

Neural Representations of Self versus Other: Visual–Spatial Perspective Taking and Agency in a Virtual Ball-tossing Game

Nicole David¹, Bettina H. Bewernick¹, Michael X Cohen²,
Albert Newen³, Silke Lux⁴, Gereon R. Fink^{4,5}, N. Jon Shah⁴,
and Kai Vogeley^{1,4}

Abstract

Human self-consciousness relies on the ability to distinguish between oneself and others. We sought to explore the neural correlates involved in self–other representations by investigating two critical processes: perspective taking and agency. Although recent research has shed light on the neural processes underlying these phenomena, little is known about how they overlap or interact at the neural level. In a two-factorial functional magnetic resonance imaging (fMRI) experiment, participants played a ball-tossing game with two virtual characters (“avatars”). During an active/agency (ACT) task, subjects threw a ball to one of the avatars by pressing a button. During a passive/nonagency (PAS) task, they indicated which of the other avatars threw the ball. Both tasks were performed from a first-person perspective (1PP), in which subjects interacted from their own

perspective, and a third-person perspective (3PP), in which subjects interacted from the perspective of an avatar with another location in space. fMRI analyses revealed overlapping activity in medial prefrontal regions associated with representations of one’s own perspective and actions (1PP and ACT), and overlapping activity in temporal–occipital, premotor, and inferior frontal, as well as posterior parietal regions associated with representation of others’ perspectives and actions (3PP and PAS). These findings provide evidence for distinct neural substrates underlying representations of the self and others and provide support for the idea that the medial prefrontal cortex crucially contributes to a neural basis of the self. The lack of a statistically significant interaction suggests that perspective taking and agency represent independent constituents of self-consciousness. ■

INTRODUCTION

The question of how to conceptualize and operationalize human self-consciousness is a long-standing philosophical debate with very different views and models. The cognitive neuroscience approach to self-consciousness conceptualizes the self as “a set of representational capacities of the physical brain” instead of an abstract, nonphysical construct (Churchland, 2002; Dehaene & Naccache, 2001). This view offers the possibility to develop experimental paradigms as operationalizations of self-consciousness.

The ability to distinguish oneself from others is undeniably central to self-consciousness. This is supported by evidence from developmental psychology that suggests that self-consciousness emerges through the infant’s interactions with others by comparing and distinguishing states of the self with those of others (Decety & Chaminade, 2003; Rochat & Striano, 2000). Other evidence comes from psychopathological syndromes (e.g.,

delusions) that affect the integrity of self-consciousness in which the ability to distinguish one’s own mental and bodily states from mental or bodily states of others can be impaired (Feinberg, 2001; Franck et al., 2001; Spence et al., 1997). Within the realm of a cognitive neuroscience approach to self-consciousness, the self–other distinction has become an intriguing topic. Processes involved in self–other distinctions have been investigated by studies that attempted to examine neural representations of self and other. These studies typically investigated the introspective ability or self versus other evaluations, for example, with respect to emotions, food preferences, or trait adjectives (Ochsner et al., 2004; Seger, Stone, & Keenan, 2004; Kelley et al., 2002), the ability to recognize one’s own face in contrast to faces of others (Uddin, Kaplan, Molnar-Szakacs, Zaidel, & Iacoboni, 2005; Turk et al., 2002; Keenan, Freund, Hamilton, Ganis, & Pascual-Leone, 2000), the ability to distinguish between actions generated by oneself versus actions generated by others (Farrer, Franck, Georgieff, et al., 2003; Farrer & Frith, 2002), or the ability to take one’s own perspective in contrast to that of another person (Vogeley, May, et al., 2004; Ruby & Decety, 2001, 2003,

¹University of Cologne, Germany, ²University of Bonn, Germany, ³University of Tuebingen, Germany, ⁴Research Center Juelich, Germany, ⁵University of Aachen, Germany

2004; Stuss, Gallup, & Alexander, 2001; Vogeley, Bussfeld, et al., 2001). These studies revealed slightly different neural networks implicated in self–other distinctions depending on the task used, but consistently implicated structures within a frontoparietal network in self–other distinctions, with particular emphasis on medial prefrontal, posterior temporal, and parietal cortices.

Here, we focused on two aspects critical to self–other distinctions: agency, the ability to experience ourselves as agents of our own actions and to attribute them to ourselves rather than to other persons (Gallagher, 2000), and the experience of a first-person perspective (in contrast to taking another person’s perspective). These two processes have been proposed to be key components of self-consciousness (Newen & Vogeley, 2003; Vogeley & Fink, 2003; Gallagher, 2000; Metzinger, 2000; Vogeley, Kurthen, Falkai, & Maier, 1999). Unfortunately, these models of self-consciousness¹ simply propose that these components are distinct dimensions of self-consciousness, without discussing how they may overlap or interact. Likewise, empirically, perspective taking and the sense of agency have mostly been studied in isolation (e.g., Sato & Yasuda, 2005; Vogeley, May, et al., 2004; Farrer & Frith, 2002), but there is reason to think that a better understanding of these processes would arise from studying them in conjunction. For example, in schizophrenia, both processes can be impaired simultaneously, leading to symptoms such as delusions of control, thought insertion, and deficits in social interactions (Frith, 2003; Franck et al., 2001; Frith & Frith, 1999; Spence et al., 1997). A common impairment of the sense of agency and perspective taking suggests that these processes may be functionally interwoven or rely on shared neural substrates. Only one previous positron emission tomography (PET) study included both perspective taking and agency by examining the effect of perspective taking on the neural networks engaged during mental simulation of action (Ruby & Decety, 2001). They found differential activation within the posterior parietal, posterior cingulate, frontopolar, and somatosensory cortex involved in action simulation from a first- versus a third-person perspective, but, unfortunately, they did not test for an interaction between these factors.

We therefore sought to investigate both perspective taking and agency in a 2×2 design using functional magnetic resonance imaging (fMRI) to identify commonalities, distinctions, and possible interactions between these factors at the neural level. Taking a first-person perspective was compared to taking another person’s perspective, and this was examined in relation to being an agent or to observing another person as being an agent. We specifically focused on visual–spatial perspective taking, although other forms of perspective taking exist (e.g., Frith & Frith, 1999; Baron-Cohen, 1997). Visual–spatial perspective taking is the ability to disengage one’s own visual–spatial perspective, for ex-

ample, by imagining what someone across the room can or cannot see (Newcombe, 1989). We utilized dynamic, lifelike stimuli that depicted a basic form of social interaction: playing a ball-tossing game with others. We manipulated visual–spatial perspective taking by letting subjects interact from their own, first-person perspective, versus interact from the perspective of another person in space (third-person perspective). Agency was manipulated by including a task in which subjects actively tossed the ball, versus a passive task in which they observed somebody else tossing the ball. Both tasks had to be performed from both perspectives.

We predicted that an experimental conjunction between perspective taking and agency would reveal overlapping neural substrates. More specifically, we expected self-representations such as taking a first-person perspective and being an agent to overlap on the one hand, and representations of others such as taking another person’s perspective and observing another person being an agent to overlap on the other hand. Although interactions between perspective taking and agency have not been previously investigated, it is possible that interactions could occur, for example, if perspective taking is more critical when observing others’ actions than acting oneself, as the goal of perspective taking is to understand and predict other people’s behavior. An interaction between perspective taking and agency would suggest that the two processes either depend on each other or share common core features and thus should not be considered independent constituents of self-consciousness.

METHODS

Subjects

Thirteen healthy male volunteers (age 25.2 ± 4.8 years) without significant psychiatric or neurological history were recruited. We studied only male volunteers to avoid variation in brain size and shape between sexes in order to improve image normalization. In addition, there is evidence for sex differences in spatial rotation tasks with regard to behavioral performance and hemispheric engagement (e.g., Parsons et al., 2004). All subjects were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Informed consent was obtained before participation. The study was approved by the ethics committee of the University of Bonn.

Stimulus Material, Tasks, and Study Design

We employed a 2×2 factorial design, with the factors Agency (active vs. passive) and Perspective Taking (first-person vs. third-person perspective) manipulated in a virtual ball-tossing game (see Figure 1). 3-D animated scenes and virtual characters (“avatars”) were generated using the software 3D Studio Max (version 4.0, Discreet,

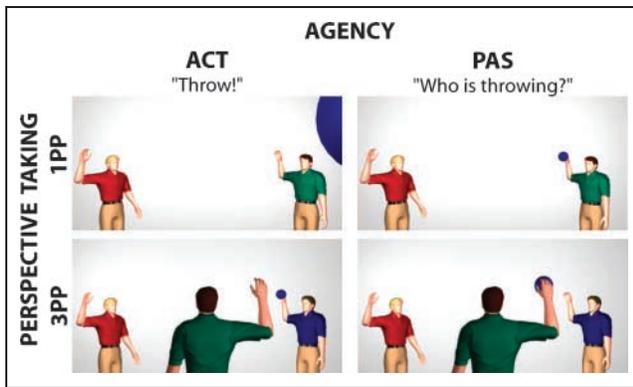


Figure 1. Experimental design and stimuli: 2×2 design with the factors Perspective Taking and Agency. Each factor comprised two levels: a first-person perspective (1PP) vs. a third-person perspective (3PP) for Perspective Taking, and an active task (ACT) vs. a passive task (PAS) for Agency. Instructions are given in quotes.

Division of Autodesk, Montreal, Canada) and Poser (version 5, Curious Labs, Inc., Santa Cruz, CA). Subjects interacted with two avatars, which differed in the color of their shirts (green or red) and hair (blond or brown). One avatar was located to the subject's left side (i.e., in the left visual hemifield), the other to the subject's right side, thus forming a triangular constellation with the subject (Figure 1, top). Avatars switched locations in a pseudorandomized fashion, standing either to the subject's left or right side.

Subjects performed two tasks (Agency manipulation). In the active (ACT) task, subjects were in possession of a ball (located in the upper right corner to render the visual impression for a right-hander with an elevated arm) and were instructed to throw it to the red avatar. Subjects threw by pressing a corresponding button (left or right) on an MRI-compatible handheld response device (Lumitouch, Lightwave Medical Industries, CST Coldswitch Technologies, Richmond, CA). In the passive task (PAS), one of the two avatars was in possession of the ball, and subjects had to indicate the ball's position in relation to themselves (left or right side) with a button press. The avatar also threw the ball, but its behavior was independent of subjects' responses. Both tasks, thus, required the subject to make left–right decisions (to locate the red avatar or the ball).

These tasks were performed from two different perspectives (Perspective Taking manipulation). During first-person perspective (1PP), subjects interacted from their own viewpoint, whereas during third-person perspective (3PP), they had to perform the task from one of the avatar's perspectives instead of from their own. To facilitate this, a third avatar (with a blue shirt) was included in the game, from whose perspective the subject had to perform both tasks (see Figure 1, bottom). The subject was told to identify with this avatar and to imagine himself standing in its position (i.e., perform a transformation of his egocentric perspective). This

avatar also changed positions but never stood in the middle front of the display to avoid an analogue of a first-person perspective. Our experimental paradigm was inspired by the mental own-body transformation (OBT) task, previously used by Blanke et al. (2005) and Zacks, Rypma, Gabrieli, Tversky, and Glover (1999), which requires the subject to make a left–right decision from either his own egocentric perspective or from a mentally transformed egocentric perspective.

The following features of the stimuli were counterbalanced and systematically varied: left/right responses of subjects, position of the red and, in case of 3PP, also of the blue avatar, and direction to which avatars threw the ball during PAS conditions. The study was conducted as a block design. There were four experimental conditions: 1PP_ACT (A), 1PP_PAS (B), 3PP_ACT (C), and 3PP_PAS (D). Each run consisted of 2×4 symmetric sets of experimental blocks of 38.4 sec (e.g., ABCDDCBA), separated by baseline blocks (crosshair) of 17.14 sec. Orders of experimental blocks were counterbalanced across runs, so that each condition appeared at each location in the 2×4 sequence. Eight stimulus events per block were presented. A stimulus event lasted 4.8 sec and consisted of a brief precue (80 msec), a cue image (max. 2250 msec), and a corresponding video outcome (2470 msec). The cue image depicted a static basic scene (see Figure 1) and was shown until the subject made a response (only in ACT conditions). To evoke a sense of agency, immediately after the subject's response a video file was played that showed the ball flying in the intended direction. Subjects lost the chance to throw the ball after 2250 msec; in this case, a static image was shown instead. In PAS conditions, the cue duration was varied (1600–2250 msec) and randomized to induce the experience of contingency of one's own (button press) and the avatar's behavior (throwing ball). Instructions were displayed for 4 sec condition before a block started. In total, there were 18 different cue images and 36 different video outcomes. The number of basic cue images and potential ball trajectories (outcome video files) differed across conditions. Whereas only two different cue images and four different video files could be randomized in the 1PP_ACT condition, there were four different cue images and eight different video outcomes in 1PP_PAS and 3PP_ACT, and eight cues and 16 videos in 3PP_PAS conditions. Stimuli were programmed and presented centered on a light gray background using the Presentation software (Version 0.76, Neurobehavioral systems, Albany, CA).

Before scanning, subjects practiced each condition outside the scanner in a standardized way. In the scanner, subjects looked through a mirror mounted on the head coil to view a screen on which stimuli were projected. To prevent systematic effects of hand lateralization on task performance and brain activation, subjects alternately used the right or left hand across runs, which was also randomized across subjects. Thus, we

also balanced visual hemifield hand interactions as being crossed and uncrossed (Iacoboni & Zaidel, 2004). In order to get an impression of the subjects' experiences during the experiment, they filled out a qualitative postscan questionnaire developed by the experimenter in which they indicated whether they experienced a sense of agency during ACT conditions and how they performed perspective taking during 3PP conditions.

Statistical Analyses of Behavioral Data

Statistical analyses were performed using SPSS for Windows (Version 11.0). Dependent variables were reaction times (RTs) and accuracy (percentage of correct responses). We used a three-way repeated measures ANOVA with the factors Perspective Taking (1PP vs. 3PP), Agency (ACT vs. PAS), and Time (four scanning runs) as within-subject factors. Furthermore, Hand was added as a factor to test whether subjects showed differences in performance when responding with their nondominant left hand. In addition, we ran two-tailed Spearman correlations to determine potential speed-accuracy trade-offs in subjects' performance. The significance level for all analyses was set at $p < .05$.

fMRI Image Acquisition

Functional and structural MRI were performed on a Siemens 1.5T MRI whole-body scanner (SIEMENS Sonata, Erlangen, Germany) using a standard head coil and a custom-built head holder to reduce head movement. Functional images were obtained using a single-shot gradient-echo, echo-planar imaging (EPI) sequence (TR 3020 msec, TE 60 msec, 90° flip angle, FOV 200 mm, matrix 64 × 64, voxel size 3 × 3 × 4 mm). Each EPI volume contained 30 axial slices covering the whole brain. Each session contained 165 functional images. To aid in localization of activation, a high-resolution T1-weighted magnetization-prepared rapid gradient-echo imaging (MP-RAGE) 3-D MRI sequence was acquired from each subject (TR 2200 msec, TE: 3.93 msec, 15° flip angle, FOV 256 mm, matrix 256 × 256, voxel size 1 × 1 × 1 mm).

fMRI Image Preprocessing and Analyses

Functional images were preprocessed and statistically analyzed using SPM2 (Wellcome Department of Imaging Neuroscience, London, UK) implemented in MATLAB 6.5 (Mathworks Inc., Sherborn, MA). The first three repetitions of each EPI series were discarded before image analyses to allow for T1 saturation effects. Images were reoriented (along the AC-PC line) and eyes were masked to avoid artifacts. Images were then corrected for movement (realigned and unwarped), coregistered, normalized to stereotactic space, and spatially smoothed with a 10-mm Gaussian kernel. Statistical analyses were performed on single-subject and group data using the

modified general linear model in SPM (Friston et al., 1995). Subject-specific, low-frequency drifts in signal changes were removed by a high-pass filter of 256 sec, and serial autocorrelation was corrected for. For each subject and each condition, a comparison of interest was implemented as an individual contrast image. For group comparisons, these contrast images were used in a second-level analysis, treating subjects as a random effect. We then performed a within-subjects ANOVA with replications over subjects (including sphericity correction) to test differences in neural activity between factor levels and the two-way interaction. We primarily report differential activation patterns associated with 1PP in contrast to 3PP (in the following just referred to as "1PP") and vice versa (referred to as "3PP") collapsed across the factor Agency, or ACT in contrast to PAS (in the following just referred to as "ACT") and vice versa (referred to as "PAS") collapsed across Perspective Taking.

Activations were identified using a corrected (with False Discovery Rate; Genovese, Lazar, & Nichols, 2002) two-tailed height threshold of $p < .05$ and an extent threshold of $k = 10$ contiguous voxels throughout the brain. We additionally report regions surviving a two-tailed uncorrected threshold of $p < .0005$ for which we had a strong a priori hypothesis, namely, medial prefrontal cortical regions during 1PP and ACT. In addition, the 1PP contrast served as a search volume for the ACT contrast in a post hoc analysis ($p < .05$, two-tailed, FDR corrected, $k = 10$), for which we used tools that allow region-of-interest (ROI) analyses such as Marsbar (marsbar.sourceforge.net/) and the WKU Pick-Atlas (www.fmri.wfubmc.edu/download.htm). Furthermore, we used an inclusive masking procedure (ACT inclusively masked by 1PP) as implemented in SPM2 to determine the voxels that were commonly activated (at $p_{(1PP)} < .0005$ and $p_{(ACT)} < .0005$, uncorrected, and $k = 10$) between the main effects 1PP and ACT that presumably concerned representations of the self. We also performed inclusive masking to show commonalities between the main effects that presumably concerned representations of others (PAS inclusively masked by 3PP) as well as between the presumably nonmatching effects (ACT inclusively masked by 3PP; PAS inclusively masked by 1PP). With Marsbar, implemented in Matlab, the percentage of overlapping voxels between the contrast images were determined. Resulting activation peaks were superimposed on a normalized high-resolution MP-RAGE (averaged across subjects) and anatomically localized using an atlas of the human brain (Duvernoy, 1999) and MRICro (www.mricro.com). Approximately corresponding Brodmann's areas (BAs) were determined using the MRICro software based on Talairach and Tournoux (1988). We note that the Talairach and Tournoux version of the Brodmann map does not reflect the complete and up-to-date cytoarchitectonic organization of the human brain (e.g., Eickhoff et al., 2005; Brett,

Johnsrude, & Owen, 2002). Nevertheless, BAs are given for the reader's convenience.

In order to evaluate the contribution of each condition to the main effects and to interpret possible interactions, we created spheres with a 5-mm radius around principally activated voxels for each main contrast on the second level and extracted parameter estimates for each condition as compared to baseline on the single-subject level. The parameter estimates were then averaged across subjects. Resulting means and standard errors of the mean (*SEMs*) were plotted. To statistically test for interaction effects, a two-way repeated measures ANOVA was performed on the parameter estimates.

RESULTS

Behavioral Data

Means and standard errors of the mean are reported in Table 1. We did not detect any significant speed-accuracy trade-offs in subjects' performances. For RTs, there was no interaction between Agency and Perspective Taking, $F(1,12) = .68$, *ns*, but there were significant main effects: Subjects were significantly slower in 3PP than in 1PP, $F(1,12) = 302.87$, $p < .001$, and faster in ACT (when making an action) than in PAS (when observing an action), $F(1,12) = 18.03$, $p < .005$.

By contrast, with respect to accuracy, we observed a significant interaction between Perspective Taking and Agency, $F(1,12) = 8.69$, $p < .05$: There is a difference in accuracy between ACT and PAS for 3PP, but not for 1PP (Table 1). Planned comparisons confirmed that subjects were significantly less accurate performing the PAS task from 3PP, $F(1,12) = 14.35$, $p < .005$. However, this result has to be interpreted with caution because it could be influenced by the very high accuracy during 1PP for either ACT or PAS, which may represent a ceiling effect. Time (i.e., potential learning or fatigue effects over runs) had no influence on RT, $F(3,36) = 1.06$, *ns*, or accuracy, $F(3,36) = 1.69$, *ns*. Hand also did not influence task performance (all F s < 1).

fMRI Data

Main suprathreshold activation clusters for all analyses reported here are presented in Tables 2–5. Increased neural activity during 1PP, relative to 3PP, was observed in

Table 1. Behavioral Data

	1PP_ACT		1PP_PAS		3PP_ACT		3PP_PAS	
	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>	<i>M</i>	<i>SEM</i>
RT (msec)	541.6	25.0	604.3	28.8	1060.7	50.2	1150.6	41.5
% Correct	99.5	0.4	99.0	0.4	93.0	1.6	86.8	2.3

Means (*M*) and standard errors of the mean (*SEM*) of reaction time (RT) and percentage of correct responses (% correct).

Table 2. Main Suprathreshold Clusters for Perspective Taking

<i>MNI Coordinates</i>	<i>t</i>	<i>Cluster Size</i>	<i>Cluster Anatomical Region</i>	<i>BA</i>
<i>1PP (1PP > 3PP)</i>				
-2 44 -8	6.84	3800	L. medial prefrontal/cingulate	10
-62 -20 -14	5.00	216	L. middle temporal	21
-56 -64 30	4.69	84	L. inferior parietal (angular)	39
-28 -4 -12	4.65	324	L. amygdala	34
-4 -24 44	4.50	704	L. cingulate	23
54 6 -32	4.20	75	R. middle temporal	21
-32 34 -12	4.02	38	L. posterior orbitofrontal	47
20 36 52	3.96	11	R. superior frontal	9
-12 -50 8	3.94	38	L. calcarine	30
6 -10 48	3.87	42	R. cingulate	~23
-8 -52 30	3.79	75	L. cingulate	23
-6 -88 30	3.78	21	L. cuneus	19
-48 -10 -8	3.75	14	L. superior temporal	~22
<i>3PP (3PP > 1PP)</i>				
-34 -56 56	9.56	29562	L. inferior parietal (angular)	~40
-44 8 34	8.80	3549	L. inferior frontal	44
38 2 54	6.14	2855	R. middle frontal, superior part	6
2 -36 -40	5.09	274	R. brainstem	
18 -26 14	4.90	325	R. thalamus	
34 22 2	4.60	399	R. insula, anterior part	47
-36 22 2	4.41	248	L. insula, anterior part	47
4 16 46	4.35	455	R. cingulate	32
-18 -22 12	3.87	208	L. thalamus	
40 56 6	3.39	44	R. middle frontal, inferior part	10
32 -64 -50	3.01	39	R. cerebellum	

$p < .05$, two tailed, corrected. MNI coordinates (*x, y, z*), *t* values of regions active in each contrast, Brodmann's area (BA) if applicable. L = left hemisphere, R = right hemisphere.

cortical midline structures such as the left medial prefrontal cortex (MPFC) (extending to the superior frontal and right anterior cingulate cortex) and bilateral posterior cingulate cortices (with subclusters in the left precentral gyrus and right supplementary motor area), and in temporal regions including bilateral middle temporal gyrus, left superior temporal gyrus, and left amygdala (extending to the left hippocampus and the left puta-

Table 3. Main Suprathreshold Clusters for Agency

MNI Coordinates			<i>t</i>	Cluster Size	Anatomical Region	BA
<i>ACT (ACT > PAS)</i>						
-14	46	10	4.55	228	L. cingulate	32
-10	40	46	4.17	68	L. superior frontal	9
-8	58	20	4.15	106	L. superior frontal	10
4	-56	-50	4.14	22	R. cerebellum	
14	46	22	4.12	18	R. cingulate/ superior frontal	32
<i>PAS (PAS > ACT)</i>						
50	-72	2	9.20	3822	R. middle occipital	37
-50	-58	16	6.87	2279	L. superior temporal, posterior part	37
6	-54	50	5.39	855	R. precuneus	
28	-78	40	4.43	274	R. superior occipital	19
-38	-46	-18	4.12	35	L. fusiform	37
44	4	50	4.11	290	R. middle frontal, superior part	6
-52	22	34	3.93	28	L. middle frontal, inferior part	44
-36	0	62	3.79	23	L. middle frontal, superior part	6
28	-82	12	3.68	29	R. middle occipital, superior part	18
58	-38	54	3.58	13	R. inferior parietal (supramarginal)	40
44	-52	54	3.39	10	R. inferior parietal (intraparietal sulcus)	40

ACT > PAS: $p < .0005$, uncorrected; PAS > ACT: $p < .05$, two-tailed, corrected. MNI coordinates (x, y, z), t values of regions active in each contrast, Brodmann's area (BA) if applicable. L = left hemisphere, R = right hemisphere.

men). Furthermore, 1PP elicited activations in the angular gyrus within the left inferior parietal lobe (IPL), in the right subcentral gyrus (rolandic operculum), bilateral posterior insula, left visual cortical areas such as the calcarine sulcus and cuneus, and left posterior orbital gyrus (Figure 2). Increased neural activity during 3PP relative to 1PP was observed in the left IPL (angular gyrus) with subclusters in the right superior parietal lobe and the right cuneus, in the left inferior frontal cortex (extending to the left middle frontal/premotor cortex), in the right middle frontal/premotor cortex (extending to the right inferior frontal), right brainstem, bilateral thalamus, bilateral anterior insula, right anterior cingulate cortex, and right cerebellum (also extending to the left hemisphere) (see Figure 2).

Table 4. Main Suprathreshold Clusters for ACT Using 1PP as a Search Volume

MNI Coordinates			<i>t</i>	Cluster Size	Anatomical Region	BA
-14	46	10	4.55	1724	L. cingulate	32
-10	40	46	4.17	175	L. superior frontal	9
-14	-48	10	3.54	24	L. cingulate	30
-14	-32	74	3.17	18	L. precentral	4
0	-28	46	3.05	28	L. cingulate	~23
10	56	32	2.73	27	R. superior frontal	10/32

$p < .05$, two-tailed, corrected. MNI coordinates (x, y, z), t values of regions active in each contrast, Brodmann's area (BA) if applicable. L = left hemisphere, R = right hemisphere.

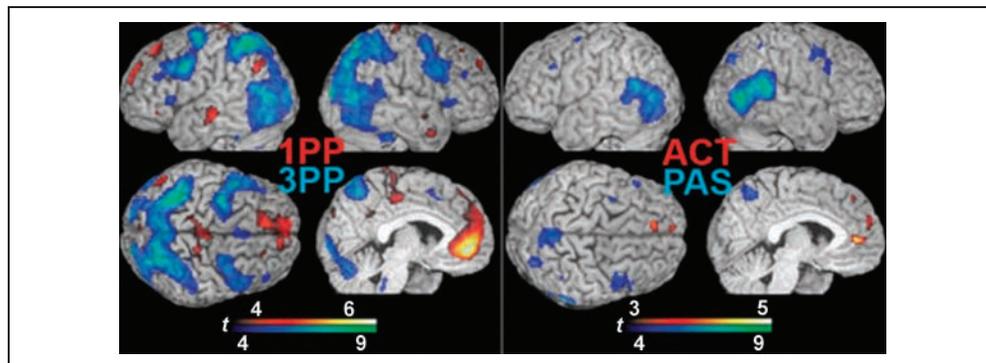
PAS, relative to ACT, yielded significant activations in bilateral temporal-occipital cortices, right precuneus, left fusiform gyrus, frontal areas such as the right middle frontal/premotor cortex (extending to inferior frontal), left inferior and left middle frontal/premotor cortex, and in the right IPL (intraparietal sulcus and supramarginal gyrus) (Figure 2). There were no areas of significantly

Table 5. Main Suprathreshold Clusters for Inclusive Masking

MNI Coordinates			<i>t</i>	Cluster Size	Anatomical Region	BA
<i>Common activation for ACT and 1PP</i>						
-14	46	10	4.55	223	L. cingulate	32
-10	40	46	4.17	35	L. superior frontal	9
-8	58	20	4.15	104	L. superior frontal	10
<i>Common activation for PAS and 3PP</i>						
50	-72	2	9.20	1840	R. middle occipital	37
-50	-58	16	6.87	1478	L. superior temporal (sulcus), posterior part	37
6	-54	50	5.39	464	R. precuneus	
28	-78	40	4.43	164	R. superior occipital	19
44	4	50	4.11	76	R. middle frontal, superior part	6
16	-62	36	4.03	14	R. parieto-occipital fissure/precuneus	~7
-52	22	34	3.93	15	L. middle frontal, inferior part	44
46	18	36	3.73	14	R. middle frontal, inferior part	44

$p < .0005$, uncorrected. MNI coordinates (x, y, z), t values of regions active in each contrast, Brodmann's area (BA) if applicable. L = left hemisphere, R = right hemisphere.

Figure 2. To demonstrate an overlap in activation patterns, statistical activation maps for all contrasts are overlaid on a single subject's rendered structural image (for better visualization). Red–yellow colors indicate activation during 1PP greater than 3PP (“1PP”), and during ACT greater than PAS (“ACT”). Blue–green colors indicate activation during 3PP greater than 1PP (“3PP”), and during PAS greater than ACT (“PAS”). Activations as shown for 1PP, 3PP, and PAS correspond to a two-tailed $p < .05$ corrected for multiple comparisons, and for ACT to $p < .0005$ uncorrected.



increased activation during ACT, compared to PAS, after correcting for multiple comparisons. However, because we had a strong a priori hypothesis about the activation associated with ACT with regard to cortical midline structures, we also examined activations using an uncorrected threshold of $p < .0005$, $k = 10$, as has been done in previous studies (e.g., Farrer, Franck, Frith, et al., 2004; Farrer, Franck, Georgieff, et al., 2003; Farrer & Frith, 2002; Fink et al., 1999). With this threshold, significant activations in cortical midline structures including the bilateral anterior cingulate cortex, left prefrontal and right cerebellum were observed (Figure 2). An additional ROI analysis for ACT (using the 1PP contrast to define a search volume) confirmed the involvement of cortical midline structures during ACT (see Table 4; Figure 3).

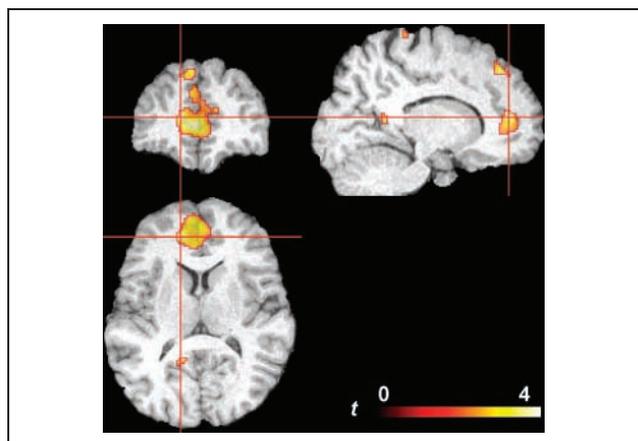


Figure 3. Statistical activation map of an ROI analysis for ACT using 1PP as a search volume (at $p < .05$, two-tailed, corrected) overlaid on a single-subject structural image (for better visualization). Crosshairs are located on the global maximum ($x = -14$, $y = 46$, $z = 10$).

Inclusive masking revealed that ACT and 1PP were both associated with activation in left medial prefrontal cortical regions, specifically the anterior cingulate sulcus and gyrus as well as superior frontal gyrus (Figure 4). Eighty-four percent of all voxels activated in ACT were also present in 1PP, whereas only 7% of all voxels activated in 1PP were also present in ACT. PAS and 3PP, on the other hand, were associated with common activations in bilateral temporal–occipital cortex, right precuneus, right middle frontal/premotor cortex, and bilateral inferior frontal cortices (Figure 4). Seventy-seven percent of all voxels activated in PAS were also present in 3PP, whereas only 15% of all voxels activated in 3PP were also present in PAS. There were no commonly activated regions when ACT was inclusively masked by 3PP or when PAS was inclusively masked by 1PP.

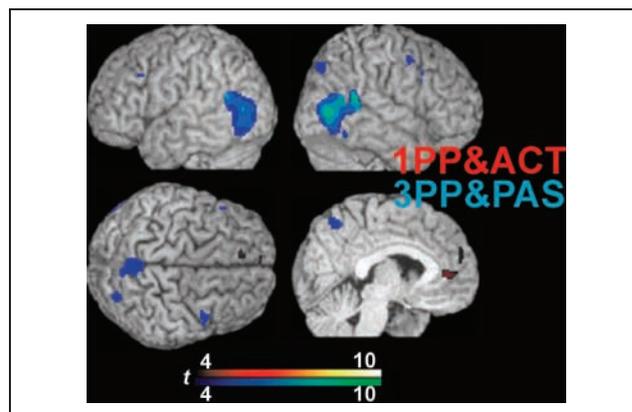


Figure 4. To demonstrate an overlap in activation patterns, statistical activation maps for ACT inclusively masked by 1PP (at $p < .0005$, uncorrected) and PAS inclusively masked by 3PP (at $p < .0005$, uncorrected) are overlaid on a single subject's rendered structural image (for better visualization). Red colors indicate activation common to 1PP and ACT. Blue–green colors indicate activation common to 3PP and PAS.

No significant neural interactions between Agency and Perspective Taking were observed. A statistical analysis of the parameter estimates also revealed no significant interactions within ROIs in the medial prefrontal, inferior parietal, or temporal–occipital cortex.

DISCUSSION

In the present study, we sought to investigate the neural correlates of two critical processes involved in self–other distinctions in conjunction, perspective taking and agency, in order to shed light onto the neural underpinnings of self-consciousness. There was an overlap of activity in medial prefrontal regions associated with representations of one’s own perspective and actions (1PP and ACT) and an overlap of activity in temporal–occipital, premotor, and inferior frontal, as well as posterior parietal regions associated with representations of others’ perspectives and actions (3PP and PAS). Levels of perspective taking and agency coactivated the same brain regions but did not interact significantly. Our findings provide evidence for distinct neural representations of the self in contrast to others and, furthermore, suggest that perspective taking and agency represent independent constituents for the formation of self-consciousness.

Levels of Perspective Taking

Prior to the present study, Vogeley, May, et al. (2004) investigated visual–spatial perspective taking using virtual, but static, stimuli. The present findings extend previous findings by Vogeley, May, et al. We were able to detect similar differential activation patterns between 1PP and 3PP in relation to dynamic action stimuli. Consistently, we found activation in cortical midline structures such as MPFC and cingulate cortices, prefrontal and temporal cortices, as well as the posterior insula, to be more active in 1PP than 3PP. In addition, we observed increased activity during 1PP in limbic structures such as the amygdala and orbitofrontal cortex. Some of these regions activated during 1PP have been discussed as being critical for self-consciousness. For example, the “default state” describes a network of brain areas that are tonically active when people are at rest and not involved in effortful cognitive tasks or goal-directed behaviors (Gusnard, Akbudak, Shulman, & Raichle, 2001; Raichle et al., 2001). Gusnard et al. (2001) speculated that MPFC, which is one component of this network, contains the neural basis of self-consciousness. Damasio’s (1999) idea of a “core self” is based on the continuous sensation of interoceptive and exteroceptive stimuli. This has also been associated with ventral MPFC and limbic structures such as the orbitofrontal cortex. In addition, several studies have consistently associated MPFC activity with the utilization of self-

referential stimuli (e.g., Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Ochsner et al., 2004; Kelley et al., 2002; Vogeley, Bussfeld, et al., 2001). Most studies observed MPFC activation when subjects reflected upon themselves. However, the ability to explicitly meta-represent one’s own mental or bodily states as one’s own is one operationalization of self-consciousness (Newen & Vogeley, 2003; Vogeley & Fink, 2003). Our operationalization of 1PP differed from those studies as it represents an immediate and prereflective process (Gallagher, 2000) as part of a “minimal self” that does not necessarily involve a reflective act of consciousness (in contrast to a “narrative self”). Here, we show that subjects also recruit MPFC regions when they were simply looking out on the world, not necessarily reflecting upon themselves.

Whereas subjects performed the tasks from their egocentric perspective or reference system during 1PP, 3PP conditions required an additional transformation of one’s own egocentric perspective/reference system onto another agent’s body axis, that is, a shift to another location in space. This transformation is crucial for the process of visual–spatial perspective taking (Vogeley & Fink, 2003; Zacks, Rypma, et al., 1999) and was associated with activation in posterior parietal cortical regions such as the left IPL and parietal–temporal–occipital junction as well as the right superior parietal lobe (activation for these regions extending to the contralateral hemisphere), consistent with other studies (Blanke et al., 2005; Vogeley, May, et al., 2004; Zacks, Rypma, et al., 1999). The IPL, especially in the right hemisphere, has been proposed to be critical for the distinction between self and other (see Jeannerod, 2004; Decety & Sommerville, 2003), especially in relation to taking others’ perspectives (Vogeley, May, et al., 2004; Ruby & Decety, 2001; Vogeley, Bussfeld, et al., 2001).

One might argue that 3PP is confounded by mental rotation processes. Zacks, Rypma, et al. (1999) compared egocentric perspective transformation (i.e., viewer rotation) and mental rotation (i.e., object rotation) showing that both can be dissociated, although they also share some features (Zacks, Vettel, & Michelon, 2003). However, performing left–right decisions from another perspective is more likely to involve the visual–spatial alignment of the egocentric perspective of one’s own body with that of another person instead of aligning the other person’s perspective to one’s own. We furthermore instructed subjects to imagine themselves at the avatar’s location in space. No subject reported to have performed a mental rotation of the scene, but rather to have performed a transformation of their own perspective.

Interestingly, we also observed activation of areas previously implicated in mental perspective taking (also referred to as “theory of mind,” “mentalizing” or “mind reading”; Frith & Frith, 1999; Baron-Cohen, 1997) during visual–spatial perspective taking. This indicates that

both kinds of perspective taking partly rely on shared neural mechanisms. For example, a region within the temporal–parietal junction was activated (here, in the right hemisphere) that has been reported to specifically respond to representations of other people’s mental states (Saxe & Kanwisher, 2003) as well as left inferior frontal, premotor, and inferior parietal cortices, all associated with the human mirror neuron system. Mirror neurons have been proposed to represent neural substrates of simulation (Rizzolatti, Fogassi, & Gallese, 2001) and have been furthermore related to the ability of mindreading (Gallese & Goldman, 1998).

Levels of Agency

Being an agent, in contrast to being an observer, elicited activations in anterior medial prefrontal regions and right cerebellum. Medial prefrontal regions were consistently reported to be involved in self-referential tasks (Northoff & Bermpohl, 2004), including awareness of agency (Frith, 2002), as well as in internal self-monitoring and error detection with respect to actions (Carter, MacDonald, Ross, & Stenger, 2001). Cerebellar activation has also been previously observed in agency tasks (Farrer, Franck, Georgieff, et al., 2003; Farrer & Frith, 2002) and is thought to predict and compare sensory consequences of actions (Blakemore, Frith, & Wolpert, 2001). In the postscan questionnaire, all subjects reported to have experienced a sense of agency throughout ACT conditions.

It is important to note that the ACT effect was less robust than the other main effects (as indicated by the uncorrected threshold). Other studies also often used ROI approaches or uncorrected thresholds when reporting activity associated with agency tasks (e.g., Farrer, Franck, Frith, et al., 2004; Farrer, Frank, Georgieff, et al., 2003; Farrer & Frith, 2002; Fink et al., 1999), which indicates that activation during agency tasks is difficult to detect at a whole-brain threshold. Because we were especially interested to see whether ACT—like 1PP—shows activation in medial prefrontal structures, we used a post hoc ROI analysis and used our 1PP contrast as a search volume for the ACT contrast. We were able to confirm activation within the MPFC during ACT (Table 4; Figure 3). More importantly, this approach did not reveal any activation in MPFC for PAS, which underlines a strong relationship between 1PP and ACT, but not between 1PP and PAS, at the neural level.

By contrast, observing other people acting (i.e., throwing a ball) during PAS yielded activation in brain areas that have been associated with representations of others, more specifically of others’ actions, intentions, and perspectives. For example, we observed increased activation in areas implicated in the perception of biological motion, others’ actions, faces, and of other socially relevant stimuli, including the posterior segment of

the superior temporal sulcus and the fusiform gyrus (Iacoboni et al., 2004; Pelphrey, Morris, & McCarthy, 2004; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004; Schultz, Imamizu, Kawato, & Frith, 2004; Grossman & Blake, 2002; Castelli, Happe, Frith, & Frith, 2000; Grossman et al., 2000; Kanwisher, McDermott, & Chun, 1997). The right IPL, as activated here, has also been reported to be involved in the observation of actions (Buccino et al., 2004) and was explicitly proposed as a key structure in self–other distinctions thereby reflecting others’ actions and perspectives (Jeannerod, 2004; Decety & Sommerville, 2003; Farrer & Frith, 2002; Ruby & Decety, 2001).

Overlap between Levels of Perspective Taking and Levels of Agency

Just by inspecting Figure 2, one can observe that activation patterns revealed by 1PP and ACT seem to overlap in the MPFC, whereas activations during 3PP and PAS seem to overlap in more posterior and premotor cortices. To formally examine this, we performed inclusive masking procedures for 1PP and ACT on the one hand, and 3PP and PAS on the other hand, which confirmed our observation (see Figure 4). Left medial prefrontal regions were commonly associated with representations of one’s own perspective and actions, whereas temporal–occipital, posterior parietal, and premotor regions (mostly bilateral) were commonly associated with representations of others’ perspectives and actions.

However, 1PP and 3PP show more extensive activation than ACT and PAS (Figure 2; Tables 2 and 3). As a consequence, there were areas uniquely activated by 1PP or 3PP that are not covered by the ACT or PAS. More importantly though, our question was if and where they would overlap. Although 1PP and ACT (or 3PP and PAS, respectively) showed a substantial amount of activation that they did not share, they coactivated certain areas, whereas the nonmatching components (1PP and PAS or 3PP and ACT) did not share any activation.

These findings provide empirical evidence for distinct neural representations of self and other with respect to visual–spatial perspective taking and agency. This may be relevant for psychopathological disorders, in which the boundaries between self and the external world are no longer intact, such as in schizophrenia: These patients exhibit deficits in both perspective taking and agency attributions (Farrer, Franck, Frith, et al., 2004; Franck et al., 2001; Frith & Frith, 1999; Spence et al., 1997). A common deficit is suggestive of common neural substrates for both processes. This hypothesis is supported by the present findings of neural overlap between levels of perspective taking and agency. We suggest that the network of brain regions commonly underlying perspective taking and agency may play a specific role in maintaining the integrity of the self.

Interaction between Levels of Perspective Taking and Levels of Agency

An interaction between these conditions would suggest that the effect of Agency was modulated by the level of Perspective Taking. Although this was partly observed on a behavioral level, no statistically significant interaction between Agency and Perspective Taking was observed at the neural level. Behaviorally, there was a difference in accuracy (not RTs) between ACT and PAS during 3PP but not 1PP. This, however, is likely to be due to very high accuracy during 1PP for both Agency conditions. ROI analyses of activation at the main effects' principally activated regions including the medial prefrontal, inferior parietal, and temporal–occipital cortex also did not reveal significant interactions at the neural level (see Figure 5).

In light of the observed overlap, a lack of interaction at the neural level suggests that the levels of perspective taking and agency engage the same brain regions probably in an additive manner. It may also provide empirical evidence that agency and perspective taking represent independent constituents of self-consciousness as proposed by several philosophical and conceptual accounts in the field (Newen & Vogeley, 2003; Vogeley & Fink, 2003; Gallagher, 2000; Metzinger, 2000; Vogeley, Kurthen, et al., 1999).

General Discussion and Conclusion

There are a few caveats that need to be discussed. First, stimuli differed across conditions with respect to visual

stimulation. For example, 3PP comprised more visual stimulation than stimuli in 1PP because they included more diverse ball trajectories. For instance, the ball in 1PP_ACT always flew from the subjects' near space to the subjects' far space (i.e., to avatars further away in space). This, however, constitutes the phenomenological experiences of a first-person perspective and agency and cannot be varied otherwise. We also cannot rule out the possibility that enhanced visual–spatial attention may have modulated activity during 3PP and PAS in some regions including the temporal–occipital or parietal cortex (Corbetta, Miezin, Shulman, & Petersen, 1991). However, such a putative increase in attention would indeed reflect real-life situations: We are more attentive when we are trying to understand what other people are doing and usually less attentive to or aware of our own state of mind or actions.

Second, behavioral performance was better during 1PP and ACT in comparison to 3PP or PAS. The difference between 1PP and 3PP conditions was especially evident, which has previously been shown (e.g., Vogeley, May, et al., 2004; Zacks, Rypma, et al., 1999). This, however, allows for the possibility of differing results due to task difficulty and is problematic when reporting activity within the default state network. Regions within this network are tonically active during rest and reported activation in the MPFC almost always represents a relative decrease (rather than an actual increase) of this tonic activity during attention-demanding cognitive tasks (Iacoboni et al., 2004; Gusnard & Raichle, 2001; Mitchell, Heatherton, & Macrae, 2001). Accordingly, tasks that are more difficult such as 3PP would yield more deactivation (i.e., less activation) of MPFC compared to 1PP, whereas easier tasks such as 1PP would yield only little deactivation. Indeed, this is what we observed for the principally activated regions during 1PP and ACT in the ventral medial prefrontal cortex for 1PP conditions and in the more dorsal cingulate cortex for ACT conditions (Figure 5A and C). This raises the question about how to interpret findings in tasks that produce only little decreases from the default state. Taking a first-person perspective, for example, may very likely simply represent a “default process” that spontaneously occurs during rest. Gusnard et al. (2001) suggested that regions associated with the default state of the brain, including the MPFC, may represent a potential neural basis of self-consciousness. Thus, the finding that conditions that implement constitutive aspects of self-consciousness, such as a first-person perspective and a sense of agency, would yield only little deviation from the default state is consistent with Gusnard et al. and supports our initial hypothesis.

In conclusion, we demonstrated overlapping brain activation associated with representations of one's own perspective and actions and an overlap of activation associated with representations of others' perspectives and actions. This is evidence for distinct neural substrates

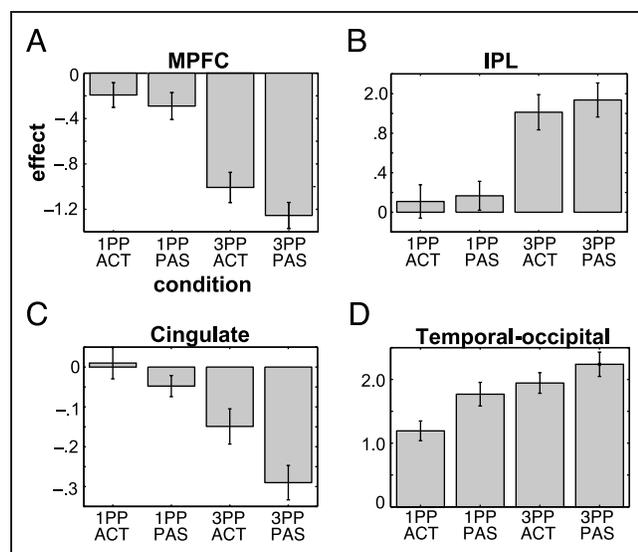


Figure 5. Parameter estimates (means and SEMs) within spherical ROIs around each main effect's principally activated voxel were plotted: (A) for 1PP, $x = 2$, $y = 44$, $z = -8$ (MPFC; BA 10); (B) for 3PP, $x = -34$, $y = -56$, $z = 56$ (IPL; BA ~40); (C) for ACT, $x = -14$, $y = 46$, $z = 10$ (cingulate; BA 32); (D) for PAS, $x = 50$, $y = -72$, $z = 2$ (temporal–occipital; BA 37).

for representations of the self, including the medial prefrontal cortex, in contrast to neural substrates for representations of others, including inferior frontal/premotor, posterior parietal, and posterior temporal–occipital areas. These findings cannot be seen as evidence against studies that argued in favor of shared representations of self and other (Decety & Chaminade, 2003; Decety & Sommerville, 2003) because our study only looked at differential contrasts. However, despite evidence for shared representations, there must exist a neural/cognitive mechanism that helps us to distinguish between our own and other people’s mental or bodily states. Taking a first-person perspective and agency represent key and seemingly independent processes for self-consciousness. Both recruit the MPFC, which supports the idea that the MPFC houses a neural basis of self-consciousness. Future studies could address the intriguing question about the connectivity between brain regions engaged in self–other representations or their potential disconnectivity that may underlie disturbances of self-consciousness, as, for example, occurring in schizophrenia.

Acknowledgments

This research was supported by a grant from the Volkswagen-Stiftung awarded to A. Newen for the research project “Self-consciousness and concept formation in humans” (AZ II/80 594). The German ministry for education and research is acknowledged for its support of the MRI scanner (BMBF 01GO 01 04/ N. J. Shah and K. Zilles). G. R. Fink was supported by the Deutsche Forschungsgemeinschaft (KFO-112). The authors thank P. Klaver and J. Schultz for their help during preparation and revision of the manuscript and R. Tepest for technical support.

Reprint requests should be sent to Nicole David, Department of Psychiatry, University of Cologne, Kerpener Str. 62, 50924 Cologne, Germany, or via e-mail: nicole.david@uk-koeln.de.

The data reported in this experiment have been deposited with the fMRI Data Center (www.fmridc.org). The accession number is 2-2005-120GH.

Note

1. In the present study, the term *self-consciousness* is primarily used and operationalized as defined by Newen and Vogeley (2003), Vogeley and Fink (2003), and Gallagher (2000).

REFERENCES

Baron-Cohen, S. (1997). *Mindblindness—An essay on autism and theory of mind*. Cambridge: MIT Press.

Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (2001). The cerebellum is involved in predicting the sensory consequences of action. *NeuroReport*, *12*, 1879–1884.

Blanke, O., Mohr, C., Michel, C. M., Pascual-Leone, A., Brugger, P., Seeck, M., Landis, T., & Thut, G. (2005). Linking out-of-body experience and self processing to mental own-body imagery at the temporoparietal junction. *Journal of Neuroscience*, *25*, 550–557.

Brett, M., Johnsrude, I. S., & Owen, A. M. (2002). The

problem of functional localization in the human brain. *Nature Reviews Neuroscience*, *3*, 243–249.

Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C. A., & Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspicuous: An fMRI study. *Journal of Cognitive Neuroscience*, *16*, 114–126.

Carter, C. S., MacDonald, A. W., Ross, L. L., & Stenger, V. A. (2001). Anterior cingulate cortex activity and impaired self-monitoring of performance in patients with schizophrenia: An event-related fMRI study. *American Journal of Psychiatry*, *158*, 1423–1428.

Castelli, F., Happe, F., Frith, U., & Frith, C. (2000). Movement and mind: A functional imaging study of perception and interpretation of complex intentional movement patterns. *Neuroimage*, *12*, 314–325.

Churchland, P. (2002). Self-representation in nervous systems. *Science*, *296*, 308–310.

Corbetta, M., Miezin, F. M., Shulman, G. L., & Petersen, S. E. (1991). Selective attention modulates extrastriate visual regions in humans during visual feature discrimination and recognition. *Ciba Foundation Symposia*, *163*, 165–175; discussion 175–180.

Damasio, A. R. (1999). *The feeling of what happens: Body and emotion in the making of consciousness*. New York: Harcourt Brace.

Decety, J., & Chaminade, T. (2003). When the self represents the other: A new cognitive neuroscience view on psychological identification. *Consciousness and Cognition*, *12*, 577–596.

Decety, J., & Sommerville, J. A. (2003). Shared representations between self and other: A social cognitive neuroscience view. *Trends in Cognitive Sciences*, *7*, 527–533.

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, *79*, 1–37.

Duvernoy, H. M. (1999). *The human brain*. New York: Springer.

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *Neuroimage*, *25*, 1325–1335.

Farrer, C., Franck, N., Frith, C. D., Decety, J., Georgieff, N., d’Amato, T., & Jeannerod, M. (2004). Neural correlates of action attribution in schizophrenia. *Psychiatry Research*, *131*, 31–44.

Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J., & Jeannerod, M. (2003). Modulating the experience of agency: A positron emission tomography study. *Neuroimage*, *18*, 324–333.

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*, 596–603.

Feinberg, T. E. (2001). *Altered egos: How the brain creates the self*. New York: Oxford University Press.

Fink, G. R., Marshall, J. C., Halligan, P. W., Frith, C. D., Driver, J., Frackowiak, R. S., & Dolan, R. J. (1999). The neural consequences of conflict between intention and the senses. *Brain*, *122*, 497–512.

Franck, N., Farrer, C., Georgieff, N., Marie-Cardine, M., Dalery, J., d’Amato, T., & Jeannerod, M. (2001). Defective recognition of one’s own actions in patients with schizophrenia. *American Journal of Psychiatry*, *158*, 454–459.

Friston, K. J., Holmes, A. P., Worsley, K. J., Poline, J.-P., Frith, C. D., & Frackowiack, R. S. J. (1995). Statistical parametric

- maps in functional imaging: A general linear approach. *Human Brain Mapping*, *2*, 189–210.
- Frith, C. D. (2002). Attention to action and awareness of other minds. *Consciousness and Cognition*, *11*, 481–487.
- Frith, C. D. (2003). *Schizophrenia: A very short introduction*. New York: Oxford University Press.
- Frith, C. D., & Frith, U. (1999). Interacting minds—A biological basis. *Science*, *286*, 1692–1695.
- Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Sciences*, *4*, 14–21.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, *2*, 493–501.
- Genovese, C. R., Lazar, N. A., & Nichols, T. E. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage*, *15*, 870–878.
- Grossman, E., Donnelly, M., Price, R., Pickens, D., Morgan, V., Neighbor, G., & Blake, R. (2000). Brain areas involved in perception of biological motion. *Journal of Cognitive Neuroscience*, *12*, 711–720.
- Grossman, E. D., & Blake, R. (2002). Brain areas active during visual perception of biological motion. *Neuron*, *35*, 1167–1175.
- Gusnard, D. A., Akbudak, E., Shulman, G. L., & Raichle, M. E. (2001). Medial prefrontal cortex and self-referential mental activity: Relation to a default mode of brain function. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 4259–4264.
- Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting brain. *Nature Reviews Neuroscience*, *2*, 685–694.
- Iacoboni, M., Lieberman, M. D., Knowlton, B. J., Molnar-Szakacs, I., Moritz, M., Throop, C. J., & Fiske, A. P. (2004). Watching social interactions produces dorsomedial prefrontal and medial parietal BOLD fMRI signal increases compared to a resting baseline. *Neuroimage*, *21*, 1167–1173.
- Iacoboni, M., & Zaidel, E. (2004). Interhemispheric visuo-motor integration in humans: The role of the superior parietal cortex. *Neuropsychologia*, *42*, 419–425.
- Jeannerod, M. (2004). Visual and action cues contribute to the self–other distinction. *Nature Neuroscience*, *7*, 422–423.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- 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.
- Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*, 785–794.
- Macrae, C. N., Moran, J. M., Heatherton, T. F., Banfield, J. F., & Kelley, W. M. (2004). Medial prefrontal activity predicts memory for self. *Cerebral Cortex*, *14*, 647–654.
- Metzinger, T. (2000). The subjectivity of subjective experience: A representationalist analysis of the first-person perspective. In T. Metzinger (Ed.), *Neural correlates of consciousness* (pp. 285–306). Cambridge: MIT Press.
- Mitchell, J. P., Heatherton, T. F., & Macrae, C. N. (2001). Distinct neural systems subserve person and object knowledge. *Proceedings of the National Academy of Sciences, U.S.A.*, *99*, 15238–15243.
- Newcombe, N. (1989). The development of spatial perspective taking. *Advances in Child Development and Behavior*, *22*, 203–247.
- Newen, A., & Vogeley, K. (2003). Self-representation: Searching for a neural signature of self-consciousness. *Consciousness and Cognition*, *12*, 529–543.
- Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*, *8*, 102–107.
- Ochsner, K. N., Knierim, K., Ludlow, D. H., Hanelin, J., Ramachandran, T., Glover, G., & Mackey, S. C. (2004). Reflecting upon feelings: An fMRI study of neural systems supporting the attribution of emotion to self and other. *Journal of Cognitive Neuroscience*, *16*, 746–772.
- Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh Inventory. *Neuropsychologia*, *9*, 97–113.
- Parsons, T. D., Larson, P., Kratz, K., Thiebaut, M., Bluestein, B., Buckwalter, J. G., & Rizzo, A. A. (2004). Sex differences in mental rotation and spatial rotation in a virtual environment. *Neuropsychologia*, *42*, 555–562.
- Pelphrey, K. A., Morris, J. P., & McCarthy, G. (2004). Grasping the intentions of others: The perceived intentionality of an action influences activity in the superior temporal sulcus during social perception. *Journal of Cognitive Neuroscience*, *16*, 1706–1716.
- 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. *Proceedings of the National Academy of Sciences, U.S.A.*, *98*, 676–682.
- Rizzolatti, G., Fogassi, L., & Gallese, V. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews Neuroscience*, *2*, 661–670.
- Rochat, P., & Striano, T. (2000). Perceived self in infancy. *Infant Behavior and Development*, *23*, 513–530.
- Ruby, P., & Decety, J. (2001). Effect of subjective perspective taking during simulation of action: A PET investigation of agency. *Nature Neuroscience*, *4*, 546–550.
- Ruby, P., & Decety, J. (2003). What you believe versus what you think they believe: A neuroimaging study of conceptual perspective-taking. *European Journal of Neuroscience*, *17*, 2475–2480.
- Ruby, P., & Decety, J. (2004). How would you feel versus how do you think she would feel? A neuroimaging study of perspective-taking with social emotions. *Journal of Cognitive Neuroscience*, *16*, 988–999.
- Sato, A., & Yasuda, A. (2005). Illusion of agency: Discrepancy between predicted and actual sensory consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. *Cognition*, *94*, 241–255.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in “theory of mind.” *Neuroimage*, *19*, 1835–1842.
- Saxe, R., Xiao, D. K., Kovacs, G., Perrett, D. I., & Kanwisher, N. (2004). A region of right posterior superior temporal sulcus responds to observed intentional actions. *Neuropsychologia*, *42*, 1435–1446.
- Schultz, J., Imamizu, H., Kawato, M., & Frith, C. D. (2004). Activation of the human superior temporal gyrus during observation of goal attribution by intentional objects. *Journal of Cognitive Neuroscience*, *16*, 1695–1705.
- Seger, C. A., Stone, M., & Keenan, J. P. (2004). Cortical activations during judgments about the self and an other person. *Neuropsychologia*, *42*, 1168–1177.

- 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*, 1997–2011.
- Stuss, D. T., Gallup, G. G., Jr., & Alexander, M. P. (2001). The frontal lobes are necessary for “theory of mind.” *Brain*, *124*, 279–286.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. Stuttgart: Thieme.
- 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. *Nature Neuroscience*, *9*, 841–842.
- Uddin, L. Q., Kaplan, J. T., Molnar-Szakacs, I., Zaidel, E., & Iacoboni, M. (2005). Self-face recognition activates a frontoparietal “mirror” network in the right hemisphere: An event-related fMRI study. *Neuroimage*, *25*, 926–935.
- Vogeley, K., Bussfeld, P., Newen, A., Herrmann, S., Happe, F., Falkai, P., Maier, W., Shah, N. J., Fink, G. R., & Zilles, K. (2001). Mind reading: Neural mechanisms of theory of mind and self-perspective. *Neuroimage*, *14*, 170–181.
- Vogeley, K., & Fink, G. R. (2003). Neural correlates of the first-person-perspective. *Trends in Cognitive Sciences*, *7*, 38–42.
- Vogeley, K., Kurthen, M., Falkai, P., & Maier, W. (1999). Essential functions of the human self model are implemented in the prefrontal cortex. *Consciousness and Cognition*, *8*, 343–363.
- Vogeley, K., May, M., Ritzl, A., Falkai, P., Zilles, K., & Fink, G. R. (2004). Neural correlates of first-person perspective as one constituent of human self-consciousness. *Journal of Cognitive Neuroscience*, *16*, 817–827.
- Zacks, J., Rypma, B., Gabrieli, J. D., Tversky, B., & Glover, G. H. (1999). Imagined transformations of bodies: An fMRI investigation. *Neuropsychologia*, *37*, 1029–1040.
- Zacks, J. M., Vettel, J. M., & Michelon, P. (2003). Imagined viewer and object rotations dissociated with event-related fMRI. *Journal of Cognitive Neuroscience*, *15*, 1002–1018.