidence that the DMPFC activity increased when Christian subjects made trait judgment about the self relative to others. Using bootstrap analysis, Han et al. demonstrated that the distinct pattern of MPFC activity in association with trait judgment of the self (i.e., decreased activity in the VMPFC but increased activity in the DMPFC) can be used to classify the two subject groups well. Since the VMPFC and DMPFC are, respectively, involved in the representation of stimulus self-relevance and the evaluation of self-referential stimuli (Northoff et al., 2006), the findings suggest that adopting Christian beliefs may result in weakened neural encoding of stimulus self-relatedness but may enhance neural activity in areas that mediate the evaluative process applied to self-referential stimuli.

Cultural difference in neurocognitive processing of self-recognition: implicit and automatic processing of the self

Another important aspect of self-processing is self-face recognition, that is, to recognize oneself in a mirror, which has been proposed to reflect the ability to become the object of one's own attention (Gallup, 1970) and to be an indicator of high-level self-awareness (Keenan et al., 2000). A number of neuroimaging studies have investigated the cortical underpinnings of self-recognition by comparing neural activity in association with one's own face and faces of other individuals. The accumulating evidence suggests that a distributed network consisting of the fusiform gyrus, middle and inferior frontal gyrus, and precuneus is involved in self-face recognition when compared with recognition of faces of other individuals (Platek et al., 2008). While both Westerners and East Asians were recruited in the previous research of self-recognition, there has been no research exploring potential cultural difference in neural mechanism underlying self-recognition. However, given the Western/East Asian cultural

difference in self-construal styles (Markus and Kitayama, 1991) and the consequent cultural modulation of neural substrates of self-referential processing (Zhu et al., 2007; Chiao et al., 2009), one would expect similar cultural influence on the neural mechanisms of self-recognition. Specifically, the Western independent self may assign greater social salience or positive association with one's own face than to others' faces (Ma and Han, in press), which in turn results in stronger attention to one's own face when presented among others' faces and induce deeper processing of the own-face. In contrast, as the East Asian interdependent self emphasizes social connections between the self and others, enhanced processing of one's own face may not be as strong as that in Westerners.

To test this hypothesis, we (Sui et al., 2009) recently recorded event-related potentials from British and Chinese subjects while they judged head orientations of their own face or a familiar face in visual displays. We first observed faster responses to one's own face relative to the familiar face in both cultural groups. However, the self-advantage in behavioral performances was greater for British than for Chinese subjects, suggesting that the own-face captures attention to a larger degree in the British than in Chinese. More interestingly, the pattern of the ERP results showed a reverse pattern in the two cultural groups. We found that one's own face elicited a larger negative activity at 280–340 ms over the frontal–central area (N2) relative to the familiar face in the British. In contrast, the Chinese showed weakened self-advantage in behavioral responses and reduced anterior N2 amplitude to the own-face compared with the familiar face. The frontal–central N2 component is sensitive to perceptual salience of stimuli (Folstein and Petten, 2008). The N2 is also involved in differentiation between different facial expressions (Kubota and Ito, 2007) and between faces of different races (Ito and Urland, 2003), suggesting that the N2 is associated with deeper processing of faces to benefit individuating. Thus, the reverse pattern of the N2 results in the cultural groups suggests that the independent self-construals endow the own-face with higher social

significance relative to familiar faces whereas the interdependent self-construals may assign higher salience to familiar faces.

To further explore the potential cause–effect relation between self-construals and self-recognition, we (Sui and Han, 2007) scanned Chinese subjects while they performed an implicit face recognition task that required judgments of orientations of one’s own face or a familiar face. The contrast between the two judgment tasks revealed the effect of implicit recognition of the own face. However, subjects were primed before the face recognition task with either independent or interdependent construals (Gardner et al., 1999) by marking independent (e.g., I, mine) or interdependent (e.g., we, ours) pronouns in an essay. We found that the neural activity in the right middle frontal cortex increased to the self-face than familiar faces. In addition, the right frontal activity differentiating between the self and familiar faces was enlarged by the independent relative to interdependent self-construal priming. The increased right frontal activity was associated with faster responses to self than familiar faces. The findings suggest that shifts of self-construal styles induced modulation of neural underpinnings of self-face recognition that is supposed to reflect self-awareness and thus provide preliminary evidence for the interplay between self-construals and the neural substrates underlying self-face recognition. The findings support the view that the influence of cultural differences on self-concept may extend beyond the processing of personal trait and modify the neural mechanism underlying the processing of the physical self (e.g., face). As mentioned above, the CMS plays a pivotal role in self-processing. A challenge for future research is to uncover the way the neural activity in the CMS interacts with the activity in other cortical areas in a specific sociocultural context and thus results in cultural specific neural underpinnings of cognitive processes.

Conclusion

Recent neuroimaging studies have shown strong evidence that humans evolve neural mechanisms

mediating self-related processing that encode the strength of stimulus’s relation to the self and to environmental contexts. In addition, as the strength of the self-stimulus relation emerges gradually through learning during development, the neural substrates underlying self-referential processing are strongly influenced by socio-cultural contexts. Culture-specific neural mechanisms afford unique self-concepts or self-construal styles that help individuals to adapt to the accompanying cultural and social environments so that individuals can function efficiently during social interactions. The transcultural neuroimaging findings of culturally distinct neural representations of the self help to understand the nature of self-construals and the social significance of self-related stimuli and their implicit and automatic processing. The findings also assist in understanding how others in different cultures are represented in terms of the relation to the self, indicating that the self–other relationship is highly flexible in its neural manifestation and dependent on the social context.

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References

- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Review Neuroscience*, *7*, 268–277.
- Beer, J. S., John, O. P., Scabini, D., & Knight, R. T. (2006). Orbitofrontal cortex and social behavior: Integrating self-monitoring and emotion-cognition interactions. *Journal of Cognitive Neuroscience*, *18*, 871–879.
- Britton, J. C., Phan, K. L., Taylor, S. F., Welsh, R. C., Berridge, K. C., & Liberzon, I. (2006). Neural correlates of social and nonsocial emotions: An fMRI study. *NeuroImage*, *31*, 397–409.
- Burns, C. (2003). “Soul-less” Christianity and the Buddhist empirical self: Buddhist-Christian Convergence? *Buddhist-Christian Studies*, *23*, 87–100.

- Cabeza, R., Prince, S. E., Daselaar, S. M., Greenberg, D. L., Budde, M., Dolcos, F., et al. (2004). Brain activity during episodic retrieval of autobiographical and laboratory events: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 1583–1594.
- Caldji, C., Tannenbaum, B., Sharma, S., Francis, D., Plotsky, P. M., & Meaney, M. J. (1998). Maternal care during infancy regulates the development of neural systems mediating the expression of fearfulness in the rat. *Proceedings of the National Academy of Sciences of the United States of America*, *95*, 5335–5340.
- Chiao, J. Y., & Ambady, N. (2007). Cultural neuroscience: Parsing universality and diversity across levels of analysis. In S. Kitayama & D. Cohen (Eds.), *Handbook of cultural psychology* (pp. 237–254). New York: Guilford Press.
- Chiao, J. Y., Harada, T., Komeda, H., Zhang, L., Mano, Y., Saito, D. N., et al. (2009). Neural basis of individualistic and collectivistic views of self. *Human Brain Mapping*, *30*, 2813–2829.
- Ching, J. (1984). Paradigms of the self in Buddhism and Christianity. *Buddhist-Christian Studies*, *4*, 31–50.
- Chiu, C. Y., & Hong, Y. Y. (2006). *Social psychology of culture*. New York: Psychology Press.
- Craig, A. D. (2002). How do you feel? Interoception: The sense of the physiological condition of the body. *Nature Review Neuroscience*, *3*, 655–666.
- Craik, F. I. M., Moroz, T. M., Moscovitch, M., Stuss, D. T., Winocur, G., Tulving, E., et al. (1999). In search of the self: A positron emission tomography study. *Psychological Science*, *10*, 26–34.
- Damasio, A. (1999). *The feeling of what happens: Body and emotion in the making of consciousness*. Harcourt Brace.
- Damasio, A. R., Grabowski, T. J., Bechara, A., Damasio, H., Ponto, L. L., Parvizi, J., et al. (2000). Subcortical and cortical brain activity during the feeling of self-generated emotions. *Nature Neuroscience*, *3*, 1049–1056.
- Fink, G. R., Markowitsch, H. J., Reinkemeier, M., Bruckbauer, T., Kessler, J., & Heiss, W. D. (1996). Cerebral representation of one's own past: Neural networks involved in autobiographical memory. *Journal of Neuroscience*, *16*, 4275–4282.
- Fossati, P., Hevenor, S. J., Graham, S. J., Grady, C., Keightley, M. L., Craik, F., et al. (2003). In search of the emotional self: An fMRI study using positive and negative emotional words. *American Journal of Psychiatry*, *160*, 1938–1945.
- Frith, C. D., & Frith, U. (1999). Interacting minds — A biological basis. *Science*, *286*, 1692–1695.
- Frith, U., & Frith, C. D. (2003). Development and neurophysiology of mentalizing. *Philosophical Transactions of the Royal Society, B*, *358*, 459–473.
- Folstein, J. R., & Petten, C. V. (2008). Influence of cognitive control and mismatch on the N2 component of the ERP: A review. *Psychophysiology*, *45*, 152–170.
- Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Sciences*, *4*, 14–21.
- Gallup, G. G. (1970). Chimpanzees: Self-recognition. *Science*, *167*, 86–87.
- Gardner, W. L., Gabriel, S., & Lee, A. Y. (1999). “I” value freedom, but “we” value relationships: Self-construal priming mirrors cultural differences in judgment. *Psychological Science*, *10*, 321–326.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 4259–4264.
- Han, S., Jiang, Y., Humphreys, G. W., Zhou, T., & Cai, P. (2005). Distinct neural substrates for the perception of real and virtual visual worlds. *NeuroImage*, *24*, 928–935.
- Han, S., Mao, L., Gu, X., Zhu, Y., Ge, J., & Ma, Y. (2008). Neural consequences of religious belief on self-referential processing. *Social Neuroscience*, *3*, 1–15.
- Han, S., & Northoff, G. (2008). Culture-sensitive neural substrates of human cognition: A transcultural neuroimaging approach. *Nature Review Neuroscience*, *9*, 646–654.
- Heatherton, T. F., Wyland, C. L., Macrae, C. N., Demos, K. E., Denny, B. T., & Keley, W. M. (2006). Medial prefrontal activity differentiates self from close others. *Social and Cognitive Affective Neuroscience*, *1*, 18–25.
- Iacoboni, M. (2006). Failure to deactivate in autism: The co-constitution of self and other. *Trends in Cognitive Sciences*, *10*, 431–433.
- Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., et al. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *NeuroImage*, *21*, 1167–1173.
- Ito, T. A., & Urland, G. R. (2003). Race and gender on the brain: Electrocortical measures of attention to the race and gender of multiply categorizable individuals. *Journal of Personality and Social Psychology*, *85*, 616–626.
- Johnson, S. C., Baxter, L. C., Wilder, L. S., Pipe, J. G., Heiserman, J. E., & Prigatano, G. P. (2002). Neural correlates of self-reflection. *Brain*, *125*, 1808–1814.
- Keenan, J. P., & Nelson, A. (2001). Self-recognition and the right hemisphere. *Nature*, *409*, 305.
- Keenan, J. P., Wheeler, M. A., Gallup, G. G., & Pascual-Leone, A. (2000). Self-recognition and the right prefrontal cortex. *Trends in Cognitive Sciences*, *4*, 338–344.
- Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*, 785–794.
- Kjaer, T. W., Nowak, M., & Lou, H. C. (2002). Reflective self-awareness and conscious states: PET evidence for a common midline parietofrontal core. *NeuroImage*, *17*, 1080–1086.
- Koole, S. L., Dijksterhuis, A., & van Knippenberg, A. (2001). What's in a name: Implicit self-esteem and the automatic self. *Journal of Personality and Social Psychology*, *80*, 669–685.
- Kubota, J. T., & Ito, T. A. (2007). Multiple cues in social perception: The time course of processing race and facial expression. *Journal of Experimental Social Psychology*, *43*, 738–752.
- Lieberman, M. D., Jarcho, J. M., & Satpute, A. B. (2004). Evidence-based and intuition-based self-knowledge: An

- fMRI study. *Journal of Personality and Social Psychology*, 87, 421–435.
- Lou, H. C., Luber, B., Crupain, M., Keenan, J. P., Nwak, M., Kjaer, T. W., et al. (2004). Parietal cortex and representation of the mental self. *Proceedings of National Academy of Sciences of the United States of America*, 101, 6827–6832.
- Ma, Y., & Han, S. (in press). Why respond faster to the self than others? An implicit positive association theory of self advantage during implicit face recognition. *Journal of Experimental Psychology: Human Perception and Performance*.
- Markus, H. R., & Kitayama, S. (1991). Culture and the self: Implication for cognition, emotion and motivation. *Psychological Review*, 98, 224–253.
- McKiernan, K. A., D'Angelo, B. R., Kaufman, J. N., & Binder, J. R. (2006). Interrupting the "stream of consciousness": An fMRI investigation. *NeuroImage*, 29, 1185–1191.
- Mitchell, J. P., Banaji, M. R., & Macrae, C. N. (2005a). The link between social cognition and self-referential thought in the medial prefrontal cortex. *Journal of Cognitive Neuroscience*, 17, 1306–1315.
- Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, 50, 655–663.
- Mitchell, J. P., Neil Macrae, C., & Banaji, M. R. (2005b). Forming impressions of people versus inanimate objects: Social-cognitive processing in the medial prefrontal cortex. *NeuroImage*, 26, 251–257.
- Moran, J. M., Macrae, C. N., Heatherton, T. F., Wyland, C. L., & Kelley, W. M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience*, 18, 1586–1594.
- Northoff, G. (2004). *Philosophy of the brain. The brain problem*. Amsterdam: John Benjamins Publishing.
- Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Science*, 8, 102–107.
- Northoff, G., Heinzel, A., de Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain – A meta-analysis of imaging studies on the self. *NeuroImage*, 31, 440–457.
- Ochsner, K. N., Beer, B. S., Robertson, E. R., Cooper, J. C., Gabrieli, J. D. E., Kihlstrom, J. F., et al. (2005). The neural correlates of direct and reflected self-knowledge. *NeuroImage*, 28, 797–814.
- Ochsner, K. N., & Lieberman, M. D. (2001). The emergence of social cognitive neuroscience. *American Psychologist*, 56, 717–734.
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. Oxford University.
- Panksepp, J. (2003). At the interface of the affective, behavioral, and cognitive neurosciences: Decoding the emotional feelings of the brain. *Brain and Cognition*, 52, 4–14.
- Panksepp, J. (2007). Neurologizing the psychology of affects: How appraisal-based constructivism and basic emotion theory can coexist. *Perspectives on Psychological Science*, 2, 281–296.
- Panksepp, J., & Northoff, G. (2009). The trans-species core SELF: The emergence of active cultural and neuroecological agents through self-related processing within subcortical-cortical midline networks. *Consciousness and Cognition*, 18(1), 193–215.
- Phan, K. L., Taylor, S. F., Welsh, R. C., Ho, S. H., Britton, J. C., & Liberzon, I. (2004). Neural correlates of individual ratings of emotional salience: A trial-related fMRI study. *NeuroImage*, 21, 768–780.
- Piefke, M., Weiss, P. H., Zilles, K., Markowitsch, H. J., & Fink, G. R. (2003). Differential remoteness and emotional tone modulate the neural correlates of autobiographical memory. *Brain*, 126, 650–668.
- Platek, S. M., Keenan, J. P., Gallup, G. G., & Mohamed, F. B. (2004). Where am I? The neurological correlates of self and other. *Cognitive Brain Research*, 19, 114–122.
- Platek, S. M., Wathne, K., Tierney, N. G., & Thomson, J. W. (2008). Neural correlates of self-face recognition: An effect-location meta-analysis. *Brain Research*, 1232, 173–184.
- Rilling, J., Gutman, D., Zeh, T., Pagnoni, G., Berns, G., & Kilts, C. (2002). A neural basis for social cooperation. *Neuron*, 35, 395–405.
- Schacter, D. L., & Addis, D. R. (2007). The cognitive neuroscience of constructive memory: Remembering the past and imagining the future. *Philosophical Transactions of the Royal Society, B*, 362, 773–786.
- Schmitz, T. W., Kawahara-Baccus, T. N., & Johnson, S. C. (2004). Metacognitive evaluation, self-relevance, and the right prefrontal cortex. *NeuroImage*, 22, 941–947.
- Schneidera, F., Bermpohl, F., Heinzl, A., Rotted, M., Waltera, M., Tempelmann, C., et al. (2008). The resting brain and our self: Self-relatedness modulates resting state neural activity in cortical midline structures. *Neuroscience*, 157, 120–131.
- Seger, C. A., Stone, M., & Keenan, J. P. (2004). Cortical activations during judgments about the self and an other person. *Neuropsychologia*, 42, 1168–1177.
- Sui, J., & Han, S. (2007). Self-construal priming modulates neural substrates of self-awareness. *Psychological Science*, 18, 861–866.
- Sui, J., Liu, C., & Han, S. (2009). Cultural difference in neural mechanisms of self-recognition. *Social Neuroscience*.
- Turk, D. J., Heatherton, T. F., Macrae, C. N., Kelley, W. M., & Gazzaniga, M. S. (2003). Out of contact, out of mind: the distributed nature of the self. *Annals of the New York Academy of Sciences*, 1001, 65–78.
- Singelis, T. M. (1994). The measurement of independent and interdependent self-construals. *Personality and Social Psychology Bulletin*, 20, 580–591.
- Vogel, K., & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Sciences*, 7, 38–42.
- Zhu, Y., & Han, S. (2008). Cultural differences in the self: From philosophy to psychology and neuroscience. *Social and Personality Psychology Compass*, 2, 1799–1811.
- Zhu, Y., Zhang, L., Fan, J., & Han, S. (2007). Neural basis of cultural influence on self-representation. *NeuroImage*, 34, 1310–1316.
- Zysset, S., Huber, O., Ferstl, E., & von Cramon, D. Y. (2002). The anterior frontomedian cortex and evaluative judgment: An fMRI study. *NeuroImage*, 15, 983–991.