Research report

Where am I? The neurological correlates of self and other

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Abstract

Although still controversial, there is growing evidence that information about the self is processed in the right hemisphere, specifically the right frontal lobe. It has also been hypothesized that self-awareness and mental state attribution (inferences about the mental experience of others) are part of a similar neurocognitive process [Am. J. Primatol. 2 (1982) 237]. Here we measured blood oxygen level-dependent (BOLD) activity when viewing self-faces and when thinking about the mental states of others. We found significant activation in right superior, middle, and inferior frontal gyri when activation associated with self-face processing was compared with activation associated with familiar famous face processing. Mental state attribution, as measured by a computerized version of the Mind in the Eyes—Revised Test, was associated with activation in the right superior and middle frontal gyri, medial superior frontal gyrus, and left middle frontal gyrus and superior temporal gyrus/temporal pole. Self-face recognition and mental state attribution were colocalized to the middle and superior frontal gyri in the right hemisphere. These data support a model developed over two decades ago by Gallup [Am. J. Primatol. 2 (1982) 237] that posits that self-awareness and mental state attribution are part of a shared neurocognitive suite of processing and that neural architecture implicated in processing knowledge about the self is called upon when inferring knowledge in others.
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1. Introduction

1.1. Self-face recognition

Although not completely resolved in the literature, there is growing evidence that information about the self is processed in the right hemisphere (Ref. [19], but see Turk et al. [50] for counterevidence). Sperry et al. [39], while investigating split-brain patients, demonstrated that the right hemisphere could recognize self-face, and Preilowski [36] discovered that when self-faces were presented to the right hemisphere in callosotomy patients, there was an increased galvanic skin response (GSR). Patients' GSRs when viewing self-faces with the right hemisphere were twice as large as when seeing other faces with the right hemisphere and four times as large as when seeing self-faces with the left hemisphere. Self-recognition dominance in the right hemisphere of a callosotomy patient has recently been replicated (Keenan et al. [24]; see Turk et al. [50] for counterevidence). In spite of the data supporting right hemisphere dominance for self-face processing using callosotomy patients, these are typically $n = 1$ studies and should be interpreted with caution.

Keenan et al. [18,19] recently demonstrated a left-hand advantage for self-face recognition, which, because of contralateral motor control, supports a right hemisphere model for self-processing. Platek and Gallup [31] and Platek et al. [32,33] have now replicated Keenan's results in three independent samples. Keenan et al. [21] recently utilized patients with intractable seizures who were undergoing intracarotid amobarbitol (IAT; i.e., WADA test) anesthetization as a way

of assessing the outcomes of anterior temporal lobectomy. Keenan et al. showed five patients' images of themselves morphed with a famous face during right and left hemispheric anesthetization. When patients recovered, they were queried about the face they were shown. When the left hemisphere was anesthetized (i.e., right hemisphere intact), subjects reported seeing their own face. However, when the right hemisphere (left hemisphere intact) was anesthetized, subjects reported seeing the famous face (see also [48]).

Further evidence of right hemisphere localization of self-recognition comes from case studies of delusional misidentification, particularly mirrored self-misidentification. Breen [5] and Breen et al. [6] have published case studies in which patients have a condition in which they think that the person in the mirror (i.e., the patient's mirrored reflection) is an imposter who follows him or her around. Breen found that it is not a patient's inability to use mirrored information (i.e., understand mirror space) that accounts for the dysfunction because both patients showed the ability to identify the experimenter and other objects using the mirrored space, but persist with the delusion that their own image is "the one who follows 'them' around." Other case reports of delusional mirrored self-misidentification demonstrate similar behavioral patterns [9,38]. It appears that right hemisphere damage is common to each of these cases.

It also appears that information about the self from other sensory domains is processed differentially in the right hemisphere. For example, Platek et al. [34] have shown a left-hand advantage when responding to adjectives that participants reported describe themselves. These findings are supported by functional neuroimaging (positron emission tomography, PET) data, which show that self-descriptive words activate specific areas of the right frontal cortex [8]. Kelley et al. [25] have recently demonstrated right lateralized activity when asked to process information in terms of the self, as well. Again, however, these data are controversial and some groups have found left hemisphere activation using similar experimental paradigms [26,27].

Additionally, we (Platek et al., unpublished data) have recently found that patients who have undergone right temporal lobectomy in order to treat intractable seizures associated with epilepsy were worse (longer response latencies and increased number of errors) when asked to respond to self-faces than patients who had undergone left anterior lobectomy. Further, one right anterior temporal lobectomy patient reported not seeing his face in the experiment; however, when the experiment was evaluated for the presence of the patient's face, the patient's face was present. This suggests that the right anterior lobe may be implicated in self-processing as well. This is consistent with other findings suggesting that the temporal pole and probably uncinate fasciculus are involved in processing information about the self. For example, Wheeler and McMillan [53] showed that episodic memory was impaired in a patient who had damage bilaterally to the temporal poles and uncinate fasciculi.

Although there is mounting evidence in favor of a right hemisphere model for self-processing, some studies have revealed left hemisphere dominance or activation. For example, Turk et al. [50] found left hemisphere advantage for self-face processing using a split-brain patient. These data obvious contradict a right hemisphere model, but one must remember that studies employing split-brain patient as participants are usually $n = 1$ studies and one must maintain some level of skepticism about the generalizability of the results. However, even in the face of these data, of the few split-brain patients tested, most [24,36,39,50] have demonstrated right hemisphere dominance for self-face, suggesting that the patient of Turk et al. may have been unusual.

Kircher et al. [26,27] also disagree with the right hemisphere model for self-processing and have conducted several experiments that have demonstrated increased left hemisphere activation when viewing images of one's own face. However, we feel that there are flaws with Kircher et al.'s procedures. First, unlike Keenan et al. [18,19] and the current study, they use images that are partly morphed and mirror-reversed (i.e., not all self-face and not how one normally sees oneself in a mirror). This represents an instance in which the subject is seeing a face that is supposed to represent an image of him/her, but is slightly altered. This slight change in appearance is tantamount to what Povinelli and Gallup (unpublished data) refer to as "perm shock" (personal communication). Povinelli and Gallup dyed the hair of several chimpanzees that were capable of seeing themselves in a mirror then provided them with mirror exposure. This change in appearance caused increased viewing times of their mirror reflection similar to anecdotal reports of how women react towards mirrors after acquiring a new hairdo (e.g., a perm, dye job, etc.) and similar to the findings of the original report of self-recognition in chimpanzees using the mark test (i.e., increased mirrored self-viewing times when the face was altered with a red mark painted above the eyebrow and on the opposite ear) [12].

Kircher et al.'s paradigm of using varying degree of morphs as a way of precluding habituation to the stimuli may have represented an information-processing load that did not differentially call on self-face recognition. In other words, if a subject is instructed to choose between self and familiar faces, but both the self and familiar faces represent varying degrees of morph between the two faces, as they were in Kircher et al.'s study, the subject may have been calling on another processing system for making mental comparisons. The subject may simply have been comparing each newly presented face with a mental representation of a face from previous trials in order to determine whether the face represented more self-face or familiar face. This is not a self-face recognition task, but rather a facial working memory task tantamount to an N-back working memory task—and working memory has been shown to primarily activate left prefrontal cortex [4]. Finally, a reanalysis of the functional magnetic resonance imaging (fMRI) data of Kircher et al. [26] actually shows a slightly greater amount

of right hemisphere activation in the self-face condition (see Keenan et al. [23]).

1.2. Importance of self-face recognition

In front of mirrors, Gallup [12] discovered an apparent cognitive discontinuity in self-recognition. Unlike several species of monkeys, who typically engage in species-specific social responses (e.g., spitting, threat yawning, and barking) while in front of a mirror, chimpanzees were observed to spontaneously use the mirror to engage in mirror-guided self-directed behaviors (i.e., the chimpanzees used the mirror to groom and inspect parts of their bodies that could not be seen without the mirror). As a way of testing whether the chimpanzees were engaging in self-recognition behaviors, Gallup [12] developed the "mark test." The chimpanzees were anesthetized and a red odorless dye, free of tactile cues, was applied to the eye brow and the opposite ear of four common chimpanzees (*Pan troglodytes*). The chimpanzees were given time to recover from anesthesia, fed, and watered. An initial baseline period served to count the number of times the chimpanzees incidentally touched the marks, which was not significantly greater than chance. When the mirror was put back into the cage, the chimpanzees immediately began investigating the marks—touching and then bringing their fingers to their nose and mouth for further investigation. This led Gallup to hypothesize that chimpanzees possessed the capacity for self-recognition.

Although there is much debate about the importance of the mark test and mirror self-recognition, Gallup [13] hypothesized that in order to recognize your own face in a mirror, you had to first have a concept of self (i.e., you have to know who you are to be able to recognize who is being reflected in the mirror). Therefore, the ability to recognize oneself in the mirror appears to represent a cognitive capacity related to a sense of self-awareness. Further, Gallup [13] hypothesized that only those species capable of self-recognition would also be able to engage in a number of introspectively based social strategies, such as empathy, sympathy, and intentional deception–mental state attribution. Gallup's model suggests that in order to infer the mental experiences of other individuals, one must have a sense of their own experiences (i.e., species that are self-aware could use their experiences to model/infer the mental states of others) (see also Keenan et al. [22]).

1.3. Mental state attribution

Mental state attribution (inferentially modeling the mental experiences of others) also appears to be localized to areas of the frontal cortex. Stone et al. [41,42] present data that suggest that the right hemisphere is implicated in correctly passing a false belief task. They inferred right hemisphere dominance in the task because stroke patients who had bilateral damage performed worse than those

patients who presented with only left hemisphere damage. Furthermore, Baron-Cohen et al. [2], using PET, showed that right orbitofrontal areas were preferentially activated during a task that entailed reading mental state terms.

Happe et al. [16] compared right hemisphere-damaged patients with those who had left hemisphere damage along with normal controls on a number of different theory-of-mind tasks. Not only were patients with damage to the right hemisphere poorer than the other groups in their interpretation of mental state attribution narratives, but they were worse at identifying the point of a joke when the humor required an understanding of the mental state of the characters. Similarly, Stone et al. [41] report that patients with damage to the right frontal cortex had difficulty representing false beliefs or states of mind in other people that were contrary to what they knew to be true. Other data implicating a relationship between damage to the right hemisphere and deficits in mental state attribution are provided by Siegal et al. [37] and Stone et al. [42] and Miler et al. [29].

Recently, Stuss et al. [17,47] provided data that the frontal lobes, primarily the right frontal lobes, are implicated in the ability to infer mental states. Stuss et al. examined a number of patients who had brain lesions in various areas of the brain: right frontal, left frontal, and nonfrontal regions. When tested on the ability to detect an instance of intentional deception, the ability to engage in visual perspective taking, and the ability to understand emotional mental states, patients with frontal lesions performed significantly worse than patients with lesions elsewhere in the brain. Furthermore, those patients with right frontal lesions performed the worst out of all of the patients, further suggesting that the right frontal lobes are necessary for theory of mind. Stuss [43] and Platek et al. [32] have also shown that empathy and the understanding of emotional mental states may also be related to processing information about the self.

Gallup [12,13] (extended in Ref. [14]) has argued that mental state attribution presupposes self-awareness and that self-awareness and mental state attribution likely reside in evolutionarily recent regions of the neocortex (i.e., the frontal lobes). In other words, in order to be in a position to infer what others think, know, want, or intend to do, you must be able to conceive of your own mental experiences. By being aware of your own mental states, you are in a unique position to then model comparable mental experiences of others. Vogeley and Fink [51] and Vogely et al. [52] have provided data in support of this model by showing colocalization in the right frontal/anterior cingulate cortex when participants were asked to think about themselves in the first-person and third-person perspectives.

In an attempt to measure whether self-awareness and mental state attribution are colocalized in the brain as suggested by the Gallup [13] model and the evidence reviewed above, we measured blood oxygen level-dependent (BOLD) activation to self-faces when subtracted from familiar famous faces and when asked to think about mental states

when viewing a computerized version of the Mind in the Eyes—Revised Test developed by Baron-Cohen et al. [3].

1.4. Hypothesis

Our model suggests that self-processing and mental state attribution are part of a shared neurocognitive network—a network dedicated to processing information about the self that is also called upon when the need to interpret other's intentions, behaviors, or thoughts arises. Recent behavioral evidence supports the notion that self-information is processed by similar mechanisms, although the exact means with which these mechanisms work is not yet clear. For example, Platek et al. [33] have recently discovered that information about the self from different sensory domains (self-odor, self-descriptive adjectives, and self-names) facilitates quicker self-face reaction times. These data suggest that self-information may be processed by similar brain substrates independent of processing information that does not pertain to the self. Further, there is growing support that the frontal cortex/prefrontal cortex is involved in processing information about the self [5,6,19,20,21,38,46,49,50]. However, it is important to note that the prefrontal cortex serves primarily as a processing center and may have no "real" function. That being the case, it appears from the existing data as well as the data we present that loci in the frontal/prefrontal cortex are implicated in processing information about the self.

2. Methods

2.1. Subjects

Five right-handed subjects volunteered for participation. All subjects were screened for right handedness using a modified version of the Edinburgh Handedness Inventory [30]. Subjects were graduate and undergraduate students at Drexel University and gave written informed consent.

2.2. Pictures

Prior to scanning, subjects had their pictures taken using a Hewlett Packard 315 digital camera. Subjects were asked not to smile or frown and to maintain a neutral facial expression. The images (self and a famous face; e.g., Albert Einstein) were processed using a 1.8-GHz Dell laptop and Paint Shop Pro (version 3.0) software. All images were converted to grayscale. After images were converted to grayscale, they were cropped just under the chin, from ear to ear, and just below the hairline and centered in the cropped space. Images were made the same size and brightness. Images were mounted on a black background and presented through goggles designed for use in the fMRI environment using Neurobehavioral Systems Presentation 0.51 (NIH-NINDS; http://www.neurobehavioralsystems.

com). Famous faces were downloaded from the Internet and made the same size, grayscale, and brightness as the pictures of the subjects.

2.3. Mind in the Eyes—Revised Test

The revised eyes test consists of 36 images of people's eyes expressing various mental states (e.g., serious or reflective; see Ref. [3] for examples). The revised eyes test appears to be sensitive to deficits in social cognition as evidenced by the fact that patients with autistic spectrum disorders consistently perform poorly when compared to normal controls. We computerized the revised eyes test by scanning each of the 36 panels of the test using a Lexmark X85 scanner. We removed all of the words using Paint Shop Pro (version 3.0) so that we would limit activation due to language processing. Subjects were instructed to think about the mental state of the person depicted in the picture. They were given practice trials prior to scanning to make sure they understood the instructions. Two modified eyes stimuli panels were presented during each 20-s block for 8 s each using Neurobehavioral Systems Presentation 0.51.

2.4. fMRI procedures

Images were collected by a Siemens Magnetom Vision 1.5-T scanner with echoplanar capability (25 mT/m, rapid switching gradients). Initially, the scanning began with collection of high-resolution T1-weighted imaging sequence acquired in the axial plane to locate the positions for in-plane structural images. Imaging parameters were: matrix size $= 256 \times 256$; TR (repetition time) $= 600$ ms; TE (echo time) $= 15$ ms; field of view (FOV) $= 21$ cm; number of excitations (NEX) $= 1$; and slice thickness $= 5$ mm. Contiguous (no gap) axial images were acquired to cover the entire brain (26 slice locations). A precise localization-based standard anatomic marker (AC-PC Line) was used for all subjects [49]. Functional images were acquired with echo planar-free induction decay (EPI-FID; T2*-weighted) sequence in the same plane as the structural images. The functional imaging parameters include: 128×128 matrix; FOV $= 21$ cm; slice thickness $= 5$ mm; TR $= 4$ s; and TE $= 54$ ms minimum. The size of the imaging voxel was $1.72 \times 1.72 \times 5$ mm.

Additional foam pads within the head coil help secure head fixation and prevent motion of the head inside the coil. All the subjects were instructed to lie still throughout the scanning procedure and to look into the goggles during the experiment and to focus on the center of the FOV.

2.5. Design

The study was designed to elicit specific BOLD responses to self-faces and mental state attribution. We used a box car/block design (Fig. 1). The design consists of six blocks that consisted of activation or rest periods that
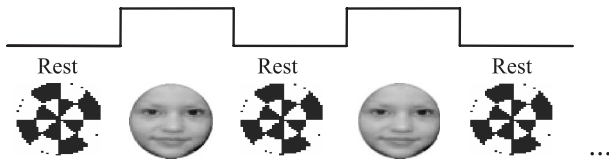
Fig. 1. Box car design. Each epoch lasted 20 s with 20 s of activation and 20 s of rest.

lasted 20 s each. During the activation blocks, subjects saw either an image of their own face, the face of a familiar famous person, or a computerized version of the Mind in the Eyes—Revised Test. Each stimulus was the same within and between blocks for the face blocks. During the face blocks, stimuli flashed on the screen for 1.5 s and was off the screen for 0.5 s; for each 20-s activation block, participants saw 10 flashes of the image. During the mind-in-the-eyes condition, the stimuli were flashed on the screen for 8 s and off for 2 ; for each 20-s activation block, the subject saw two mind-in-the-eyes images. Rest images consisted of a circular checkerboard for the face conditions and a crosshair for the mind-in-the-eyes condition. Rest stimuli flashed on and off the screen at the same rate as activation stimuli.

During the face conditions, subjects were instructed to look at the image being presented and think about whom it was (i.e., subjects were asked to mentally identify the face being presented). During the mind-in-the-eyes condition, subjects were instructed to try and think about what the mental state of the person in the image was. They were instructed to concentrate on the checkerboards and crosshairs during rest conditions. Stimuli were delivered through stereoscopic goggles designed for use within the fMRI environment using Neurobehavioral Systems Presentation version .051 experimental design software (NINDS).

2.6. Spatial preprocessing

The postacquisitional spatial and statistical selections of the analysis were performed using SPM99 (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology, University College of London, UK), run under the MATLAB® (The Mathworks, Natick, MA) environment.

All images were converted from the Siemens format into the ANALYZE (AnalyzeDirect, Lenexa, KY) format adopted in the SPM package. Slice timing correction was performed to compensate for delays associated with acquisition time differences between slices during the sequential imaging. This correction adjusts an MR signal's phase shift so that each volume has the signal values that would have been obtained had each slice been acquired first. A 3D automated image registration routine (six-parameter ridged body, sinc interpolation; second-order adjustment for movement) was applied to the volumes to realign them with the first volume of the first series

used as a spatial reference. All functional and anatomical volumes were then transformed into the standard anatomical space [49] using the T2 EPI template and the SPM normalization procedure [1]. This procedure uses a sinc interpolation algorithm to account for brain size and position with a 12-parameter affine transformation, followed by a series of nonlinear basic function transformations seven and eight, and seven nonlinear basis functions for the x, y, and z directions, respectively, with 12 nonlinear iterations to correct for morphological differences between the template and the given brain volume. Next, all volumes underwent spatial smoothing by convolution with a Gaussian kernel of $3.44 \times 3.44 \times 10$ mm full width at half maximum (FWHM) (two times the voxel size) to increase the signal-to-noise ratio (SRN) and account for residual intersession differences.

To determine the spatial extent of the fMRI activation and to subsequently determine the BOLD signal, the SPM General Linear Model (GLM) procedures were used to identify the voxels associated with the self-face and famous face images and the mind-in-the-eyes active conditions. Voxel-based ANCOVAs were performed and statistical parametric maps (SPM$\{t\}$) were obtained, reflecting significantly activated voxels for the task and model used ($p < 0.05$). SPM incorporates voxel-wise statistical corrections (Bonnferoni) and allows for confidence using small sample sizes.

A priori comparisons were made between self-images and famous images, and mind-in-the-eyes and rest (checkerboard) conditions. Initially, activation involved with viewing self-faces was compared to rest and famous face conditions. Mind-in-the-eyes task was compared with rest condition.

3. Results

3.1. Self-face−famous face

Subtraction analysis between self-face and famous face conditions revealed significant activations for self-face recognition in the right frontal cortex. When subtracting activations common to self-faces and famous faces, there were significant activations for self-face in the right superior ($p < 0.01$), middle ($p < 0.01$), and inferior gyri ($p < 0.05$; see Table 1 and Fig. 1).

Table 1
Brain activations (Talairach coordinates) comparing activation when viewing self-faces with famous faces

Right hemisphere	Coordinates			BA	p value
	x	y	z		
Middle frontal gyrus	42	22	47	8	< 0.01
Superior frontal gyrus	39	22	49	9	< 0.01
Inferior frontal gyrus	42	8	27	–	< 0.05

Table 2
Brain activations (Talairach coordinates) during Mind in the Eyes—Revised Test [3]

Right Hemisphere	Coordinates			BA	p value
	x	y	z		
Middle frontal gyrus	42	22	47	8	< 0.05
Superior frontal gyrus	39	22	49	9	< 0.05
Inferior frontal gyrus	42	8	27	–	n.s.
Medial frontal lobe					
Medial superior frontal gyrus	5	34	57	6	< 0.01
Left hemisphere					
Middle frontal gyrus	– 46	28	19	46	< 0.01
Superior temporal gyrus temporal pole	– 46	20	– 18	38	< 0.01

3.2. "Mind in the Eyes" test

The Mind in the Eyes—Revised Test [3] activated frontal regions bilaterally and medial frontal lobe as well. Significant activation was observed in the middle frontal gyrus bilaterally, left superior temporal gyrus/temporal pole, and medial superior frontal gyrus (Table 2).

4. Discussion

These data provide support for the right hemisphere model of self-awareness [14,19,22,23] by demonstrating right frontal lateralized activation for self-face recognition. Further, these data support the model posited by Gallup [13] by showing an overlap in neural activation between self-face and a mental state attribution task [52]. The areas, active during the Mind in the Eyes—Revised Test in the right hemisphere, corresponded almost exactly with right hemisphere activation in the self-face condition (see Figs. 1 and 2, panel a). These data suggest that the areas of the brain responsible for an ability to inferentially model another's mind may presuppose an underlying neural capacity for self-processing and that neurocognitive mechanisms implicated in social cognition (e.g., self-awareness, mental state attribution) may be processed by similar regions of neocortex. These findings also support recent data suggesting that the frontal lobes are implicated in

processing the theory of mind and the Mind in the Eyes test [15] (Fig. 3 panel c).

Further, our data support previous data that mental state attribution is associated with activation outside of the right frontal lobe. We found activation in temporal pole and medial prefrontal cortex (MPFC) as well. For example, Fletcher et al. [10] found MPFC when comparing activation associated with reading mentalizing stories with reading physical stories. Gallagher et al. [11] and Vogely et al. [52] found a similar MPFC activation associated with mental state processing. In a test similar to the test of understanding intention in chimpanzees by Povinelli et al. [35], Berthoz et al. (2002) reported temporal polar and MPFC activation associated when reading social transgressions that were both deliberate and accidental. These data extend those of Castelli et al. [7] and Klin et al. [28], which demonstrated activation in temporal pole and MPFC when observing motion in inanimate objects that could be interpreted as having intention or desire. Whereas our study replicates most previous works on mental state attribution in showing MPFC activation, our study differs in that we only found superior temporal gyrus/temporal pole activation in the left hemisphere.

A large variability in findings has produced controversy surrounding the localization of important constructs such as self-awareness and mental state attribution. For example, some researchers champion a left hemisphere model of self [26,27,50]. However, in light of the current study, we think that much of the variance surrounding studies of this type lies in the stimuli used. Almost every test of theory of mind has used a different assay of the capacity, suggesting that the neural correlates for theory of mind extend beyond only the right frontal cortex. Indeed, we agree with the notion that mental state attribution is processed in areas other than the right hemisphere, but we believe that the ability to process information about other minds rests in one's ability to process information about their own mind (i.e., self-processing). It is from the development of an ability to process information about the self that we believe mental state attribution develops. This is an empirical statement (e.g., one could use fMRI to measure the developmental trajectory of mirror self-recognition while simultaneously observing neural activity to theory-of-mind tasks as a function of age and mental
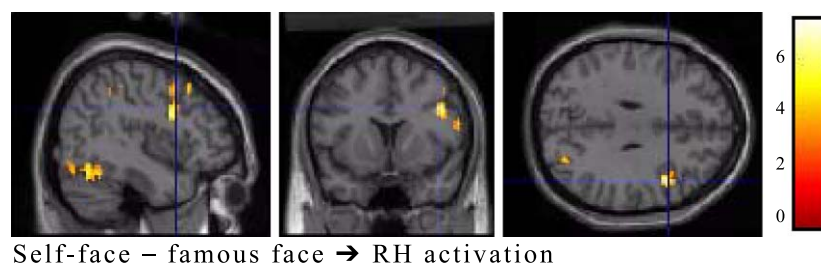

Self-face − famous face ➔ RH activation

Fig. 2. Right frontal activation associated with viewing self-faces (self-face−famous face). Bar indicates *t* statistic value: range 1−6.

(a)

"Mind in the eyes" (right hemisphere activation)

(b)

"Mind in the eyes task" (left hemisphere activation)
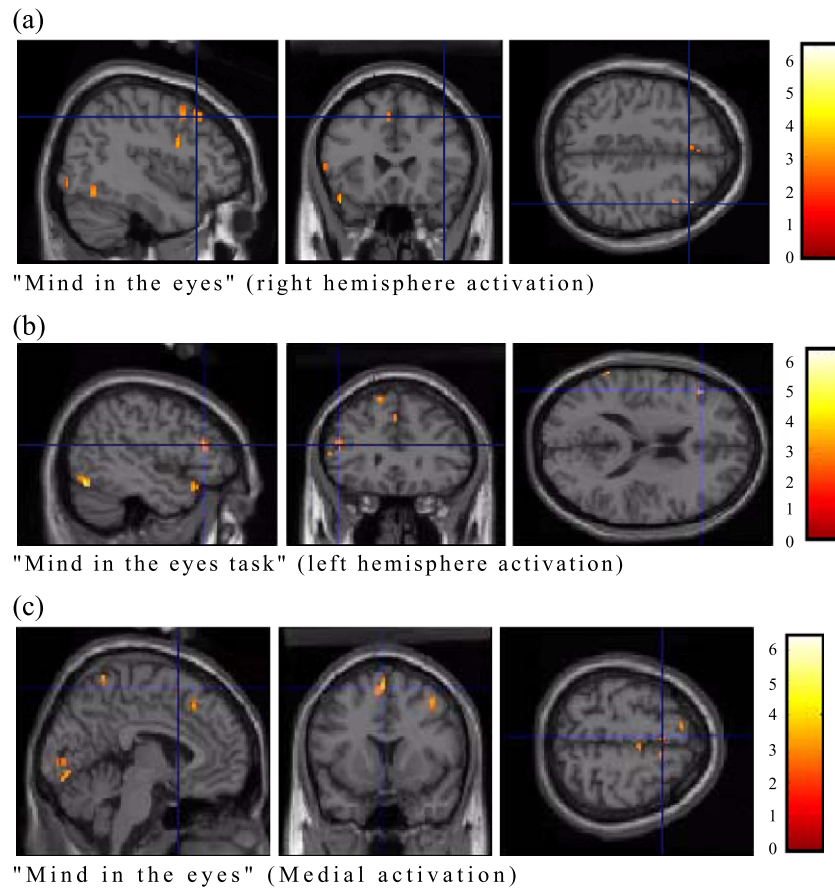
(c)

"Mind in the eyes" (Medial activation)

Fig. 3. Bilateral frontal (panels a and b) and medial frontal (c) activation associated with the "mind-in-the-eyes task" (Baron-Cohen et al., 2001 [3]). Bar indicates t statistic value: range $1-6$. (a) "Mind in the eyes" (right hemisphere activation); (b)"mind-in-the-eyes task" (left hemisphere activation); and (c)"mind in the eyes (medical activation)."

sophistication). Baron-Cohen et al. [2,3] have performed some of the preliminary investigations of this type by investigating how autistic and Asperger patients process theory-of-mind tasks. They have consistently found that patients with autism and Asperger exhibit deficits in theory-of-mind tasks. It is interesting to note that these patients also show delayed onset, and sometimes absence of mirror self-recognition [40].

In conclusion, these data are consistent with the hypothesis that the right hemisphere is important for self-awareness [44,45,47]. Further, damage to the right hemisphere, but not the left hemisphere, tends to alter one's personality and sense of self [25]. Recently, Keenan et al. [24], by testing a patient who had undergone corpus callosotomy, demonstrated that the right hemisphere was more likely to detect self in a self-famous morph when less of the self-face was in the morph.

It is important to note that this study and the interpretation of our results were guided by an a priori theoretical perspective suggesting that mental state attribution and self-processing share neural substrates. These data support the model that individuals (and species) that can conceive of themselves, or process information about their self, may be in a position to mentally model the experiences of others and that damage to regions implicated in self-processing should effectively damage an individual's ability to engage in self-awareness, mental state attribution, and hence appropriate social cognitive behaviors.

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