Out of Contact, Out of Mind

The Distributed Nature of the Self

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ABSTRACT: A truly remarkable aspect of human existence is the unitary sense of self that exists across time and place. Understanding the nature of self—what it is and what it does—has challenged scholars since antiquity. How can empirical research measure what it is to have a sense of self? We propose that the sense of self may emerge from the functions of a left hemisphere "interpreter" (Gazzaniga, 2000). First, we examine evidence for the existence of self-processing mechanisms in the intact brain, from behavioral and functional neuroimaging research. The available evidence suggests that the sense of self is widely distributed throughout the brain. Second, we discuss these findings in relation to what is known about higher cognitive functions in humans who have undergone a surgical procedure to sever the connection between the two cerebral hemispheres. Split-brain research has facilitated an understanding of the way in which each cerebral hemisphere independently processes information. Research in this area has shown that each cerebral hemisphere features distinct information-processing capabilities. This cognitive asymmetry is reflected in the notion of a left hemisphere *interpreter* module which, we have argued, generates a unitary sense of consciousness even in the disconnected brain. This chapter describes how this *interpreter* may also give rise to a unified sense of self.

KEYWORDS: callostomy; split-brain; self; interpreter; left hemisphere; recognition; lateralized; face recognition

WHAT IS THE SELF?

Although the term *self* is widely used in everyday speech, and most people have an intuitive sense of what the term means, formal definitions have proved more elusive. Kihlstrom and Klein (1997) offered a conceptual defi-

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nition of the self as being a representation of what we know about ourselves. This knowledge, they argued, can be broadly categorized against four types:

(1) a concept comprising a fuzzy set of context-specific selves;

(2) a set of narratives that address our past, present, and future;

(3) an image- or percept-based representation containing face, body, and gesture represinformation; and

(4) an associative network that contains information about personality traits, autobiographical memories, thoughts, and behaviors separated on the basis of episodic and semantic self-knowledge.

These definitions suggest that any notion of a cognitive self may be implemented across a distributed network of cortical representation. However, such a model does not directly specify or confer any special status to the representation of the self from other forms of episodic and semantic knowledge. Indeed, it has been argued that the apparent special status of self-referential processing can be accommodated by semantic processing accounts. However, we will argue that the representation of self is special, and is subserved by a unique cortical network that differs from brain regions involved in other forms of semantic processing.

SELF-KNOWLEDGE AS DISTINCT FROM OTHER REPRESENTATIONS OF KNOWLEDGE

With respect to memory function, knowledge about the self is often remembered better than other types of semantic knowledge (Rogers et al., 1977; for review see Symons & Johnson, 1997). Why does this memory advantage occur? One possibility is that distinct brain regions are engaged during self-referential processing that enhance memory for this material. Recent evidence that the cortical representation of the self is distinct from other forms of semantic knowledge is provided from two different strands of cognitive neuroscience. In an event-related fMRI study, Kelley et al. (2002) recorded brain activation while participants made judgments about trait adjectives under three conditions: whether the adjective was self-descriptive, whether the adjective described U.S. President George W. Bush, or whether the word was presented in uppercase font. Compared to case judgments, judgments about the self and a familiar other (President Bush) were characterized by increased activation in the left inferior frontal cortex, a region that has been implicated in a wide range of semantic appraisal tasks. Of interest, activity in this area did not differ between self judgments and judgments about a familiar other, even though self-judgments led to better memory on a surprise recognition test. When the self-reference judgments were compared directly to judgments about a familiar other, however, self-referential processing selectively activated regions of the medial pre-frontal cortex (MPFC).

In subsequent work, the level of activity in MPFC was shown to predict, on average, whether a word judged in reference to the self would later be remembered or forgotten (Macrae et al., submitted for publication). Collectively, these findings demonstrate that self-referential processing is functionally dissociable from other forms of semantic processing.

Klein et al (2002) provided further evidence for a distinct self-processing network. They report the case of patient D.B., a 78 year-old man who, as a result of cardiac arrest with presumed anoxia, was left with a dense anterograde and retrograde amnesia. Although D.B. was unable to recall information from autobiographical or from more general semantic memory, he was able to accurately identify trait adjectives that best described his personality. Thus, even with the most impoverished episodic and semantic memory, he is able to accurately reflect on personal attributes. This provides further support for the existence of a distinct cortical network specific to self-knowledge that remained intact in this individual.

NEUROPSYCHOLOGICAL INVESTIGATIONS OF THE CORTICAL LOCUS OF SELF-REPRESENTATION

While the first two tenets of Kihlstrom and Klein's (1997) categorization of self-knowledge do not lend themselves easily to empirical investigation using standard cognitive neuropsychological methodologies, the concept of the self as being percept-based, or a collection of semantic and episodic knowledge, has received a great deal of recent attention.

THE SELF AS A PERCEPT

The ability to recognize oneself from a photograph or from a mirror image seems to develop in humans around the middle of the second year. This ability can be seen to play a pivotal role in the development of other higher-order cognitive capacities, including a theory of mind (Keenan et al., 2000). However, a definitive anatomical substrate of self-recognition remains elusive.

Neuroimaging and neuropsychology have identified regions of the right cerebral hemisphere as being central to the ability to process information about familiar faces, and damage to these cortical areas impairs our ability to recognize others (De Renzi, 1994; Gazzaniga & Smylie, 1983). It is not surprising therefore that recent imaging (and behavioral) studies have identified regions in the right cerebral hemisphere as being specialized for self-recognition. Keenan et al. (1999) presented participants with photographs of themselves, familiar others (co-workers), and strangers. They reported that identification of self-images was faster when participants responded with the left hand. As each hand is predominantly controlled by the contralateral cerebral hemisphere, this indicated the importance of right cerebral hemisphere in self-recognition.

Keenan et al. (2001) tested self-recognition in individuals who underwent a sodium amytal (Wada) procedure and showed a right-hemisphere superiority for self-recognition. At encoding, a morphed facial photograph (generated by combining the patient's face with a famous face) was presented while a portion of one hemisphere was anesthetized. When patients had recovered from the effects of the anesthesia they were shown two photographs (self and a famous other) and asked to report which one they had seen before (although note, in fact, that they had seen neither face, only a morph of the two). A bias towards perception of the morph as "self" occurred when it was presented to the right- rather than the left hemisphere, whereas the left hemisphere appeared better at recognizing famous faces. It is unclear, however, the extent to which this is a memory effect or an indication of right hemispheric specialization in self-recognition.

Keenan et al. (2000) showed movie sequences comprising the transition from a self-image to a famous-other image (or familiar-other to famous-other). They demonstrated that left hand (and consequently right hemisphere) responses to self were faster than for a movie sequence that involved a familiar other-to-famous face, providing additional support for the notion of structures in the right hemisphere mediating self-recognition.

However, imaging studies of self-recognition undertaken by Kircher and colleagues (Kircher et al., 2001; Kircher et al., 2000) have shown a different pattern of results. Participants were shown morphed self or familiar-other images. Self-recognition was characterized by increased activity in the right hemisphere limbic system and the left pre-frontal cortex. These studies demonstrate that while it is possible to study a percept-based model of the self, the resulting anatomical locus of this process from studies of the normal brain remains elusive.

THE SELF AS AN ASSOCIATIVE NETWORK

The study by Kelley et al. (2002) described earlier demonstrated regions of the medial frontal lobes associated with making trait judgments relevant to the self. However, this region could not easily be lateralized to a single cerebral hemisphere. Furthermore, the neurological profile of the patient reported by Klein et al. (2002) is not well documented and does not permit any clear insight into the lateralization of any self-trait processing.

The distributed nature of the self is further characterized by recent imaging studies on autobiographical memory. It has been argued that autobiographical memories are strongly related to the concept of self. Indeed, it has been suggested that it is the intrinsic self-referential nature of autobiographical memories that dissociates them from other forms of long-term knowledge (Brewer, 1986). Others have suggested that autobiographical memory is actually a component of the self (Conway & Taachi, 1996; Robinson, 1986). So is autobiographical memory lateralized to one cerebral hemisphere?

Conway and Pleydell-Pearce (2000) proposed that autobiographical memories were constructed in what they referred to as a self-memory system (SMS). This system contains a knowledge base and a set of control processes that mediate access to that knowledge. Contained within the knowledge base are layers of autobiographical knowledge that are arranged from conceptual and abstract, through to highly specific details of single events. Access to this knowledge is mediated by the active goals set by the control process (or what they referred to as the "working self"). The role of generating goals and evaluating responses to those goals for autobiographical memory retrieval would seem to fit the characteristics of the *interpreter* module in left hemisphere (Gazzaniga, 2000). Moreover, several imaging studies identified regions of the left pre-frontal cortex as the locus for the retrieval process in autobiographical memory (Conway et al., 1999; Conway et al., 2001; Nolde et al., 1998; see also Maguire, 2001, for a review).

This then would seem to imply a left hemisphere–lateralized autobiographical memory system. However, Markowitsch and colleagues (Fink et al., 1996; Markowitsch, 1998; Markowitsch, 1995) have demonstrated greater right hemisphere activation during the retrieval of autobiographical memories. It may be possible to explain the differences in cortical activity associated with retrieval from autobiographical memory in terms of the methodological differences across these studies (for a review see Conway et al., 2002). It is also conceivable that one hemisphere sets retrieval goals while the other reconstructs the resultant episode. The latter process is more likely to include imagery and emotional constituents that would trigger activation in the right hemisphere, but does not preclude a left hemisphere goal-directed approach to the retrieval of that information. This hypothesis necessitates temporal differences in brain activation for retrieval and reconstruction that can not easily be dissociated in the PET or fMRI studies cited earlier. To address this issue, Conway and Pleydell-Pearce (2000) utilized temporally superior EEG techniques to measure regions of the brain associated with autobiographical retrieval and reconstruction. They demonstrated that the early retrieval processes in autobiographical memory are indeed mediated by frontal regions in the left hemisphere.

In summary, it is clear that the self appears to be a measurable construct both behaviorally and cortically, and that aspects of self-knowledge are distributed throughout the cortex. While there is some evidence that frontal regions of the left hemisphere may play a pivotal role at least in setting the goals for the retrieval and reconstruction of autobiographical knowledge (Conway et al., 2002; Conway et al., 2001), the issue of hemispheric laterality remains equivocal.

THE LEFT HEMISPHERE INTERPRETER

Split-brain research has identified different cognitive processing styles for the two cerebral hemispheres. The right hemisphere appears to process what it receives and no more, while the left hemisphere appears to make elaborations, associations and searches for logical patterns in the material, even when none are present. In lateralized memory experiments, for example, the right hemisphere retains a veridical representation of each to-be-remembered item and tends to accurately recognize previously viewed items and correctly reject new items, even when they are similar to the target material. The left hemisphere tends to elaborate and make inferences about the material presented, often at the expense of veracity (Metcalfe et al., 1995; Phelps & Gazzaniga, 1992).

In addition to elaboration of information, the left hemisphere also attempts to assign a coherent explanation to events or behavior, even when in reality none is present. Wolford et al. (2000) tested a split-brain patient on a probability-guessing paradigm. In this procedure there are two events (e.g., the presentation of either a red or green circle) that each have a different probability of occurring (e.g., 75% red & 25% green). However, the assignment of these events is stochastic. The two main strategies employed for making responses are *matching* and *maximizing*. The matching strategy takes account of the ratio of occurrences of each event type. Therefore, red stimuli appear 75% of the time, so 75% of responses made are for red. It is possible to get a maximum of 100% correct responses using this strategy if all responses are correctly aligned with the different trial types. However, it is also possible with incorrect predictions to fall as low as 50% accuracy on this task. This is because every incorrect prediction made essentially represents two errors. An incorrect prediction for one trial type must be mirrored by a subsequent prediction error on the other trial type. Thus while this matching strategy would seem to follow a logical vein and carries with it the highest potential gain, it also results in the highest potential loss to the individual. The second strategy, maximizing, involves choosing the response associated with the highest frequency event on every trial (in this case, red). This strategy results in only 25% errors and thus maximizes the number of correct responses. It is noteworthy that human participants tend to use the matching strategy whereas animals like the rat or goldfish tend to maximize. In the split-brain, the right hemisphere tends to maximize responses whereas the left hemisphere tends to look for order and match responses.

The left hemisphere of the split-brain patient also attempts to explain the behaviors elicited from the disconnected right hemisphere. In a classic study (see Gazzaniga & LeDoux, 1978) using the simultaneous concept test, a split-brain patient was presented with two pictures (one to each cerebral hemisphere), and asked to select an associated picture from an array placed in front of him or her. When a picture of a chicken claw was presented to the left hemisphere and a snow scene presented to the right hemisphere, subject P.S. responded by selecting a picture of a shovel with the left hand and a picture of a chicken with the right hand. These choices would seem to be logical since a shovel might be used to clear snow and the chicken claw obviously goes with the chicken. However, when asked to explain why he selected these items, P.S. responded "Oh that's simple. The chicken claw goes with the chicken, and you need a shovel to clean out the chicken shed." Thus the left hemisphere explains the response of the disconnected the right hemisphere (left hand) in terms of its own experience, which does not include information about the snow scene (perceived only by the right hemisphere). In fact, this same interpretive process can also be demonstrated in participants with an intact connection between the two hemispheres (Schachter & Singer, 1962).

A further example of this type of biased interpretation of events or behavior by the left hemisphere is evident from studies of patients with various delusional disorders (see Cooney & Gazzaniga [2003] for a review). One such disorder, anosognosia for hemiplegia (Prigatano & Schacter, 1991; see also Ramachandran, 1995) resulting from damage to the right parietal cortex, renders patients unable to maintain a representation of the left side of the body. However, when confronted with resulting paralysis the patient generates a plausible excuse. For example, patient B.M. was asked to explain her inability to use her left hand to point to a student in the room. "Because I didn't want to" she replied (Ramachandran, 1995, p. 24). The same patient then goes on to identify her left hand as belonging to her son. The absence of sensory input to the left hemisphere *interpreter* from the right parietal system essentially means that for her subjective experience the limb does not exist as a part of her anatomy and as a result she engages in elaborate confabulations to explain its presence. The left hemisphere's drive to interpret and explain its world, no matter how bizarrely, is also evident in Capgras' syndrome (Doran, 1990). Here the visual representation of a familiar loved one is divorced from the accompanying emotional feelings for that person. Therefore when meeting a spouse, for example, the patient recognizes the individual physically, but not on an emotional level. As a result, the patient's interpretation is that the person is an imposter. Thus, the "interpreter' attempts to make sense of its input both from the external environment and from its own body. Where the information it receives is nonsensical or even absent, it constructs a plausible reality, such that in the case of delusional syndromes "bizarre information yields bizarre results" (Cooney & Gazzaniga, 2003).

What is the advantage of hemispheric asymmetry in processing the world? The left hemisphere strives to provide an understanding of not only the event, but also the underlying cause of that event. In this way, one can develop a mechanism to cope with future occurrences of that (or a related) event. However, this strategy carries a cost in terms of the accuracy with which specific perceptual inputs can be matched and with which other information can be recalled from memory. The right hemisphere does not engage in interpretive processing of information and maintains a veridical representation of its input. In the normal brain, these two cognitive styles complement each other and facilitate elaborative information processing (and by definition comprehension of the world) without the associated cost to immediate memory. Thus novel events can be accommodated within the existing knowledge base, but concomitant access to an episodic record of the specific incident in question is also available. Gazzaniga (2000) has argued that this difference in processing style between the two hemispheres might be seen as adaptive and represents an underlying role for the left hemisphere in the generation of a unified consciousness experience. More specifically:

> Insertion of an interpreter into an otherwise functioning brain creates many by-products. A device that begins by asking how one thing relates to another, a device that asks about an infinite number of things, in fact, and that can get productive answers to its questions cannot help but give birth to the concept of self" (Gazzaniga, 2000, p. 1320).

There are evident parallels between the notion of conscious experience and a self-construct. Kihlstrom (1995) states that conscious experience necessitates a specific connection between a mental representation of a current or past event and of the "self" as the agent of that event. Any notion of a conscious left hemisphere must also include the notion of a similarly lateralized concept of the self. While the self appears to be constructed from information located throughout the brain, even in the most extreme cases, such as the callosotomized brain, a unified self-construct is still possible. This unified experience of self is the result of the actions of the left hemisphere "interpreter" (Gazzaniga, 1985 and 1989; Gazzaniga & LeDoux, 1978), which integrates all of the available information to form a coherent explanation of the world. Where some of the information is either missing or inaccessible, the interpreter creates an explanation of reality based upon what it does know, no matter how bizarre.

THE INTERPRETER AND SELF-RECOGNITION

Neuropsychological disorders, such as anosognosia for hemiplegia and Capgras delusions described earlier, provide an insight into the way the left hemisphere interpreter creates its own virtual reality from information received via intact neural pathways, even when this reality is or appears implausible. However, studies of the normal brain have not yielded any definitive insight into a laterally biased representation of self-referential information processing (although Conway et al. reported evidence for early-onset left hemisphere processing of autobiographical memory retrieval). This may in part be seen as the result of the employment of differing empirical methods and the variety of self-processing investigated via such methods. In addition, there appears to be an inherent difficulty in investigating some processes in the normal brain, what Martin (2000) refers to as the "contamination problem." Despite attempts to invoke a particular process, complete isolation of that process appears to be problematic in the intact brain.

In order to assess the contribution of a specific cerebral hemisphere to any given self-referential task, and to reduce the risk of "contamination" from the opposite hemisphere, one can readdress these questions in persons with a callosotomized brain. Such individuals are unable to transfer information between the two cerebral hemispheres and as a result are only able to process information within the hemisphere to which it was encoded. However, owing to the asymmetry of inter-hemispheric cognitive aptitudes in the split brain (language mediated by the left cerebral hemisphere and attentional processing mediated by the right), verbal responses load unevenly on the language-dominant hemisphere. As a result, the paradigms utilized for self-knowledge and autobiographical memory-retrieval tasks reported earlier do not lend themselves easily to split-brain research. The most appropriate methodology for identifying the lateral locus of the self in the disconnected brain would appear to be self-face recognition.

Turk et al. (2002) assessed person-recognition (self and familiar-other person) in a split-brain patient. This provided an excellent test of hemispheric differences in person-recognition as information (i.e., photographs of self or familiar others) can be independently presented to a single hemisphere in isolation. We tested J.W., a 48 year-old right-handed male who, at the age of 25, underwent two-stage callosal surgery with sparing of the anterior commissure. The surgery was undertaken as a treatment for pharmacologically intractable epilepsy. In this experiment, J.W. viewed a series of morphed facial photographs that ranged from 0% to 100% self-images. The 0% self-image was a photograph of Dr. Michael Gazzaniga (M.G.), (i.e., a familiar other). The remaining nine images were generated using computer morphing software with each image representing a 10% incremental shift from J.W. to M.G. (FIG. 1).

The images were laterally presented in a random order to each cerebral hemisphere for 250 ms. In the self-recognition condition, J.W. was asked to indicate whether the presented image was himself; in the familiar other condition, he was asked to indicate whether the image was of Dr. Gazzaniga. The same morphed images were used for each judgment task. The only difference across the two conditions was the judgment that was required ("Is it me?" vs. "Is it Mike?"). Data were collected across six separate sessions. In each session, the 11 images (i.e., self or Mike plus 9 intermediate morphs) were presented four times to each cerebral hemisphere. The results revealed a double dissociation in J.W.'s face-recognition performance. J.W.'s right hemisphere was biased towards recognizing the morphed faces as a familiar other, whereas his left hemisphere was biased in favor of self-recognition.

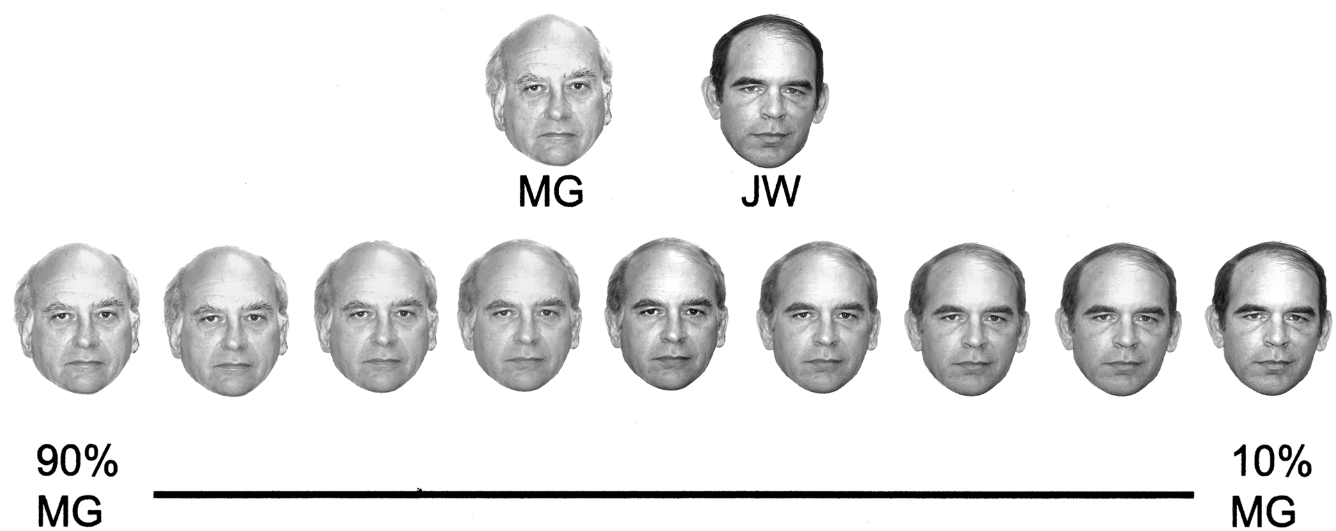

FIGURE 1. A sequence of nine faces was created by morphing M.G.'s image with J.W.'s face in 10% incremental shifts. The initial image contained 10% of J.W. and 90% M.G. and the end image was the reverse. These images, together with the two original photographs of M.G. and J.W., were randomly presented to each hemisphere. In one condition J.W. was asked to determine whether the image was self, while in the other condition J.W. was asked to determine whether the image was M.G.

To ensure that this dissociation was not dependent on the identity of the familiar other (M.G.), we repeated the entire procedure (again across six testing sessions) using three additional targets (Dr. Paul Corballis, a personally known individual; current U.S. President George W. Bush; and former U.S. President, Bill Clinton). The same double dissociation was observed across all four targets. This demonstrated that while both hemispheres were capable of recognizing faces, J.W.'s left hemisphere displayed a recognition bias for self and his right hemisphere displayed a recognition bias for others.

The results presented here support the viewpoint that, although both hemispheres are capable of self-recognition (Gazzaniga, 1998), cortical networks in the left hemisphere play a significant role in this process (Kircher et al., 2000; Kircher et al., 2001; Kircher et al., 2002). The observed double dissociation in J.W.'s person-recognition performance is theoretically important since it provides further evidence that that self-recognition is functionally dissociable from general face processing, which itself has important implications for contemporary models of social cognition.

The objectives set by the self-memory system (SMS) guide behavior in a deliberate and meaningful manner (Conway & Pleydell-Pearce, 2000). Distributed across a discrete cortical network, the SMS comprises autobiographical knowledge, personal beliefs, currently active goal states, and conceptions of self (Conway et al., 1999; Conway & Pleydell-Pearce, 2000; Conway et al., 2002). Through its enhanced ability to recognize and reconstruct aspects of self, the left hemisphere may play an important role in the functioning of the SMS. In the case of self-recognition, the left hemisphere appears to think that it sees itself, even when the image contains as much information about a familiar other as it does about the self. Thus even in the disconnected brain, the self appears to be a unified construct. This unified self-construct is underpinned by the "interpreter" within the left cerebral hemisphere.

The left hemisphere also shows a bias towards the self in experiments on spatial frames of reference conducted on the split-brain. Funnell, Johnson and Gazzaniga (2001) reported different patterns of hemispheric lateralization associated with mental rotation. The left hemisphere was shown to be superior when mental rotation was undertaken with an egocentric (internal) frame of reference. In contrast, the right hemisphere showed an advantage on tasks that demand representing spatial information relative to an external (allocentric) frame. Results from an fMRI study on neurologically intact participants indicates that the right superior parietal lobule may play a key role in representing spatial information in allocentric coordinates, while left parietal areas may be involved in the formation of egocentric representations. Interestingly, brain regions involved in motor planning and preparation are activated during egocentric mental rotation but not during allocentric rotation. These parietal-frontal circuits in the motor-dominant left hemisphere appear to be specialized for spatial transformations within a frame of reference centered on one's own body.

SUMMARY

This paper addresses the question of whether the self is unique from other forms of semantic and episodic representation, and whether there is a specific role for a left hemisphere "interpreter" in the generation of a unified sense of self. The evidence available in the literature so far suggests that self-referential trait processing is somehow special, not simply an extension of other forms of semantic information processing, and is subserved by a unique cortical network. However, until now the cortical locus of critical components of this self-processing network was equivocal. Imaging studies of autobiographical memory retrieval and of self-face recognition had not elicited clear laterality effects for these self-referential processes, although there is some compelling evidence that left hemisphere frontal systems mediate the retrieval of autobiographical information. To further investigate the laterality of self-processing, Turk et. al (2002) examined person-recognition processes (self vs. familiar other) in a split-brain patient. This work revealed a left hemisphere bias toward recognizing the self, whereas the right hemisphere was biased to recognize the faces of familiar other people.

We argue that the findings from our split-brain study, together with data from other self-referential processing studies, reflect a critical role for the left hemisphere *interpreter* in self-recognition. This interpretive function of the left hemisphere takes available information from a distributed self-processing network and creates a unified sense of self from this input. When information from the entire network is available, a realistic interpretation can be made, but when portions of the network are disconnected, the interpretation verges on fantasy. However, in all cases, this left hemisphere interpretation results in a unified sense of self, even in the disconnected brain. Thus, even when there appear to be two brains, there is still only one self.

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