



ELSEVIER

NeuroImage

www.elsevier.com/locate/ynimg
NeuroImage xx (2004) xxx–xxx

Self-face recognition activates a frontoparietal “mirror” network in the right hemisphere: an event-related fMRI study

Lucina Q. Uddin,^{a,*} Jonas T. Kaplan,^{b,d} Istvan Molnar-Szakacs,^{b,c,d}
Eran Zaidel,^{a,c} and Marco Iacoboni^{b,c,d,e}

^aDepartment of Psychology, University of California, Box 951563, B627 Franz Hall, Los Angeles, CA 90095, USA

^bAhmanson-Lovelace Brain Mapping Center, University of California, Los Angeles, CA 90095, USA

^cBrain Research Institute, University of California, Los Angeles, CA 90095, USA

^dFPR-UCLA Center for Culture, Brain and Development, University of California, Los Angeles, CA 90095, USA

^eDepartment of Psychiatry and Biobehavioral Sciences, David Geffen School of Medicine, University of California, Los Angeles, CA 90095, USA

Received 30 July 2004; revised 1 December 2004; accepted 7 December 2004

Self-recognition has been demonstrated by a select number of primate species and is often used as an index of self-awareness. Whether a specialized neural mechanism for self-face recognition in humans exists remains unclear. We used event-related fMRI to investigate brain regions selectively activated by images of one's own face. Ten right-handed normal subjects viewed digital morphs between their own face and a gender-matched familiar other presented in a random sequence. Subjects were instructed to press a button with the right hand if the image looked like their own face, and another button if it looked like a familiar or scrambled face. Contrasting the trials in which images contain more “self” with those containing more familiar “other” revealed signal changes in the right hemisphere (RH) including the inferior parietal lobule, inferior frontal gyrus, and inferior occipital gyrus. The opposite contrast revealed voxels with higher signal intensity for images of “other” than for “self” in the medial prefrontal cortex and precuneus. Additional contrasts against baseline revealed that activity in the “self” minus “other” contrasts represent signal increases compared to baseline (null events) in “self” trials, while activity in the “other” minus “self” contrasts represent deactivations relative to baseline during “self” trials. Thus, a unique network involving frontoparietal structures described as part of the “mirror neuron system” in the RH underlies self-face recognition, while regions comprising the “default/resting state” network deactivate less for familiar others. We provide a model that reconciles these findings and previously published work to account for the modulations in these two networks previously implicated in social cognition.

© 2004 Elsevier Inc. All rights reserved.

Keywords: Self-recognition; Self-awareness; Social cognition; Laterality; Hemispheric specialization; Mirror neurons; Default resting state

Introduction

The self–other distinction is fundamental to a variety of complex cognitive processes. As early as 1889, Preyer used mirrors to assess cognitive development in general, and self-concept in particular, noting that “. . .the behavior of the child toward his image in the glass shows unmistakably the gradual growth of the consciousness of self out of a condition in which objective and subjective changes are not yet distinguished from each other” (Preyer, 1889). It has since been demonstrated that infants around 2 years of age begin to show behavior indicative of self-recognition in front of a mirror (Amsterdam, 1972), a developmental period which coincides with the onset of the use of the personal pronouns “I” and “me” (Preyer, 1889). The ability to mirror-self-recognize has only been reliably demonstrated in humans, chimpanzees (Gallup, 1970; Povinelli et al., 1997), and orangutans (Lethmate and Ducker, 1973). These observations led Gallup to conclude that self-recognition is predicated on a sense of identity, and led him to suggest that this capacity is indicative of an underlying self-concept (Gallup, 1977).

Although the development of self-awareness has been a central theme in psychological approaches to consciousness, the topic has been somewhat neglected in neuroscientific approaches. In 1977, it was noted that skin resistance (SR) responses (as an index of arousal) in normal subjects were greater and more persistent in response to one's own face than to unknown faces, faces of friends, or faces of relatives. Using the “Z-lens” to restrict complex visual input to one hemisphere (Zaidel, 1975, 1979), Preilowski (1977) studied two split-brain patients and found that both showed the largest responses to pictures of their own faces and that this was most pronounced when the right hemisphere (RH) was targeted. The fact that these SR changes were observed even when stimuli could not be verbally identified by the mute RH led Preilowski to “assume the existence of conscious awareness in the ‘mute, minor’ as well as in the ‘speaking, major’ cortical half”. Sperry et al. (1979) also tested the abilities of the disconnected hemispheres to

* Corresponding author. Fax: +1 310 206 3655.

E-mail address: lucina@ucla.edu (L.Q. Uddin).

Available online on ScienceDirect (www.sciencedirect.com).

respond to self-images and reported that commissurotomy patients had no trouble identifying portraits of themselves with either hemisphere. Further, both disconnected hemispheres had similar associations with self, including social preferences, and narrative self-concepts. The authors concluded that a well developed sense of self and social awareness is indeed present in the previously described as “minor” RH.

Recent studies have attempted to identify the neuroanatomical substrates of the self. Keenan et al. (2000b) proposed that the right hemisphere, specifically the right prefrontal cortex, is recruited during self-recognition tasks. In a behavioral study, where subjects viewed digital morph movie sequences and indicated by a button-press when they judged them to be “more self than not self”, participants were more likely to identify self-to-famous morphed images as self when responding with their left hand. The authors concluded that the RH, controlling the left hand, is specialized for processing images of self (Keenan et al., 2000a). This group has also demonstrated a RH self-bias using transcranial magnetic stimulation (TMS), showing that motor evoked potentials were significantly greater for the right hemisphere than the left hemisphere (LH) while subjects viewed self-famous morphs but not familiar-famous morphs. Likewise, patients undergoing the intracarotid amobarbital (Wada) test (involving presurgical anesthetization of one cerebral hemisphere at a time to reveal the dominant hemisphere for language) are more likely to identify a self-famous morphed face as a “self” face after inactivation of the LH (Keenan et al., 2001b). Keenan et al. (2003) also cited behavioral evidence from a split-brain patient corroborating their claim of a RH processing advantage for self-faces. In addition, this group has presented preliminary event-related potential (ERP) and fMRI data supporting the claim of right frontal lateralization for self-related processing (Keenan et al., 2001a).

Clinical neuropsychological evidence for RH involvement in maintaining an integrated self-concept also exists. Devinsky argues that the RH is crucial for generating a sense of physical and emotional self, specifically for constructing an individual’s awareness of his or her own corporeal being and its relation to the environment and to his or her affective state. He cites examples of the deficits produced by right parietal lesions (neglect, anosognosia), right parietotemporal lesions (topographic orientation), right frontotemporal lesions (impulse control), right frontal lesions (social behavior, relation of self to others, social self), and various others to conclude that consciousness of the corporeal, emotional, and social self may be RH dominant (Devinsky, 2000). Patients with RH damage often show poor insight into their condition (Bisiach and Geminiani, 1991), indicating a RH role in self-concept and self-monitoring. This view of the RH is corroborated by behavioral data in normal subjects showing that the RH is often better than the LH at using external feedback to self-monitor (Kaplan and Zaidel, 2001). Likewise, evidence from patients with frontotemporal dementia suggests that those with asymmetric loss of function in the RH show dramatic changes in self-concept, defined as temporally stable, trans-situational consistencies in behavior, dress, or political or religious ideology (Miller et al., 2001). Similarly, patients exhibiting the syndrome referred to as “mirror sign”, or the inability to recognize one’s own reflected image, reportedly show striking RH dysfunction with relatively spared LH function, as revealed by neuropsychological testing (Breen et al., 2001).

However, claims of RH specialization for self-recognition are not universally accepted (Turk et al., 2003). Evidence suggesting LH or bilateral involvement in self-recognition also exists. An

fMRI study by Kircher et al. (2001) revealed increased blood oxygenation in the right limbic, left prefrontal, and left superior temporal cortex when subjects viewed pictures of themselves, while only right insula activated during viewing of a familiar other. A behavioral study cites evidence from a split-brain patient using the morphing method to suggest that it is actually the LH that shows a bias for self, and the RH that shows a bias for familiar others (Turk et al., 2002). An earlier PET study looking at the effects of active recognition versus passive recognition of the self-face found activity in a bilateral network (Sugiura et al., 2000). Behavioral evidence in favor of LH dominance (Brady et al., 2004) also exists, and we found dual hemispheric competence in recognition of the self in normals (Uddin et al., 2002) as well as in split-brains (Uddin et al., 2003). These inconsistencies may in part be accounted for by differences in methodologies and control tasks utilized. One factor that has previously been poorly controlled is that of familiarity. As the self-face is highly overlearned and familiar, an appropriate control face is difficult to obtain. Many previous studies have compared the self-face to famous faces or unknown faces, for example, Keenan et al. (2000b) and Kircher et al. (2001). An alternative is to use the face of a highly familiar individual (e.g., a personal friend) as a control. Indeed, we might expect that comparing the self to a highly familiar famous face is different from comparing the self to a personally familiar face, which invokes social and emotional attachment. Such a differential neural response between personally relevant familiar faces and famous familiar faces has recently been reported (Gobbini et al., 2004).

In summary, a review of the current literature reveals that whether and to what extent the ability to self-recognize is lateralized is still an open question, though a majority of studies support the idea of a special role for the RH. Much of the neuropsychological and clinical data suggest that there may be a specific role for frontoparietal networks in maintaining the integrity of the self (Feinberg, 2001). Dysfunction in frontoparietal networks have been linked to abnormalities in awareness of action and self-monitoring deficits (Frith et al., 2000a,b). Some have suggested that right frontoparietal networks specifically are involved in interpersonal awareness and self–other differentiation (Decety and Sommerville, 2003). Interestingly, “mirror neurons”, with the property of responding both during action observation and action execution, were reportedly found in frontal (F5) and parietal (PF) areas of the monkey brain (Buccino et al., 2004; Gallese et al., 1996; Rizzolatti et al., 1996). Homologous areas of the human brain, including the inferior frontal gyrus (BA 44) and inferior parietal lobule (BA 40), also display mirror properties. These areas are recruited during both observation and imitation of hand movements (Iacoboni et al., 1999; Molnar-Szakacs et al., 2004), and of facial expressions of emotion (Carr et al., 2003). These frontoparietal mirror areas are recruited in a variety of paradigms and are thought to be part of an action observation/execution matching system underlying action understanding. Recently, Buccino et al. (2004) reported the striking finding that while left parietal regions of the human brain activate regardless of the species performing the action, right parietal activation is stronger during observation of action by a conspecific. This evidence suggests a possible RH parietal mirror mechanism that detects a match between an external stimulus and the self.

The lack of convergence as to the laterality and precise anatomical locations underlying self-recognition motivated the current study, where we used event-related fMRI to investigate

cortical mechanisms subserving this high-level ability. Subjects were instructed to view static morphed images of themselves and a highly familiar other (a suitable control for the overlearned and highly familiar self-face) and to indicate by a button press whether they saw a “self” or “other”. If indeed frontoparietal areas in the RH play an instrumental role in recognizing the self, we would expect to see increasing activation in a such a network as the images presented contain more of the subject’s own face. Here, we show just such an increase in a right frontoparietal “mirror neuron” network as subjects view images containing greater and greater amounts of their own face. Additionally, we show modulation of midline “default/resting state” areas, previously shown to exhibit task-independent decreases in activity (Gusnard and Raichle, 2001), which deactivate less to images of a familiar other. We propose a social cognitive model to reconcile these findings with previous reports that suggest these areas are involved in some aspects of self-related processing.

Materials and methods

Subjects

Ten right-handed subjects (seven females, three males, mean age: 26.9 ± 2.6) were recruited and compensated for their participation. Subjects gave informed consent according to the guidelines of the UCLA Institutional Review Board. All participants were screened to rule out medication use, head trauma, and history of neurological or psychiatric disorders, substance abuse, or other serious medical conditions.

Image acquisition

Images were acquired using a Siemens Allegra 3.0 T MRI scanner. Two sets of high-resolution anatomical images were acquired for registration purposes. We acquired an MP-RAGE structural volume (TR = 2300, TE = 2.93, flip angle = 8°) with 160 sagittal slices, each 1 mm thick with 0.5 mm gap and $1.33 \text{ mm} \times 1.33 \text{ mm}$ in-plane resolution. We also acquired a T2-weighted coplanar volume (TR = 5000, TE = 33, flip angle = 90°) with 36 transverse slices covering the whole brain, each 3 mm thick with 1 mm gap, a 128×128 matrix and an in-plane resolution of $1.5 \text{ mm} \times 1.5 \text{ mm}$.

Each functional run involved the acquisition of 152 EPI volumes (gradient-echo, TR = 2000, TE = 25, flip angle = 90°), each with 36 transverse slices, 3 mm thick, 1 mm gap, and a 64×64 matrix yielding an in-plane resolution of $3 \text{ mm} \times 3 \text{ mm}$. A functional run lasted 5 min and 4 s, and each subject completed 4 functional runs.

Stimuli and task

Stimuli were individually tailored to each subject, and consisted of a series of static color images constructed from pictures of the subjects’ own face and the face of a gender-matched highly familiar other acquired on a Kodak 3400C digital camera. Subjects were asked to choose their own familiar control, a personal friend or colleague they encounter on a daily or almost daily basis. MorphEditor (SoftKey Corporation, Cambridge, MA) was used to create digital morphs between the subjects’ and the familiar face, resulting in 6 unique faces, each morphed to a varying extent (0%, 20%, 40%, 60%, 80%, 100%) (Fig. 1). Images were edited using Adobe Photoshop 7.0 to remove external features (hair, ears) and create a uniform gray background. A scrambled control face was created by randomly rearranging one image. The software package Presentation (Neurobehavioral Systems Inc., <http://www.neuro-bs.com/>) was used to present stimuli and record responses. Stimuli were presented through magnet-compatible goggles (Resonance Technology Inc.) and responses were recorded using two buttons of a four-button fMRI compatible response pad. During each 5 min, 4 s functional run, each of the six morphed faces and the scrambled control were presented 10 times in a random sequence optimized and counterbalanced using the optseq algorithm (<http://www.surfer.nmr.mgh.harvard.edu/optseq/>), which provides temporal jitter to increase signal discriminability (Dale, 1999). Each of the four runs consisted of a different optimized random sequence. Each stimulus was presented for 2 s, and there was at least a 1-s gap between each stimulus presentation.

Subjects pressed a button with their right index finger if the image presented looked like “self”, and another button with their right middle finger if it looked like an “other” or scrambled face.

Data processing and statistical analysis

Analysis was carried out using FEAT (fMRI Expert Analysis Tool) Version 5.1, part of FSL (FMRIB’s Software Library, <http://www.fmrib.ox.ac.uk/fsl>). After motion correction, images were temporally high-pass filtered with a cutoff period of 75 s and smoothed using a 5-mm Gaussian FWHM algorithm in 3 dimensions. The BOLD response was modeled using a separate explanatory variable (EV) for each of the seven stimulus types. For each stimulus type, the presentation design was convolved with a gamma function to produce an expected BOLD response. The temporal derivative of this timecourse was also included in the model for each EV. Data were then fitted to the model using FSL’s implementation of the general linear model.

Each subject’s statistical data was then warped into a standard space based on the MNI-152 atlas. We used FLIRT (FMRIB’s Linear Image Registration Tool) to register the functional data to

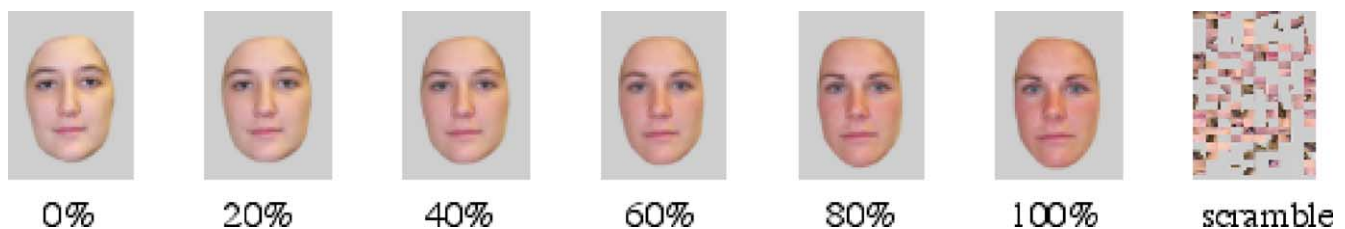


Fig. 1. Examples of stimuli. For each individual subject, an image of the subject was digitally morphed into an image of a highly familiar other in 20% increments.

the atlas space in three stages. First, functional images were aligned with the high-resolution co-planar T2-weighted image using a 6 degrees of freedom rigid-body warping procedure. Next, the coplanar volume was registered to the T1-weighted MP-RAGE using a 6 degrees of freedom rigid-body warp. Finally, the MP-RAGE was registered to the standard MNI atlas with a 12 degrees of freedom affine transformation.

Higher-level analysis was carried out using FLAME (FMRIB's Local Analysis of Mixed Effects) (Behrens et al., 2003). Z (Gaussianised T/F) statistic images were thresholded using clusters determined by $Z > 2.3$ and a (corrected) cluster significance threshold of $P = 0.05$ (Forman et al., 1995; Friston et al., 1994; Worsley et al., 1992).

Results

Behavioral

Due to technical problems, only 65% of total behavioral responses were recorded. For one subject, no behavioral responses were recorded at all. For another, all responses from all four runs were recorded. For yet another, only responses from one run were recorded. Of the other seven subjects, responses from three runs per subject were recorded. Due to these missing data points, we are unable to conduct meaningful statistics on the behavioral data. The available data are included to illustrate that the subjects were able to perform the required task. As expected, subjects had little difficulty correctly identifying 0% morphed images as “self”, and the number of “self” responses diminished as the images morphed increasingly into “other” (Fig. 2).

fMRI

Self–other contrast

A contrast subtracting the last three images in the morph series (60%, 80%, and 100% grouped) from the first three (0%, 20% and 40% grouped) revealed activation in the right hemisphere, including the inferior parietal lobule (IPL; BA 40), the inferior frontal gyrus (IFG; BA 44), the inferior occipital gyrus (IOG; BA 19), and the superior parietal lobule (SPL; BA 7) (Fig 3a, Table 1).

Other–self contrast

The opposite contrast, subtracting the three “self” images from the three “other” images shows signal changes in the precuneus (BA 31), ventromedial prefrontal cortex (VMPFC; BA 10), dorsomedial prefrontal cortex (DMPFC; BA 9), left superior frontal gyrus (SFG; BA 8), left superior temporal gyrus (STG; BA 22), right middle temporal gyrus (MTG; BA 21), and right anterior superior temporal sulcus (aSTS; BA 38) (Fig. 3b, Table 2).

Self–rest and other–rest contrasts

To ascertain whether these observed signal changes are indeed true increases relative to baseline, additional “self” minus rest and “other” minus rest contrasts were computed. For the “self” minus rest contrast, activated areas included primary visual cortex and primary motor areas in addition to right IFG, right IPL, right SPL, and right IOG. The “other” minus rest contrast showed similar but much weaker activations than the “self” minus rest. No signal changes in medial areas were observed in this contrast. These comparisons showed that activity in the “self” minus “other” contrasts are true signal increases compared to baseline in “self” trials, while those in the “other” minus “self” contrast are deactivations relative to baseline during “self” trials, as shown also in Fig. 4.

ROI analyses

To determine the percent signal change in the above-mentioned areas as a function of stimulus type, regions of interest (ROIs) were defined based on the self–other and other–self contrasts. The percent signal change from baseline (null events) was calculated for each stimulus type (Morphs 0–100%) in each of the areas. As depicted in Fig. 4, the RH structures revealed by the self–other contrast show true increases from baseline in signal intensity as the stimuli contain more “self”. Conversely, the signal changes in the other–self contrast show decreasing signal intensity as the stimuli contain more “self”, with their activity remaining below baseline in most cases.

Discussion

Our results provide clear evidence for a RH network including the inferior frontal gyrus, inferior parietal lobule, superior parietal lobule, and inferior occipital gyrus activated by recognition of the

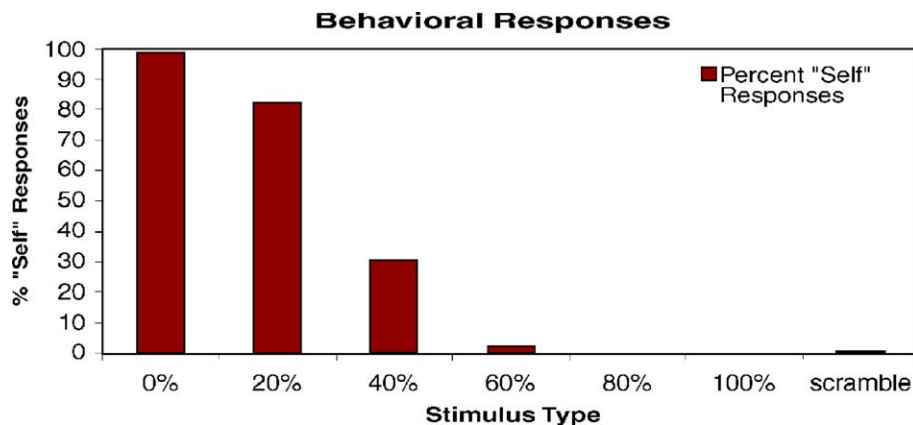


Fig. 2. Subjects viewed morphed self–other images (0–100%, 20% increments) and judged whether they were “self” or “other”. All subjects had no difficulty correctly judging the unmorphed endpoints.

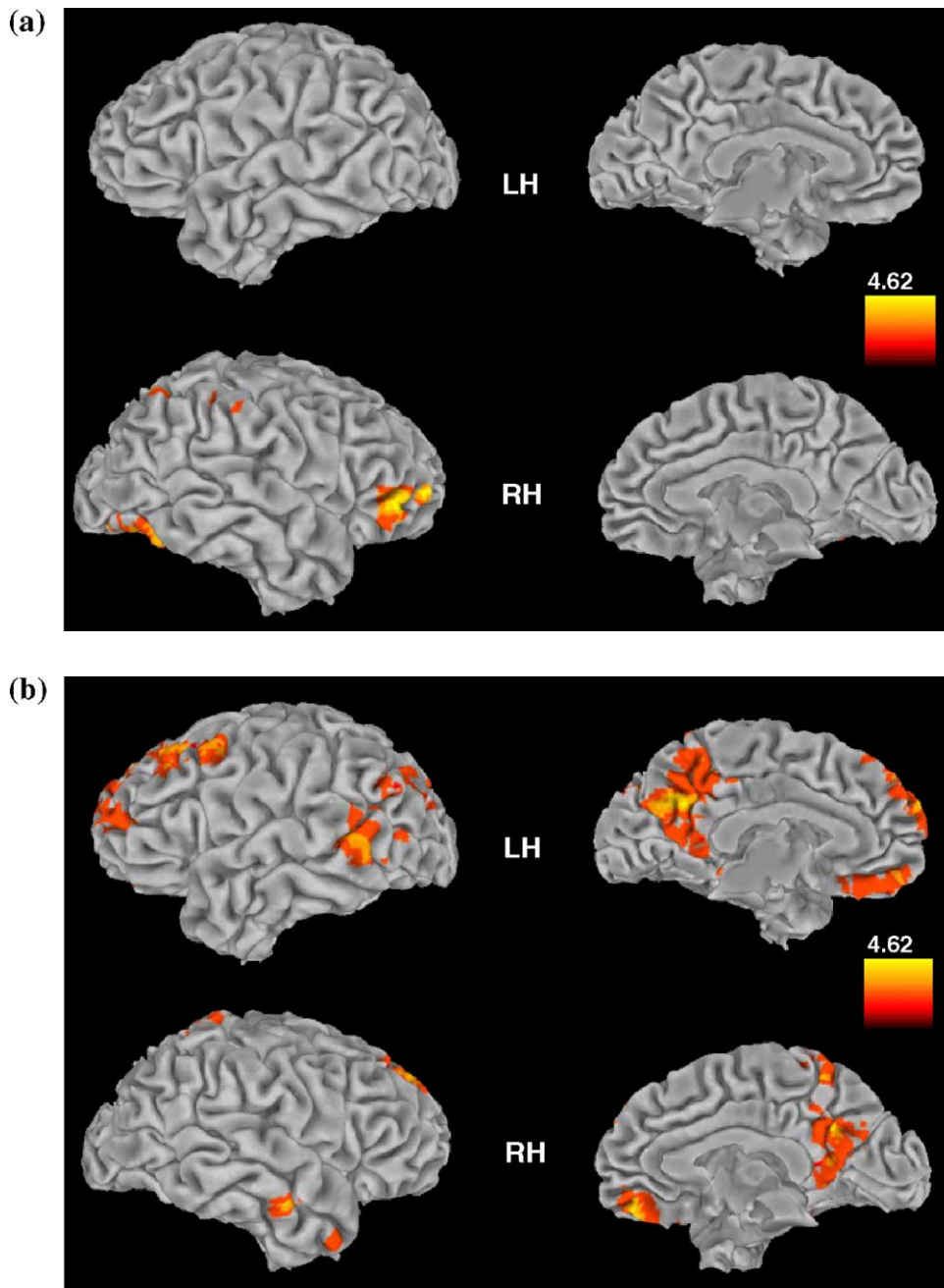


Fig. 3. (a) Voxels activated during observation of Self minus Other. (b) Voxels activated during observation of Other minus Self.

self-face. The pattern of signal increases observed in these areas as the stimuli contain more “self” suggest that these areas comprise a unique system extending beyond mere recognition of faces and of familiar others. The RH involvement we observe is consistent with several previous neuropsychological and behavioral reports, and our data provide the first functional neuroimaging study to confirm these reports.

Areas activated by “self”

The only other comparable imaging study to date was conducted by Kircher et al. In their study, subjects were scanned while viewing static morphed images between themselves and an

unknown face. The activity during this condition was compared to activity during viewing of morphs between the subject’s significant other and an unknown face, revealing greater responses in left fusiform gyrus, left inferior frontal gyrus, left supramarginal gyrus/inferior parietal lobule, and right middle temporal gyrus, right insula, and right hippocampal formation during “self” viewing (Kircher et al., 2001). A major discrepancy between this study and our own is their use of faces of significant others as a control. Though highly familiar, these faces are typically not gender-matched. We instead chose to use gender-matched highly familiar others to provide a more perceptually-matched control. Additionally, Kircher et al. tested only six male subjects, and their blocked design did not emphasize the discrimination component of the task

Table 1

Coordinates (MNI) and peak activation statistics for self–other contrast					
Hemisphere	Region	Coordinates			Max Z score
		x	y	z	
Right	SPL	32	–60	52	3.31
Right	IPL	64	–24	50	3.79
Right	IPL	42	–34	38	3.51
Right	IOG	46	–58	–12	3.79
Right	IFG	48	42	–2	3.59

MNI = Montreal Neurological Institute; SPL = superior parietal lobule; IPL = inferior parietal lobule; IOG = inferior occipital gyrus; IFG = inferior frontal gyrus.

since each block contained mostly stimuli from one category. The additional activations reported by this group may be due to perceptual processing emphasized by the block design. Also, no part of the task required direct comparison between a self and a highly familiar other face. In our study, both male and female subjects were used, and our event-related design forced subjects to make a “self–other” discrimination for each trial. Thus, the activations in our study may be more related to self–other discrimination than to perceptual processing of the images. Our design allowed for a direct comparison between the “self” and the familiar “other” faces. Additionally, our event-related design allowed us to avoid the habituation issues inherent to block designs.

A previous preliminary study (two subjects) also reports right inferior frontal gyrus activation, specifically in the pars triangularis, when subjects attended to self-, compared to famous-, faces (Keenan et al., 2001a). A recent report using a block design shows activation in the right middle, superior, and to a lesser extent inferior frontal gyrus during viewing of self compared to famous faces in five subjects (Platek et al., 2004). A PET study attempting to tease apart the effects of active recognition versus passive recognition found that active self-recognition involves the right inferior frontal gyrus, right medial frontal gyrus, right anterior cingulate and left anterior insula (Sugiura et al., 2000). These data come from six males, and while consistent with some of our findings, the activations in additional areas may be a result of the specific paradigm, which required subjects to perform a dual task. Here, we extend these previous findings with a greater number of subjects, a more optimized event-related design, and a better-matched familiar face control (Gobbini et al., 2004).

We found that the right inferior parietal lobule was one area in which activity correlated with increasing “self” component in the stimuli. The inferior parietal lobule has consistently been reported as contributing to a sense of agency, or the feeling of being the one generating an action (Farrer and Frith, 2002). In a PET study by Chaminade and Decety (2002), the authors find stronger right IPL activity when subjects were the agent of a performed action, a result consistent with previous reports of this area’s role in distinguishing internally produced actions from those generated by others (Decety et al., 2002). Patients with right frontoparietal damage often present with asomatognosia, or the lack of recognition of parts of the body (Feinberg, 2001). The phenomenon of out-of-body experience has been associated with stimulation of the right IPL, specifically the angular gyrus, leading to the suggestion that the angular gyrus may be part of a circuit mediating complex own-body perception (Blanke et al., 2002). Spence et al. (1997) show that schizophrenics experiencing passivity phenomenon (with delusions of alien control) show

differential activity in the supramarginal gyrus of the right IPL compared to schizophrenics without such delusions. Thus, in accordance with our results, a number of studies have implicated the right IPL in own-body representations and self-referential processing.

It has been suggested that the right inferior parietal cortex along with the prefrontal cortex comprise a neural network underlying self–other representations and are important in distinguishing the self from the other. According to this model, the self is thought of as a multi-dimensional construct relying on a distributed neural network encompassing shared self–other discriminations (Decety and Sommerville, 2003). Here, we provide evidence supporting this view of social cognition. While the frontoparietal regions we describe activate during both self and other perception, they show increasing levels of activity as the subjects perceive more self in the stimuli, thus distinguishing self from other. Our result implicating the IPL in a visual self–other discrimination task is consistent with previous views, and further suggests that this area may be responsible for maintaining self–other distinctions across a variety of sensory modalities.

The co-activation of the right IPL and IFG induced by our self-recognition task suggests a specific role for the frontoparietal mirror neuron network in self–other discriminations. Our result implicating both of these regions in self-recognition is particularly intriguing, given the numerous recent reports of the mirror properties of these areas (Buccino et al., 2004; Molnar-Szakacs et al., 2004; Rizzolatti and Craighero, 2004). Here, we report the first empirical link between the self and the entire mirror circuitry. Motor or simulation theories of perception posit that perception occurs through motor simulation, or a mapping of the “other” onto one’s own motor system. We may be seeing mirror areas more active for self-recognition because their role is to establish communication between individuals via a simulation mechanism that maps actions of others onto one’s own motor repertoire (make others “like me” (Meltzoff and Brooks, 2001)). Recently, even passive viewing of static face stimuli has been shown to induce premotor activity (Leslie et al., 2004). Thus, watching faces may induce motor imagery. Perhaps, when one sees one’s own image, these mirror areas are highly activated because of the ease with which one can map oneself onto one’s own motor system. This mapping produces the best “match” or correspondence, reflected in activity of the RH mirror system. Previous work has shown modulation in human “mirror” areas (BA 40 and 44) during imitation of hand movements. In particular, mirror neuron areas are

Table 2

Coordinates (MNI) and peak activation statistics for other–self contrast					
Hemisphere	Region	Coordinates			Max Z score
		x	y	z	
Left	Precuneus	0	–48	38	4.56
Left	DMPFC	–6	52	44	4.26
Left	SFG	–18	34	52	4.25
Left	SFG	–22	22	52	4.15
Left	STG	–54	–42	12	4.62
Right	VMPFC	2	44	–20	4.38
Right	MTG	70	–12	–16	4.06
Right	aSTS	62	–4	–18	3.66

DMPFC = dorsomedial prefrontal cortex; SFG = superior frontal gyrus; STG = superior temporal gyrus; VMPFC = ventromedial prefrontal cortex; MTG = middle temporal gyrus; aSTS = anterior superior temporal sulcus.

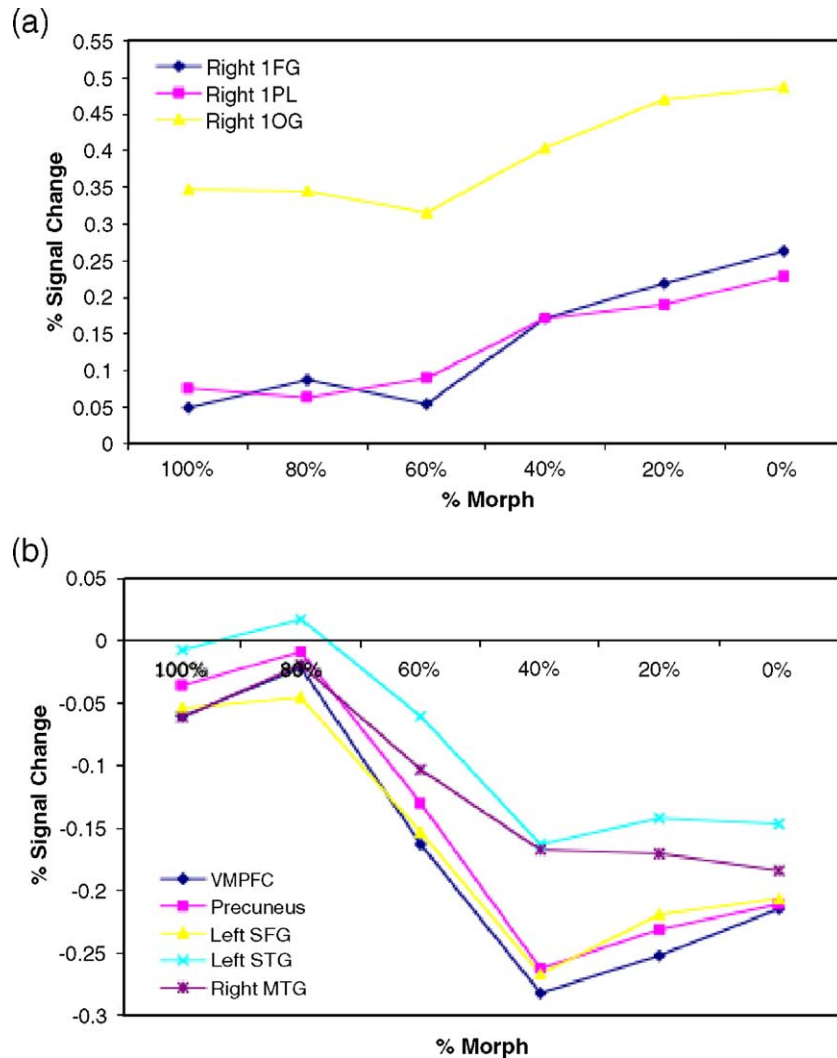


Fig. 4. (a) Activity in IFG, IPL and IOG expressed as signal intensity normalized to average signal intensity at rest in each region. 100% Morph refers to stimuli containing the most other, while 0% Morph refers to those containing the most self. (b) Activity in VMPFC, Precuneus, SFG, STG, and MTG expressed as signal intensity normalized to average signal intensity at rest in each region.

more active when subjects imitate others as in a mirror (specular imitation, i.e., when they see the movements of others as a reflection of their own movements) than during anatomically congruent imitation (Koski et al., 2003). We suggest that the mirror neuron system is thus engaged to the greatest extent when comparing the self to an external stimulus that is most similar to the self. Though some previous self-recognition studies have reported right IFG activation (Keenan et al., 2001a; Platek et al., 2004), none prior to the current study have shown activation of the entire frontoparietal mirror network (Rizzolatti and Craighero, 2004). This may be due to the fact that we controlled for familiarity in such a way that made self–other discriminations more difficult, leading to increased recruitment of the mirror neuron system.

The right inferior occipital gyrus was also active during self-face viewing. It is now fairly widely accepted that face perception activates specific areas in the fusiform gyrus (Kanwisher et al., 1997, but see Haxby et al., 2001). Additionally, the right inferior occipital gyrus has also been shown to exhibit greater responses to faces than to other stimuli (Gauthier et al., 2000), and a recent combined lesion and neuroimaging study has demonstrated that the

right inferior occipital gyrus is necessary for normal face perception (Rossion et al., 2003a). This area has also been shown to discriminate between familiar and unfamiliar faces (Rossion et al., 2003b). Here, we report enhanced right IOG activity for the self-face, perhaps reflecting increased attention towards this salient stimulus, or, alternatively, perceptual familiarity due to numerous exposures. Given that we also found activation in the superior parietal lobule (SPL), the attentional account seems more plausible, as activity in the SPL has previously been shown to increase linearly with attentional load (Jovicich et al., 2001; Mazoyer et al., 2002).

Areas activated by “other”

Interestingly, our task minus rest contrasts reveal that what appears to be activation in midline structures including MPFC and precuneus during viewing of “other” actually results from deactivation compared to baseline in these areas during viewing of “self”. It has been proposed that activity within these midline structures represents a tonic or default mode of cerebral function (Raichle et al., 2001). These areas exhibit task-independent

decreases in activity during goal-directed behavior, generally showing deactivations during cognitive tasks requiring attention to external stimuli (Gusnard and Raichle, 2001), and thus we might expect such deactivations during our task. A recent study by Iacoboni et al. reports increased activity in precuneus and dorsomedial prefrontal cortex compared to a resting baseline during viewing of social interactions. The authors suggest that processing social relationships may be one of the functions of the default network (Iacoboni et al., 2004). This study, along with one conducted by Greene et al. (2001) in which subjects process moral dilemmas, are, to the best of our knowledge, the only two existing reports of joint increased activity compared to baseline in medial parietal and medial prefrontal areas.

Our results show decreased activity in precuneus, ventromedial prefrontal cortex, dorsomedial prefrontal cortex, and posterior superior temporal gyrus (all areas in the default network, (Gusnard and Raichle, 2001; Raichle et al., 2001)) only during processing of “self” stimuli. We propose that the familiar “other” stimuli trigger various social representations, and thus the task-related deactivation is compensated during viewing of the “other” by an increase in activity due to social processing. Thus, the overall result is lack of deactivation for “other”, not a true activation. Our finding here of more activity in these areas during processing of the “other” is consistent with this interpretation. It is possible that during viewing of the familiar “other”, with whom the subjects have a positive social relationship, the subjects automatically activate social representations to a greater extent than when viewing the “self”. In summary, the generalized decrease in these areas due to the task demands is offset in the “other” condition by triggering some social cognitive processing, which previously has been shown to engage these regions (Gobbini et al., 2004; Greene et al., 2001; Iacoboni et al., 2004).

Some previous studies have proposed a link between resting state activity and the self (Gusnard et al., 2001; Wicker et al., 2003). Others have reported instances of self-referential processing and first-person perspective-taking activating these cortical midline structures (Northoff and Bermpohl, 2004; Voegeley and Fink, 2003). An important distinction to be made here is between the self as the subject of experience (as in tasks requiring introspection, self-evaluation, and monitoring one’s own mental state) and the self as an object (as in our task). The “resting state” self-related processing treats the self as the subject of experience, and thus activations reported in such studies likely underlie a very different cognitive process from that evoked by self-face recognition, which treats the self as an object. Additionally, in many of these studies, the self-related activations are contrasted to conditions that require no social cognitive processing. Perhaps, it is this comparison that leads to greater activity in midline structures during “self” processing. If the self is compared to a socially irrelevant condition, as in many previous reports, then the self actually triggers more social representations, which may explain why these studies show differential midline activity (less deactivation) for self-referential processing. In our study, the self is directly compared to a familiar other who is socially relevant to the subject, thus, we see greater midline activity during viewing of that other (Gobbini et al., 2004).

Implications for mirror neurons and mirror self-recognition

An interesting question raised by our finding of mirror neuron areas activating during self-recognition is the following: The main source of mirror neuron data comes from recordings of neurons in

the monkey brain, yet why is it that monkeys do not recognize their own faces (Inoue-Nakamura, 1997b)? The primate literature suggests that only the great apes can recognize themselves in a mirror, and that this may be due to the absence of a sufficiently well integrated self-concept in most primates (Gallup, 1982). It is likely that the mirror neuron system in monkeys is less developed than that in humans. Whereas in monkeys, it has been shown to be involved in simple motor behavior, we hypothesize that in humans the system has evolved to mediate more complex social behaviors, such as imitation (Iacoboni et al., 1999), intention understanding (Iacoboni et al., in press), and maintaining representations of self and others. The exact nature of the source and development of such differences is an open question.

Conclusion

Our data provide evidence for a neural network activated by self-face perception involving right hemisphere structures with mirror properties, including the inferior frontal gyrus and the inferior parietal lobule. These areas show signal increases as the stimuli contain more of the self-face and comprise a network that is likely engaged in maintaining self–other distinctions. Additionally, we observed decreases in activity in “default/resting state” areas during self vs. other recognition. Thus, self-face recognition appears to involve a simulation-like mechanism that recruits right hemisphere mirror neurons networks matching the face stimulus to an internal representation of the self, while other-face recognition recruits midline structures that have previously been implicated in social processing. We provide a model based on the social cognitive aspects of this task to explain the response of these midline structures to highly familiar others and to reconcile our findings with previously published reports. Recognition of the self is one of the most basic yet poorly understood cognitive operations. Using functional neuroimaging allows us to understand its neural mechanisms and develop richer models of the representations of self and other in the brain.

Acknowledgments

Support for this study was provided by NIH Grant RO1 NS20187 and a NSF Graduate Research Fellowship. We thank Julian Keenan for providing the MorphEditor software, and Katie Karlsgodt and Vikas Rao for help with data analysis.

References

- Amsterdam, B., 1972. Mirror self-image reactions before age two. *Dev. Psychobiol.* 5, 297–305.
- Behrens, T., Woolrich, M.W., Smith, S., 2003. Multi-subject null hypothesis testing using a fully bayesian framework: theory. Annual Meeting of the Organization for Human Brain Mapping.
- Bisiach, E., Geminiani, G., 1991. Anosognosia related to hemiplegia and hemianopia. In: Prigatano, G., Schacter, D. (Eds.), *Awareness of Deficit After Brain Injury*. Oxford Univ. Press, New York, pp. 17–39.
- Blanke, O., Ortigue, S., Landis, T., Seeck, M., 2002. Stimulating illusory own-body perceptions. *Nature* 419 (6904), 269–270.
- Brady, N., Campbell, M., Flaherty, M., 2004. My left brain and me: a dissociation in the perception of self and others. *Neuropsychologia* 42, 1156–1161.

- Breen, N., Caine, D., Coltheart, M., 2001. Mirrored-self misidentification: two cases of focal onset dementia. *Neurocase* 7 (3), 239–254.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., et al., 2004. Neural circuits involved in the recognition of actions performed by nonconspicuous: an fMRI study. *J. Cogn. Neurosci.* 16 (1), 114–126.
- Carr, L., Iacoboni, M., Dubeau, M.C., Mazziotta, J.C., Lenzi, G.L., 2003. Neural mechanisms of empathy in humans: a relay from neural systems for imitation to limbic areas. *Proc. Natl. Acad. Sci. U. S. A.* 100 (9), 5497–5502.
- Chaminade, T., Decety, J., 2002. Leader or follower? Involvement of the inferior parietal lobule in agency. *NeuroReport* 13 (15), 1975–1978.
- Dale, A.M., 1999. Optimal experimental design for event-related fMRI. *Hum. Brain Mapp.* 8, 109–114.
- Decety, J., Sommerville, J.A., 2003. Shared representations between self and other: a social cognitive neuroscience view. *Trends Cogn. Sci.* 7 (12), 527–533.
- Decety, J., Chaminade, T., Grezes, J., Meltzoff, A.N., 2002. A PET exploration of the neural mechanisms involved in reciprocal imitation. *NeuroImage* 15 (1), 265–272.
- Devinsky, O., 2000. Right cerebral hemisphere dominance for a sense of corporeal and emotional self. *Epilepsy and Behav.* 1, 60–73.
- Farrer, C., Frith, C.D., 2002. Experiencing oneself vs. another person as being the cause of an action: the neural correlates of the experience of agency. *NeuroImage* 15 (3), 596–603.
- Feinberg, T.E., 2001. *Altered Egos: How the Brain Creates the Self*. Oxford Univ. Press, New York.
- Forman, S.D., Cohen, J.D., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D.C., 1995. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): use of cluster-size threshold. *Magn. Reson. Med.* 33, 636–647.
- Friston, K.J., Worsley, K.J., Frakowiak, R.S.J., Mazziotta, J.C., Evans, A.C., 1994. Assessing the significance of focal activations using their spatial extent. *Hum. Brain Mapp.* 1, 214–220.
- Frith, C.D., Blakemore, S., Wolpert, D.M., 2000a. Explaining the symptoms of schizophrenia: abnormalities in the awareness of action. *Brain Res., Brain Res. Rev.* 31 (2–3), 357–363.
- Frith, C.D., Blakemore, S.J., Wolpert, D.M., 2000b. Abnormalities in the awareness and control of action. *Philos. Trans. R. Soc. Lond., B Biol. Sci.* 355 (1404), 1771–1788.
- Gallese, V., Fadiga, L., Fogassi, L., Rizzolatti, G., 1996. Action recognition in the premotor cortex. *Brain* 119 (Pt. 2), 593–609.
- Gallup, G.G., 1970. Chimpanzees: self-recognition. *Science* 167, 86–87.
- Gallup, G.G.J., 1977. Self-recognition in primates: a comparative approach to the bidirectional properties of consciousness. *Am. Psychol.* 32 (5), 329–338.
- Gallup, G.G., 1982. Self-awareness and the emergence of mind in primates. *Am. J. Primatol.* 2 (3), 237–248.
- Gauthier, I., Tarr, M.J., Moylan, J., Skudlarski, P., Gore, J.C., Anderson, A.W., 2000. The fusiform “face area” is part of a network that processes faces at the individual level. *J. Cogn. Neurosci.* 12 (3), 495–504.
- Gobbini, M.I., Leibenluft, E., Santiago, N., Haxby, J.V., 2004. Social and emotional attachment in the neural representation of faces. *NeuroImage* 22, 1628–1635.
- Greene, J.D., Sommerville, R.B., Nystrom, L.E., Darley, J.M., Cohen, J.D., 2001. An fMRI investigation of emotional engagement in moral judgment. *Science* 293 (5537), 2105–2108.
- 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. *Proc. Natl. Acad. Sci. U. S. A.* 98 (7), 4259–4264.
- Gusnard, D.A., Raichle, M.E., 2001. Searching for a baseline: functional imaging and the resting human brain. *Nat. Rev., Neurosci.* 2 (10), 685–694.
- Haxby, J.V., Gobbini, M.I., Furey, M.L., Ishai, A., Schouten, J.L., Pietrini, P., 2001. Distributed and overlapping representations of faces and objects in ventral temporal cortex. *Science* 293 (5539), 2425–2430.
- Iacoboni, M., Woods, R.P., Brass, M., Bekkering, H., Mazziotta, J.C., Rizzolatti, G., 1999. Cortical mechanisms of human imitation. *Science* 286 (5449), 2526–2528.
- 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 (3), 1167–1173.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J.C., Rizzolatti, G. Grasping the intentions of others with one’s own mirror neuron system. *PLoS Biology*, in press.
- Inoue-Nakamura, N., 1997. Mirror self-recognition in nonhuman primates: a phylogenetic approach. *Jpn. Psychol. Res.* 39, 266–275.
- Jovicich, J., Peters, R.J., Koch, C., Braun, J., Chang, L., Ernst, T., 2001. Brain areas specific for attentional load in a motion-tracking task. *J. Cogn. Neurosci.* 13 (8), 1048–1058.
- Kanwisher, N., McDermott, J., Chun, M.M., 1997. The fusiform face area: a module in human extrastriate cortex specialized for face perception. *J. Neurosci.* 17 (11), 4302–4311.
- Kaplan, J.T., Zaidel, E., 2001. Error monitoring in the hemispheres: the effect of lateralized feedback on lexical decision. *Cognition* 82 (2), 157–178.
- Keenan, J.P., Freund, S., Hamilton, R.H., Ganis, G., Pascual-Leone, A., 2000. Hand response differences in a self-face identification task. *Neuropsychologia* 38, 1047–1053.
- Keenan, J.P., Wheeler, M.A., Gallup Jr., G.G., Pascual-Leone, A., 2000. Self-recognition and the right prefrontal cortex. *Trends Cogn. Sci.* 4 (9), 338–344.
- Keenan, J.P., McCutcheon, N.B., Pascual-Leone, A., 2001. Functional magnetic resonance imaging and event-related potential suggest right prefrontal activation for self-related processing. *Brain Cogn.* 47, 87–91.
- Keenan, J.P., Nelson, A., O’Conner, M., Pascual-Leone, A., 2001. Self-recognition and the right hemisphere. *Nature* 409, 305.
- Keenan, J.P., Wheeler, M., Platek, S.M., Lardi, G., Lassonde, M., 2003. Self-face processing in a callosotomy patient. *Eur. J. Neurosci.* 18 (8), 2391–2395.
- Kircher, T.T., Senior, C., Phillips, M.L., Rabe-Hesketh, S., Benson, P.J., Bullmore, E.T., et al., 2001. Recognizing one’s own face. *Cognition* 78 (1), B1–B15.
- Koski, L., Iacoboni, M., Dubeau, M.C., Woods, R.P., Mazziotta, J.C., 2003. Modulation of cortical activity during different imitative behaviors. *J. Neurophysiol.* 89 (1), 460–471.
- Leslie, K.R., Johnson-Frey, S.H., Grafton, S.T., 2004. Functional imaging of face and hand imitation: towards a motor theory of empathy. *NeuroImage* 21 (2), 601–607.
- Lethmate, J., Ducker, G., 1973. Untersuchungen am selbsterkennen im spiegel bei orangutans einigen anderen affenarten (Self-recognition by orangutans and some other primates). *Z. Tierpsychol.* 33, 248–269.
- Mazoyer, P., Wicker, B., Fonlupt, P., 2002. A neural network elicited by parametric manipulation of the attention load. *NeuroReport* 13 (17), 2331–2334.
- Meltzoff, A.N., Brooks, R., 2001. “Like Me” as a building block for understanding other minds: bodily acts, attention, and intention. In: Malle, B.F., Moses, L.J., Baldwin, D.A. (Eds.), *Intentions and Intentionality: Foundations of Social Cognition*. MIT Press, Cambridge, pp. 171–191.
- Miller, B.L., Seeley, W.W., Mychack, P., Rosen, H.J., Mena, I., Boone, K., 2001. Neuroanatomy of the self: evidence from patients with frontotemporal dementia. *Neurology* 57 (5), 817–821.
- Molnar-Szakacs, I., Iacoboni, M., Koski, L., Mazziotta, J.C., 2004. Functional segregation within pars opercularis of the inferior frontal gyrus: evidence from fMRI studies of imitation and action observation. *Cereb. Cortex*, (Oct. 28).
- Northoff, G., Bermpohl, F., 2004. Cortical midline structures and the self. *Trends Cogn. Sci.* 8 (3), 102–107.
- Platek, S.M., Keenan, J.P., Gallup Jr., G.G., Mohamed, F.B., 2004. Where

- am I? The neurological correlates of self and other. *Brain Res. Cogn. Brain Res.* 19 (2), 114–122.
- Povinelli, D.J., Gallup, G.G.J., Eddy, T.J., Bierschwale, D.T., Engstrom, M.C., Perilloux, H.K., et al., 1997. Chimpanzees recognize themselves in mirrors. *Anim. Behav.* 53, 1083–1088.
- Preilowski, B., 1977. Self-recognition as a test of consciousness in left and right hemisphere of “split-brain” patients. *Act. Nerv. Super. (Praha)* 19 (Suppl. 2), 343–344.
- Preyer, W., 1889. *The Mind of the Child Part II: the Development of the Intellect*. Appleton, New York.
- Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G.L., 2001. A default mode of brain function. *Proc. Natl. Acad. Sci. U. S. A.* 98 (2), 676–682.
- Rizzolatti, G., Craighero, L., 2004. The mirror-neuron system. *Annu. Rev. Neurosci.* 27, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V., Fogassi, L., 1996. Premotor cortex and the recognition of motor actions. *Brain Res. Cogn. Brain Res.* 3 (2), 131–141.
- Rossion, B., Caldara, R., Seghier, M., Schuller, A.M., Lazeyras, F., Mayer, E., 2003. A network of occipito-temporal face-sensitive areas besides the right middle fusiform gyrus is necessary for normal face processing. *Brain* 126 (Pt. 11), 2381–2395.
- Rossion, B., Schiltz, C., Crommelinck, M., 2003. The functionally defined right occipital and fusiform “face areas” discriminate novel from visually familiar faces. *NeuroImage* 19 (3), 877–883.
- Spence, S.A., Brooks, D.J., Hirsch, S.R., Liddle, P.F., Meehan, J., Grasby, P.M., 1997. A PET study of voluntary movement in schizophrenic patients experiencing passivity phenomena (delusions of alien control). *Brain* 120 (Pt. 11), 1997–2011.
- Sperry, R.W., Zaidel, E., Zaidel, D., 1979. Self recognition and social awareness in the disconnected minor hemisphere. *Neuropsychologia* 17 (2), 153–166.
- Sugiura, M., Kawashima, R., Nakamura, K., Okada, K., Kato, T., Nakamura, A., et al., 2000. Passive and active recognition of one’s own face. *NeuroImage* 11, 36–48.
- Turk, D.J., Heatherton, T.F., Kelley, W.M., Funnell, M.G., Gazzaniga, M.S., Macrae, C.N., 2002. Mike or me? Self-recognition in a split-brain patient. *Nat. Neurosci.* 5 (9), 841–842.
- 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. *Ann. N. Y. Acad. Sci.* 1001, 65–78.
- Uddin, L.Q., Keenan, J.P., Mooshagian, E., Rayman, J., Zaidel, E., 2002. Self-recognition in the two cerebral hemispheres. *Annual Conference of the Society for Neuroscience*.
- Uddin, L.Q., Rayman, J., Zaidel, E., 2003. Self-recognition: lessons from the split-brain. *Annual Meeting of the Cognitive Neuroscience Society*.
- Vogeley, K., Fink, G.R., 2003. Neural correlates of the first-person-perspective. *Trends Cogn. Sci.* 7 (1), 38–42.
- Wicker, B., Ruby, P., Royet, J., Fonlupt, P., 2003. A relation between rest and the self in the brain? *Brain Res. Rev.* 43 (2), 224–230.
- Worsley, K.J., Evans, A.C., Marrett, S., Neelin, P., 1992. A three-dimensional statistical analysis for CBF activation studies in human brain. *J. Cereb. Blood Flow Metab.* 12 (6), 900–918.
- Zaidel, E., 1975. A technique for presenting lateralized visual input with prolonged exposure. *Vision Res.* 15, 283–289.
- Zaidel, E., 1979. On measuring hemispheric specialization in man. In: Rybak, B. (Ed.), *Advanced Technobiology*, pp. 365–404.