Neural Correlates of First-Person Perspective as One Constituent of Human Self-Consciousness

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Abstract

■ Taking the first-person perspective (1PP) centered upon one's own body as opposed to the third-person perspective (3PP), which enables us to take the viewpoint of someone else, is constitutive for human self-consciousness. At the underlying representational or cognitive level, these operations are processed in an egocentric reference frame, where locations are represented centered around another person's (3PP) or one's own perspective (1PP). To study 3PP and 1PP, both operating in egocentric frames, a virtual scene with an avatar and red balls in a room was presented from different camera viewpoints to normal volunteers (n = 11) in a functional magnetic resonance imaging experiment. The task for the subjects was to count the objects as seen either from the avatar's perspective (3PP) or one's own perspective (1PP). The scene was presented either from a ground view (GV) or an aerial view (AV) to investigate the effect of view on perspective taking. The factors perspective (3PP vs. 1PP) and view (GV vs. AV) were arranged in a two-factorial way. Reaction times were increased and percent correctness scores were decreased in 3PP as opposed to 1PP. To detect the neural mechanisms associated with perspective taking, functional magnetic resonance imaging was employed. Data were analyzed using SPM'99 in each subject and non-parametric statistics on the group level. Activations common to 3PP and 1PP (relative to baseline) were observed in a network of occipital, parietal, and prefrontal areas. Deactivations common to 3PP and 1PP (relative to baseline) were observed predominantly in mesial (i.e., parasagittal) cortical and lateral superior temporal areas bilaterally. Differential increases of neural activity were found in mesial superior parietal and right premotor cortex during 3PP (relative to 1PP), whereas differential increases during 1PP (relative to 3PP) were found in mesial prefrontal cortex, posterior cingulate cortex, and superior temporal cortex bilaterally. The data suggest that in addition to joint neural mechanisms, for example, due to visuospatial processing and decision making, 3PP and 1PP rely on differential neural processes. Mesial cortical areas are involved in decisional processes when the spatial task is solved from one's own viewpoint, whereas egocentric operations from another person's perspective differentially draw upon cortical areas known to be involved in spatial cognition. ■

INTRODUCTION

Self-consciousness includes the consciousness of one's own mental states, such as perceptions, attitudes, opinions, and intentions to act. Representing and integrating such mental states into a common framework, which represents the integrity of our own mind, requires the ability to take a self- or first-person perspective (1PP) among other constitutive features, such as experiences of agency or transtemporal unity (Vogeley, Kurthen, Falkai, & Maier, 1999). 1PP can thus be considered as a basic constituent of a "minimal self" (Gallagher, 2000). It enables us to experience the subjective multimodal experiential space centered on our own body. This transient relationship between oneself and objects in the world is the key component of perceptual processes and thus the underlying basis of every cognitive process dealing with the content of these perceptions (Vogeley & Fink, 2003).

At a phenomenal level, 1PP means the centralization of the subjective multidimensional and multimodal experiential space around one's own body. It can be opposed to the third-person perspective (3PP), in which mental states are ascribed to someone else. This phenomenal level needs to be clearly distinguished from an underlying representational level, on which different reference frames representing the locations of entities in space can be differentiated. A reference frame can be defined as "a means of representing the locations of entities in space" (Klatzky, 1998). In an egocentric reference frame, constituted by subject-to-object relations (best described in a polar coordinate system), locations are represented related to a personal agent and his physical configuration. As such, an egocentric reference frame crucially depends on the avatar's position in space and relation to the objects present. In contrast to egocentric frames, so-called allocentric reference frames refer to object-

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to-object relations, that are independent from an agent's position (Aguirre & D'Esposito, 1999; Klatzky, 1998).

The cognitive operations when perceiving a visual scene from another person's viewpoint (3PP) are likely to differ from taking a view of the same scene from one's own perspective (1PP). Although the cognitive operations differ phenomenally, when perceiving a visual scene from another person's viewpoint (3PP) or from one's own perspective (1PP), both tasks are centered on the body of the agent (other or self). To clearly separate these two levels of descriptions, the perspective-related terms 3PP and 1PP are used to indicate the phenomenal level, whereas the egocentric reference frame studied here refers to the cognitive or neural level as conceptualized by the onlooking scientific observer. The crucial difference is that 3PP necessitates an additional translocation of the egocentric viewpoint from 1PP to 3PP.

To date, it remains unclear which neural mechanisms are associated with the ability to differentiate between mental processes "belonging" to either oneself or to another person. In the present functional magnetic resonance imaging (fMRI) study, we therefore systematically varied 3PP and 1PP in a simple 3-D visuospatial task, for which visual stimuli were constructed that showed a virtual scene with an avatar surrounded by a variable number of red objects (Figure 1). Subjects were asked to assess the number of red balls (ranging from 1 to 3) as seen from either the avatar's (3PP) or their own perspective (1PP). To determine whether taking 3PP or 1PP interacts with the camera view on the scene, two views of the scene, namely, a ground view (GV) and an aerial view (AV) were presented. The two factors perspective (3PP vs. 1PP) and view (GV vs. AV) were arranged in a two-factorial way (Figure 1). It is important to note that both target conditions were based on egocentric operations (on a representational or cognitive level), as the objects had to be located in relation to an agent in both conditions, either the subject or the avatar. The experiment thus focuses on the differential activations due to perspective taking on the phenomenal level of the agent. Accordingly, this study addresses the issues, whether (a) 3PP and 1PP rely on the same or different brain regions and (b) whether the neural mechanisms underlying 3PP and 1PP are modified by the view onto the scene.

Our study thus focuses on the egocentric or viewer-centered frame of reference. Egocentric reference frames can be further subdifferentiated, as they may be defined with respect to the midline of the visual field, the head, the trunk, or the longitudinal axis of the limb involved in the execution of a certain action (Behrmann, 1999). We here refer to an egocentric reference frame with respect to the midline of the visual field, as perceived from either 3PP or 1PP, but we are unable to differentiate between further subtypes of egocentric reference frames, as the center of the visual field, head, and trunk were all in alignment to each other.

RESULTS

Behavioral Data and Eye Movement Data during fMRI Scanning

Dependent variables were the mean reaction times and the percent correctness scores of correct answers averaged over all blocks for each particular condition. Overall means and standard deviations (*SD*) of reaction times and percent correctness scores are given in Table 1. For statistical analysis of the reaction times and correctness scores, the general linear model with the factors perspective and view as within-subject factors was used. In 3PP conditions, subjects needed significantly more time (1095 msec, $SD = 185.6$ msec) than during 1PP conditions (760 msec, $SD = 123.4$ msec), $F = 111.157$, $p < .0001$. There were no significant differences between conditions with respect to view, $F = 1.365$, $p = .270$, nor was there a significant interaction between the two main factors, $F = 0.002$, $p = .964$. The number of correct answers differed significantly with respect to both factors perspective, $F = 221.10$, $p < .001$, where

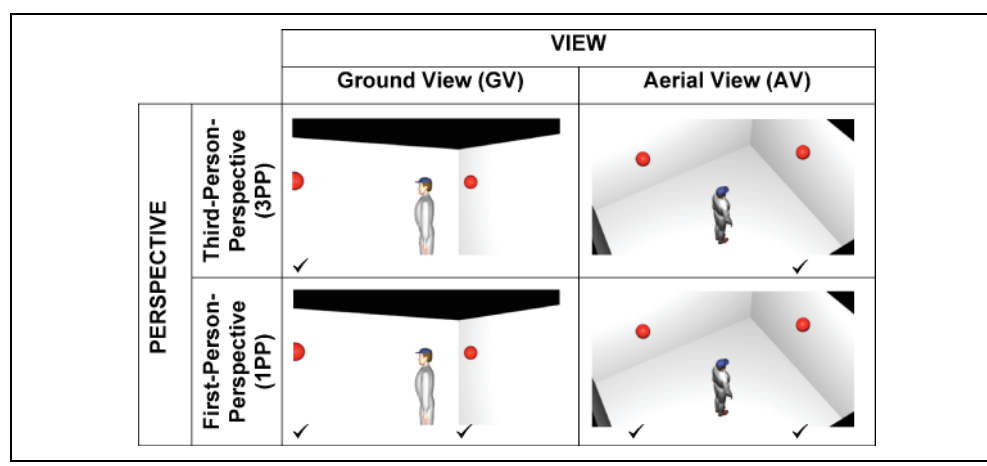

Figure 1. Two-factorial design. Two cognitive factors, perspective (3PP vs. 1PP) and view (GV vs. AV), were arranged in a two-factorial design. Typical stimulus images with room scenery, avatar, and objects are shown. Symbols ("✓") below the depicted stimulus image indicate the objects to be counted in the different conditions of 1PP and 3PP.

Table 1. Behavioral Data

	3PP-GV		*3PP-AV*		*1PP-GV*		*1PP-AV*	
	Mean	*SD*	*Mean*	*SD*	*Mean*	*SD*	*Mean*	*SD*
Reaction time (msec)	1102	207.9	1089	170.3	768	110.8	752	139.6
Correctness score (%)	90.0	1.8	87.3	2.6	99.4	0.7	97.3	1.7

This table summarizes the behavioral data of the relevant target conditions of the study. Mean values and standard deviations for the target conditions are given.

subjects made more errors during 3PP conditions, and view, $F = 80.72$, $p < .001$, where subjects made more errors during AV conditions. Again, no significant interaction between the two factors was observed, $F = 0.418$, $p = .532$.

Statistical analysis of the dependent variables of gaze position in the center of the stimulus image and of the mean distance between eye fixation points (in arbitrary units) did not reveal any significant differences between the four conditions, neither with respect to perspective or view nor the interaction thereof.

Neural Correlates of Perspective, View, and Their Interaction

The main effects are summarized in Table 2a–e. Table 2a–d corresponds to Figure 2A–D. Figure 2 provides the pseudo-*t* maps provided by nonparametric statistics on the group level as overlay images onto a normalized 3-D data set of one participant of the study. Areas with significantly increased (Figure 2A) and significantly decreased neural activity (Figure 2B) associated with all four experimental conditions are shown in addition to the main effect of 3PP (in contrast to 1PP) (Figure 2C) and of 1PP (in contrast to 3PP) (Figure 2D) (all images: nonparametric test; height threshold: $p < .05$, corrected; extent threshold = 10 voxels).

Activations common to all conditions (3PP-GV + 3PP-AV + 1PP-GV + 1PP-AV relative to baseline) were found in the occipito-parietal and frontal regions bilaterally and in the left cerebellum (Table 2a, Figure 2A). Deactivations common to all conditions (baseline relative to 3PP-GV + 3PP-AV + 1PP-GV + 1PP-AV) were found basically in mesial cortical structures, lateral temporal, and frontal cortex bilaterally, cerebellum bilaterally, and right postcentral cortex (Table 2b, Figure 2B).

Differential neural activity during 3PP (3PP > 1PP) was associated with increased neural activity in the precuneus, the frontal cortex bilaterally, cerebellum bilaterally, left temporal cortex, and occipitoparietal cortex on the left side (Table 2c, Figure 2C). 3PP activations show a substantial overlap with the areas activated by all four conditions suggesting an augmentation of neural activity in these areas rather than the recruitment of additional areas. In contrast, neural activity during 1PP (1PP > 3PP) could be demonstrated in lateral superior temporal cortex bilaterally including the insula, mesial cortical areas (both frontal and parietal), left frontal cortex, and the right postcentral gyrus (Table 2d, Figure 2D). Notably, 1PP associated increases of neural activity show a substantial overlap with deactivations of all four conditions.

These findings are illustrated by plots of the mean BOLD signal changes (%) (Figure 3). It can be demonstrated that the principally activated voxel (2, −60, 56) of the key contrast (3PP > 1PP) shows a relative BOLD signal change during 3PP that is positive compared to 1PP, where the opposite is true accordingly for the key contrast (1PP > 3PP) at its principally activated voxel (40, −20, 8).

With respect to the second main factor, view, differential neural activity during GV (GV > AV) was associated with increased neural activity in the right occipital pole (Table 2e, no figure).

No area of significantly increased neural activity associated with the main effect of AV (AV > GV) or the interaction of perspective and view were observed.

DISCUSSION

This study reveals both common and differential neural correlates for perspective taking in a simple visuospatial task to be performed from either someone else's viewpoint (3PP) or one's own viewpoint (1PP). Both viewpoints require egocentric cognitive processes. In addition to joint neural mechanisms common to both 1PP and 3PP, our data clearly demonstrate differential brain activations associated with taking 3PP as opposed to 1PP. Whereas specific activations in the precuneus, the right superior parietal and right premotor cortex were found during 3PP, a differential increase of activation in mesial cortical regions was observed during 1PP.

During 3PP, subjects are under a higher cognitive demand as they have to translocate the egocentric point of reference onto the avatar's position. Behaviorally, this leads to increased reaction times and higher error rates. The principally activated region of the precuneus has been shown in several studies to be involved in spatial cognition, including spatial location as opposed to form discrimination (Rao, Zhou, Zhuo, Fan, & Chen, 2003), spatial location in relation to egocentric reference frame (Misaki, Matsumoto, & Miyauchi, 2002), and in retrieval

Table 2. Neural Correlates of 3PP and 1PP

Region	*Cluster Size*	*x*	*y*	*z*	*t*
(a) Common activations of 3PP and 1PP (3PP-GV plus 3PP-AV plus 1PP-GV plus 1PP-AV > baseline)					
Right medial occipital gyri	8103	46	−76	8	13.00
Left precuneus	356	−12	−72	52	8.49
Left inferior occipital gyri	560	−44	−80	0	8.03
Right inferior frontal gyrus	274	54	12	28	7.74
Left cerebellum	22	−28	−42	−42	7.71
Left inferior parietal lobule	685	−42	−32	40	7.62
Left superior frontal gyrus	192	−32	−4	58	7.46
Left precentral gyrus	127	−52	6	30	7.28
Left superior frontal gyrus	34	−4	4	48	6.34
(b) Common deactivations of 3PP and 1PP (baseline > 3PP-GV plus 3PP-AV plus 1PP-GV plus 1PP-AV)					
Right medial temporal gyrus	11051	44	−18	−6	12.30
Right medial frontal gyrus	202	36	38	−20	9.40
Left medial temporal gyrus	4207	−54	−2	−20	9.18
Left superior frontal gyrus	5278	−12	66	14	8.86
Right cerebellum	240	28	−84	−36	7.84
Left cerebellum	230	−34	38	−20	7.47
Right posterior cingulate gyrus	902	24	−42	14	6.99
Left angular gyrus	116	−44	−72	36	6.25
Right insula	33	34	8	6	6.00
Left cerebellum	49	−12	−56	−22	5.97
Right supramarginal gyrus	12	56	−62	32	5.77
(c) 3PP relative to 1PP (3PP-GV plus 3PP-AV > 1PP-GV plus 1PP-AV)					
Precuneus	2303	2	−60	56	10.01
Right inferior frontal gyrus	339	48	12	24	7.65
Left cerebellum	32	−28	−42	−42	7.39
Left inferior occipital gyri	388	−38	−88	−6	7.15
Right cerebellum	309	50	−66	−16	7.13
Left inferior frontal gyrus	57	−46	8	28	6.09
Left inferior parietal lobule	115	−40	−46	50	6.04
Left medial frontal gyrus	16	−30	0	52	5.54
Left occipital gyri	55	−30	−78	28	5.52
(d) 1PP relative to 3PP (1PP-GV plus 1PP-AV > 3PP-GV plus 3PP-AV)					
Right insula	1008	40	−20	8	8.13
Left inferior temporal gyrus	651	−60	−8	−16	7.80
Superior frontal gyrus	810	−2	58	6	7.19
Posterior cingulate gyrus	529	0	−22	40	6.86

Table 2. (*continued*)

Region	*Cluster Size*	*x*	*y*	*z*	*t*
Left medial temporal gyrus	248	−52	−60	26	6.75
Left posterior cingulate gyrus	420	−6	−54	28	6.44
Anterior cingulate gyrus	104	2	34	6	6.40
Left medial frontal gyrus	205	−18	36	40	5.99
Right postcentral gyrus	40	46	−16	54	5.78
Right posterior cingulate gyrus	37	22	−40	16	5.61
(e) GV relative to AV (1PP-GV plus 3PP-GV > 1PP-AV plus 3PP-AV)					
Right inferior occipital gyri	92	24	−98	−4	7.66

Summary of volume statistics under the calculations of common activations and deactivations and the main effects of 3PP, 1PP, and GV (nonparametric permutation test on the group level, significance threshold $p < .05$, corrected, extent threshold: 10 voxels). Data in panels a–d correspond to Figure 2A–D. Brodmann's areas are provided according to Talairach and Tournoux (1988).

Nonparametrical permutations test on the group-level height threshold: $p < .05$, corrected extent threshold = 10 voxels.

of spatial information of lifelike events (Burgess, Maguire, Spiers, & O'Keefe, 2001; Fink et al., 1996). Furthermore, precuneus activation has been found in deductive reasoning, lending support for the hypothesis that mental models might be generated and "inspected" during deductive inference problems (Knauff, Mulack, Kassubek, Salih, & Greenlee, 2002). The additional activation sites in the right superior parietal cortex and right premotor cortex are known for their involvement in spatial tasks (Colby & Goldberg, 1999), including tasks with respect to action (Jeannerod, 1994) and spatial transformation of objects (Lamm, Windischberger, Leodolter, Moser, & Bauer, 2001). Interestingly, these regions are also activated in egocentric tasks, in which subjects make judgments on the midsagittal position of objects in relation to themselves (Misaki et al., 2002; Galati et al., 2000; Vallar et al., 1999).

The partial overlap of these activations with activations common to 1PP and 3PP might suggest that these parietal regions are involved in more general processes of perspective taking. From a clinical viewpoint, lesions of right posterior parietal cortex may lead to disturbances of visuospatial processing, such as extinction or spatial neglect (Marshall & Fink, 2001; Behrmann, 1999). Other clinical syndromes related to the right superior parietal cortex are deficits in representing the relative location of objects or other persons with respect to one's own body, also referred to as "egocentric disorientation" (Farrell & Robertson, 2000; Aguirre & D'Esposito, 1999). In essence, patients, predominantly with lesions in the posterior parietal cortex, have "deficits in representing the relative location of objects with respect to the self" (Aguirre & D'Esposito, 1999). Lesions, as summarized by Aguirre and D'Esposito (1999), comprise lesions of the superior parietal cortex, either bilaterally or only on the right side.

The parietal lobe thus appears to be a convergence zone in which spatial information is stored irrespective of the sensory modality of the information provided to maintain and constantly update a multimodal body-centered representation of space (Halligan, Fink, Marshall, & Vallar, 2003; Andersen, Synder, Bradley, & Ying, 1997). Accordingly, activations of posterior parietal cortex during 3PP are likely to reflect increased demands to the spatial reference system. An interesting study in this context was performed by Goel and Dolan (2001) presenting a three-term relational reasoning task showing that reasoning with concrete content recruited predominantly the left hemisphere, whereas more abstract reasoning recruited right hemisphere structures (Goel & Dolan, 2001).

The main finding concerning 1PP is that of significantly differential task-related increases of activation during 1PP as opposed to 3PP. In the direct contrast between 1PP as opposed to 3PP, it appears that during 1PP mesial cortical and superior temporal cortical sites are recruited if contrasted with 3PP, as illustrated by the BOLD signal change plot, which demonstrates an increase in the direct comparison of 1PP as opposed to 3PP (Figure 3). This finding does not contradict the observation that the 1PP activation pattern as opposed to 3PP appears as a subset of the deactivation pattern of all four conditions compared to the low-level baseline. Note, this factorial experiment focuses on the differential neural mechanisms of 1PP and 3PP rather than the changes of both 1PP and 3PP relative to an unspecific baseline. In the literature, it has been previously shown that these regions belong to a network of regions that, in general, exhibit task-related decreases in comparison to (unspecific) baseline tasks (Shulman et al., 1997).

More recently, the concept of a "default mode of brain function" was proposed reflecting "states of self," which

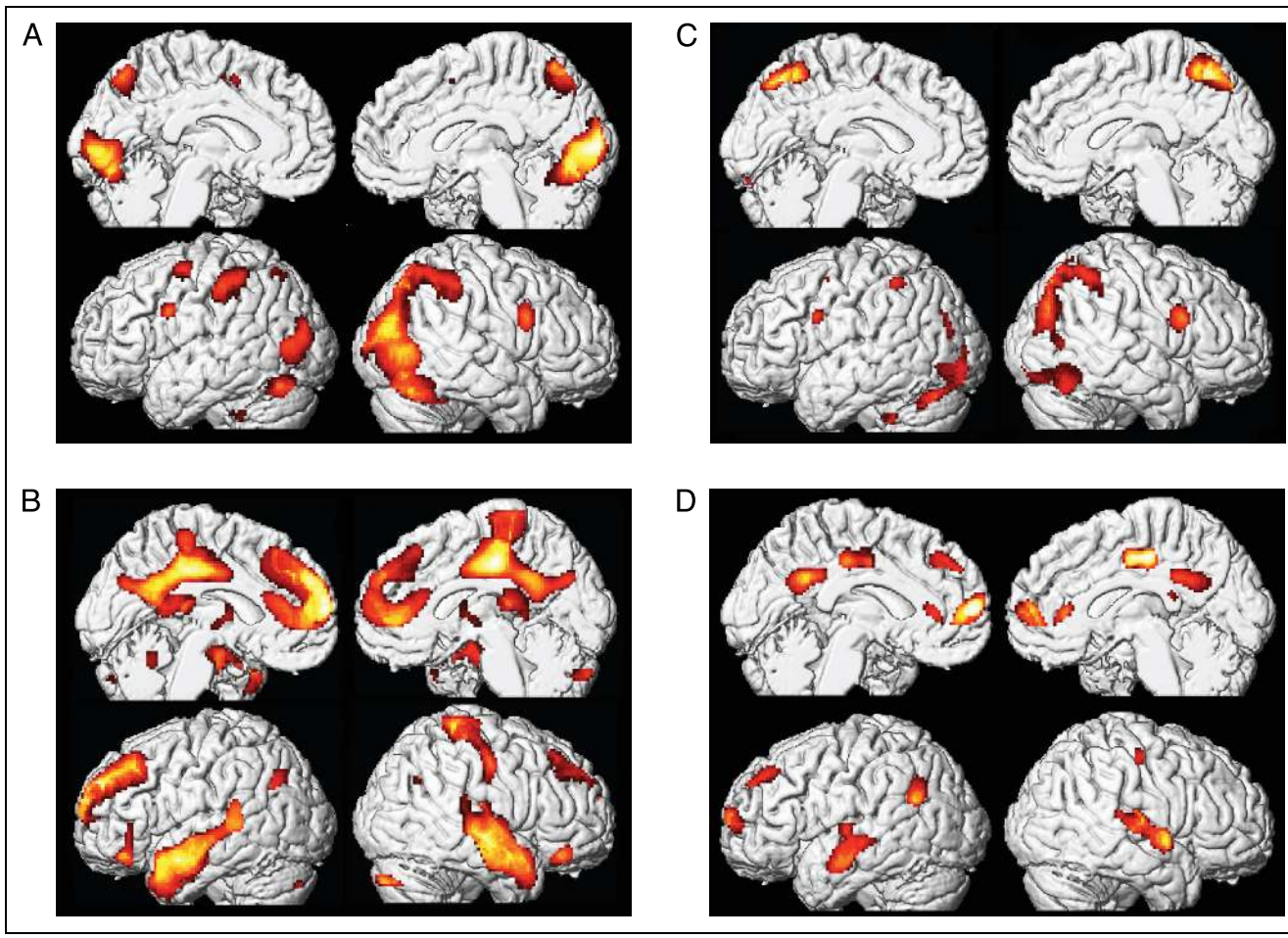

Figure 2. Neural correlates of perspective taking. Activations are projected onto a 3-D data set of one particular participant of the study (chosen randomly from the sample) to provide a background for anatomical orientation of activation sites. Aspects show the left (left column) and right hemispheres (right column) and the medial (upper row) and lateral aspects of the brain (lower row). Activation patterns were calculated with a nonparametric permutation test on the group-level (height threshold $p = .05$, corrected, extent threshold 10 voxels). (A) Activations common to all four conditions (3PP-GV plus 3PP-AV plus 1PP-GV plus 1PP-AV relative to baseline). These widespread activations comprise occipito-parietal regions, frontal regions bilaterally, and the left cerebellum. (B) Deactivations common to all four conditions (baseline relative to 3PP-GV plus 3PP-AV plus 1PP-GV plus 1PP-AV). Regions significantly deactivated during the target conditions are mesial cortical structures, lateral temporal and frontal cortex bilaterally, cerebellum bilaterally, and right postcentral cortex. (C) Main effect of 3PP (3PP-GV plus 3PP-AV relative to 1PP-GV plus 1PP-AV). Taking 3PP is associated with increased activity in the precuneus, the frontal cortex bilaterally, cerebellum bilaterally, left temporal cortex, and occipitoparietal cortex on the left side. (D) Main effect of 1PP (1PP-GV plus 1PP-AV relative to 3PP-GV plus 3PP-AV). Taking 1PP is associated with increased neural activity in lateral superior temporal cortex bilaterally including the insula, mesial cortical areas (both frontal and parietal), left frontal cortex, and the right postcentral gyrus as opposed to 3PP conditions. This pattern is a subset of the common deactivation pattern.

have been associated with a mesial cortical activation pattern, predominantly in the anterior and posterior cingulate and medial parietal cortex (Greicius, Krasnow, Reiss, & Menon, 2003; Gusnard, Akdubak, Shulman, & Raichle, 2001; Raichle et al., 2001). The empirical observation is that the medial frontal and parietal regions tend to decrease their activity during demanding cognitive tasks (Raichle et al., 2001). According to speculations of Gusnard et al. (2001), this might reflect a "continuous simulation of behavior" or "an inner rehearsal as well as an optimization of cognitive and behavioral serial programs for the individual's future," in short, a state of a "multifaceted self." What appears as "state of self" on the phenomenal level, appears as "default brain state" on the neural level. The 1PP condition modeled in our study could be taken as such a state of self, especially in comparison with the 3PP condition. That 3PP in our particular study had higher cognitive demands is reflected by the significant increase in reaction times.

In a similar vein, Burgess et al. (2001) argue that medial parietal cortex might support the "inspection" of internal images. This interpretation is also in line with the view of Vogt, Finch, and Olson (1992), who developed a differential concept of the anterior and posterior parts of the cingulate cortex, such that the anterior part primarily subserves executive functions, whereas the posterior cortex subserves evaluative functions such as monitoring sensory events and the

organism's own behavior in the service of spatial orientation and memory.

The view that these activations might constitute part of the neural basis of the core self is supported by studies suggesting executive functions for the anterior cingulate cortex and evaluative functions for the posterior cingulate cortex (Vogt et al., 1992). As our study focuses on a simple visuospatial task, the theoretical framework of the concept of a "core self" (Damasio, 1999) as a constituent of human self-consciousness also seems to apply for self-related visuospatial processes. Our data are in good accordance with studies on the neural correlates of emotional experiences related to the "core self": Self-generated emotions during recall of emotionally salient personal life episodes are associated with increased activity in the anterior and posterior cingulate cortex bilaterally (Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; Damasio et al., 2000; Fink et al., 1996). A similar result during emotional experience is reported in a PET study by Critchley, Mathias, and Dolan (2001).

With respect to the differential activations of 1PP versus 3PP, a systematic study on the shift of perspectives in a motor imagery task was recently performed by Ruby and Decety (2001), who studied imagined manipulation of objects performed either by themselves or the experimenter. Neural correlates associated with 1PP were observed in the left hemisphere only, and 3PP simulation activated right hemisphere regions only. These findings are consistent with our results. Furthermore, we recently studied the effects of 1PP and 3PP in

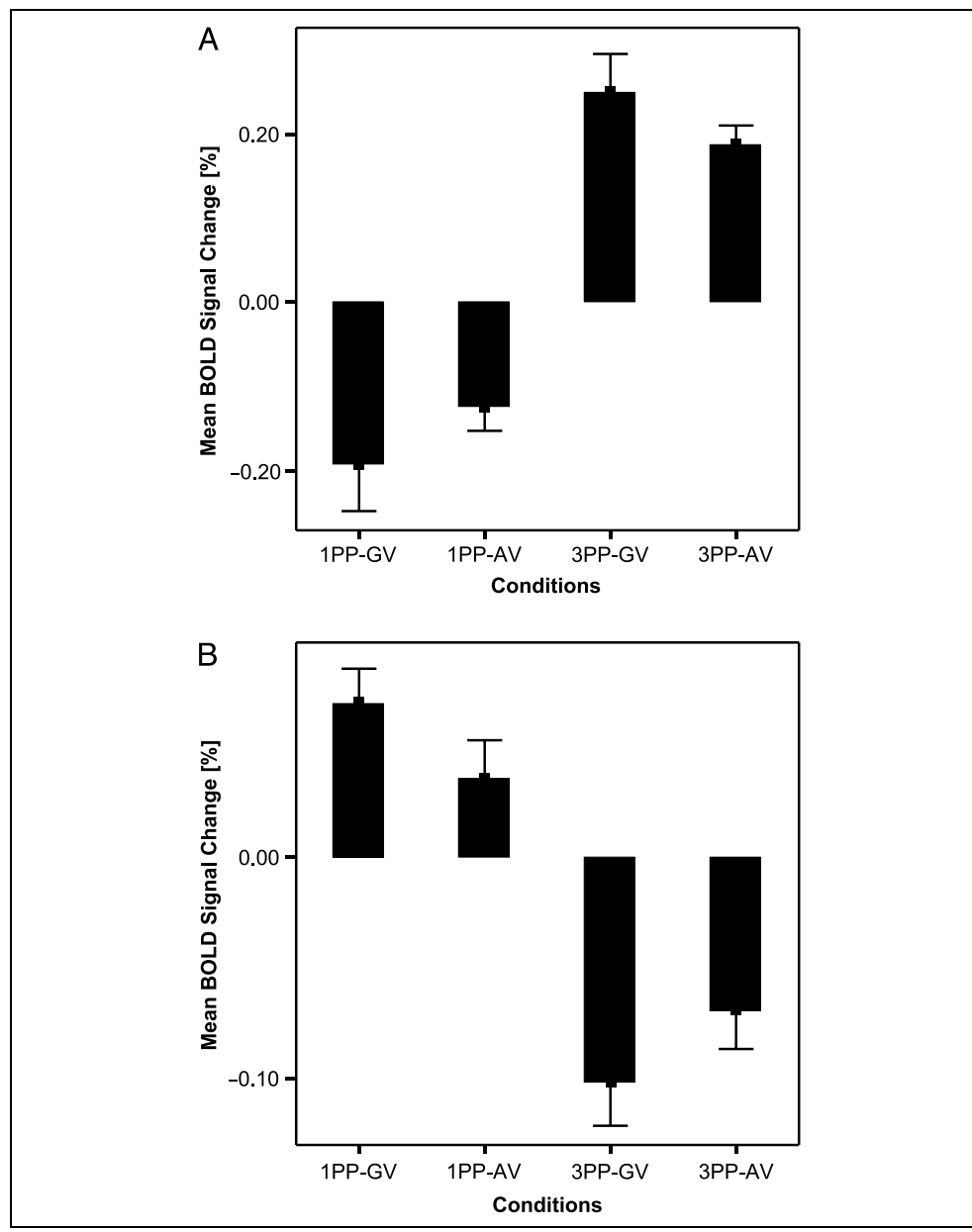

Figure 3. Mean percent signal changes of the key contrasts. (A) Mean percent signal changes and their mean standard errors (error bars) are provided for the principally activated voxel 2, −60, 56 of the key contrast 3PP > 1PP (3PP-GV plus 3PP-AV relative to 1PP-GV plus 1PP-AV). Mean values of the raw data for the four conditions, 3PP-GV, 3PP-AV, 1PP-GV, and 1PP-AV, were taken for this contrast at this voxel for each participating subject of the study. The plots show the differential increase of 3PP as opposed to 1PP. All voxel coordinates are provided according to Talairach and Tournoux (1988). (B) Mean percent signal changes and their mean standard errors (error bars) are provided for the principally activated voxel 40, −20, 8 of the key contrast 1PP > 3PP (1PP-GV plus 1PP-AV relative to 3PP-GV plus 3PP-AV). Mean values of the raw data for the four conditions, 3PP-GV, 3PP-AV, 1PP-GV, and 1PP-AV, were taken for this contrast at this voxel for each participating subject of the study. The plots show the differential increase of 1PP as opposed to 3PP. All voxel coordinates are provided according to Talairach and Tournoux (1988).

an extended theory of mind task, in which mental states had to be ascribed either to oneself or someone else. In that study, we observed an activation comprising the medial prefrontal cortex and the right temporo-parietal region associated with 1PP (Vogeley et al., 2001). The activation site of the medial prefrontal cortex is corroborated by the present study. The right temporo-parietal activation was only found in the language-based theory of mind task during 1PP, but not in the present visuospatial task. It therefore seems plausible to assume that this activation site is stimulus- and/or context-dependent. With respect to language tasks, right hemispheric activations are observed during pragmatic language tasks under normal conditions (Bottini et al., 1994; Brownell, Simpson, Birhle, Potter, & Gardner, 1990). Patients with right hemispheric lesions demonstrate difficulties with the understanding of metaphors, indirect meaning, (or indirect questions), the emotional–prosodic quality of expressions, and theory of mind (Happé, Brownell, & Wnner, 1999; Weylman, Brownell, Roman, & Gardner, 1989; Bryan, 1988; Brookshire & Nicholas, 1984; Ross, 1981).

With respect to the more general issue of spatial reference frames our study focuses on a specific type of a spatial cognitive task performed in egocentric reference frames. As summarized by Behrmann (1999), egocentric reference frames can be constituted with respect to the midline of the visual field, the head, the trunk, or the longitudinal axis of the limb involved in the execution of a certain action. Our study focuses on the aspect of translocations of different positions in space, which all involve the same type of egocentric reference frame. In other words, the center of the polar coordinate system constituting an egocentric reference frame is shifted (Vogeley & Fink, 2003). Our data show that such a translocation involves predominantly the precuneus region and the right superior parietal cortex on the neural level.

In conclusion, the results of our study reveal neural correlates of 1PP as a particular constituent of human self-consciousness. Taking one's own perspective appears to be a key component of human self-consciousness together with at least the experience of agency and the experience of transtemporal unity (Vogeley et al., 1999). Distinct mesial cortical structures are involved if the perspective is 1PP. This conclusion can be drawn based on a differential activation of these regions as opposed to 3PP conditions.

METHODS

Subjects

Eleven right-handed, healthy male volunteers (age 25–32 years) with no record of neurological or psychiatric illness participated in the study. Informed consent was obtained before participation. Volunteers were naïve with respect to the experimental task as well as the purpose of the study.

Stimulus Material, Tasks, and Study Design

Fully controlled 3-D visual scenes were generated with the software package 3-D Max (release 4.0, discreet, division of Autodesk, Montreal, Canada). Virtual scenes consisted of a quadrangular room with an avatar positioned in the center of the room with red balls around the avatar's head at constant distances (Figure 1). The virtual scene showed a quadrangular room with light gray walls and no additional visual cues like windows, doors, or furniture. An avatar was positioned in the center of the room. A variable number of red balls ranging from 1 to 3 were arranged around the avatar's head at constant distances. The virtual room was illuminated with a central light shining onto the scene from above. This basic scenery was used to generate the stimulus material used in this study. To control for potential confounds, the following features of the scenery were varied systematically: The number of red balls arranged on a circle around the avatar's head ranged from 1 to 3; the position of the avatar was varied in a way that it either looked frontally onto a wall or into a room corner with a disparity of 45°; the position of the camera was rotated around the avatar's position in the center of the room in different positions with a spacing of 60°. The objects were posted randomly at different positions around the avatar's head in steps of 30° with the distance to the head held constant. Half of the rendered images of these scenes were presented in GV with the camera position parallel to the ground floor on the level of the avatar's head. The other half was presented in AV, which was generated by applying an elevated camera perspective at a 60° angle to the floor. A total of 384 different scenes was generated. Each stimulus image was presented only once for each subject in a blocked order. Stimulus images were stored and later presented as jpg files with a spatial resolution of 400 × 200 pixels.

All stimulus images were presented only once per subject. Stimuli were presented on a display in the center of a 29-cm screen on a black background for 3 sec using the software program Presentation (Neurobehavioral Systems, Albany, CA). Twelve stimuli were presented per block, which lasted 36 sec. Subjects were instructed by a standardized slideshow before the experiment. Instructions contained example stimuli, the general instruction to count objects from different perspectives, and the field of view (FOV) of the avatar (150°). Before each block, either the instruction "How many balls does he see?" (3PP instruction) or "How many balls do you see?" (1PP instruction) were shown for 8 sec. There was no specific instruction with respect to view. During the low-level baseline (rest), a black screen with a gray fixation cross was presented for 16 sec and instructions were presented for 8 sec. Per subject,

eight blocks in randomized order covering the four conditions, 3PP-GV, 3PP-AV, 1PP-GV, and 1PP-AV, were presented in four experimental runs. The baseline condition was presented between each block of stimuli (eight blocks per run; four runs) and at the beginning and at the end of each run, equaling nine repetitions of the baseline per run. The instructions for the target conditions 1PP and 3PP were presented during these baseline conditions. There were no particular instructions for the baseline nor was there a task other than to attend and read the task instructions. Subjects had to perform four runs (two blocks for each of the four conditions) in a randomized order. One hundred twenty-six images were acquired per run (four runs total) corresponding to nine MR scans per block at a repetition time (TR) of 4 sec with the first two scans of each experimental run, but not of each block, being discarded to allow for T1 saturation effects. The overall duration of the scanning session was approximately 40 min. Reaction times and the number of objects counted were recorded using an fMRI-compatible response device with four response buttons (Lightwave Medical Industries, CST Coldswitch Technologies, Richmond, Canada). All behavioral answers were given by fingers 1–4 of the right hand. 3PP and 1PP systematically differed in so far, as during 3PP not all objects were visible for the avatar (to whom the specific perception had to be ascribed), whereas during 1PP all objects were visible for the test person. As the number of objects in the scene was systematically varied over all conditions to ensure comparable stimulus material of the same complexity, responses were consequently necessarily unbalanced with systematically lowered numbers of detected objects during 3PP as compared to 1PP. To avoid differential hemispheric activation due to unbalanced responses during 1PP and 3PP, we let the test person respond only with one hand throughout the experiment. Correctness scores and reaction times were calculated per block and subject.

Eye Movement Measurement and Analysis

All tasks were performed under free vision, first, because the answer to the question required the detection of both the avatar's position and gaze direction, the number of objects and the spatial relation of the objects and the avatar's FOV, and, second, to avoid any additional spatial cognitive activity that could arise from a fixation task. As previously shown, the factor of free versus fixed vision might influence visuospatial attention tasks (Fink, Dolan, Halligan, Marshall, & Frith, 1997). To assess whether the conditions differed by eye movements, on-line monitoring of eye positions relative to the screen, on-line monitoring of eye positions relative to the stimuli was performed using an infrared video-based eye-tracking device (ASL 504, fitted with a long-distance optics module; Applied Science Laboratories ASL, Bedford, MA). Data were analyzed with respect to the number of gaze fixations in a rectangular region-of-interest centered upon the head of the avatar and for the mean distance between two particular gaze fixations by averaging the particular distances between subsequent fixation points. Mean values of experimental conditions were calculated and compared using a two-way ANOVA.

Functional Magnetic Resonance Imaging

fMRI was carried out using echo planar imaging with whole-brain coverage and a 1.5-T MRI system (Siemens Magnetom Vision, Erlangen, Germany) with the standard head coil. Sequences with the following parameters were employed: TR = 4000 msec, echo time (TE) = 66 msec, FOV = 200 × 200 mm^2, $\alpha = 90^\circ$, matrix size = 64 × 64, voxel size = 3.125 × 3.125 × 4.4 mm^3. Using a midsagittal scout image, 30 axial slices (0.3 mm interslice gap) were positioned to cover the whole brain. Scanning was performed continuously over one run and restarted for the subsequent three runs. In addition, anatomical whole brain images were obtained by using a T1-weighted, 3-D gradient-echo pulse sequence (MP-RAGE, magnetization-prepared, rapid acquisition gradient-echo) with the following parameters: TR = 11.4 msec, TE= 4.4 msec, 15° flip angle, FOV = 256 × 256 mm^2, matrix size = 200 × 256, 128 sagittal slices with 1.33 mm thickness.

Image Processing and Analysis

Image processing and analysis including realignment, normalization, and statistical analysis was performed using SPM'99 (Wellcome Department of Cognitive Neurology, London, UK) implemented in MATLAB (Mathworks, Sherborn, MA). Analysis was carried out using the general linear model and a boxcar waveform convolved with the hemodynamic response function. Subject-specific, low-frequency drifts in signal changes were removed by a high-pass filter and global signal changes were treated as a covariate of no interest. The mean activity of each voxel throughout the whole experiment was used as a dependent variable. Specific effects for each voxel were tested by applying appropriate linear contrasts to the parameter estimates for each condition (Friston et al., 1995).

For group analysis, a standard nonparametric multiple comparisons procedure as implemented in SnPM (www.fil.ion.ucl.ac.uk/spm/snpm) was used, which is based on randomization/permutation testing (Nichols & Holmes, 2001). A multiple comparison procedure was implemented by applying a single threshold test in which the maximum voxel statistic of the image was considered. Because of the large number of possible permutations, an approximate permutation test was used, employing a subset of 1000 permutations with

no tradeoff in accuracy. Data described and displayed are significant at a height threshold of $p = .05$ (corrected) and an extent threshold of 10 voxel throughout.

To determine the increases in neural activity for a given contrast pseudo-*t* tests (in the sense of nonparametric testing with smoothed residual variance) with appropriate contrast images for each single subject were calculated. This method was applied for determination of activation common to all four conditions (relative to the low level baseline) (3PP-GV plus 3PP-AV plus 1PP-GV plus 1PP-AV relative to baseline) and deactivation common to all four conditions (relative to the low level baseline) (baseline relative to 3PP GV plus 3PP AV plus 1PP GV plus 1PP AV), as well as to determine the main effects, for which the following contrast images were calculated for every subject: relative activation during 3PP (3PP-GV plus 3PP-AV relative to 1PP-GV plus 1PP-AV), relative activation during 1PP (1PP-GV plus 1PP-AV relative to 3PP-GV plus 3PP-AV), relative activation during GV (3PP-GV plus 1PP-GV relative to 3PP-AV plus 1PP-AV), and relative activation during AV (3PP-AV plus 1PP-AV relative to 3PP-GV plus 1PP-GV). To determine the main effects of the factors perspective and view, corresponding contrast images were calculated and analyzed as described above on the group level. Stereotactic coordinates of the voxels of local maximum significant activation were determined within regions of significant relative activity change associated with the different tasks. The anatomic localization of local maxima was assessed by reference to the standard stereotactic atlas (Talairach & Tournoux, 1988) and superposition of the respective pseudo-*t* map on the mean anatomical image of all subjects who participated in the study (which had undergone the same anatomical stereotactic transformation). Approximately corresponding Brodmann's areas are provided based on Talairach and Tournoux (1988). The atlas by Talairach and Tournoux provides frequently used associations between Brodmann's areas and stereotactic coordinates. However, it should be kept in mind that Talairach and Tournoux's version of the Brodmann map does not reflect the complete and up-to-date cytoarchitectonic organization of the human brain. Likewise, the macroscopic landmark-based transformation of the schematic Brodmann map to the Talairach brain does not provide sufficiently precise localization of areal borders in relation to landmarks of the brain surface. Nevertheless, association of stereotactic coordinates with Brodmann's areas is given in the tables for the convenience of readers used to this parcellation scheme. The data were analyzed for the main effects of perspective and view and their interactions.

Mean percent signal changes were taken from raw data of every study participant for the key contrasts 3PP > 1PP (3PP-GV plus 3PP-AV relative to 1PP-GV plus 1PP-AV) and 1PP > 3PP (1PP-GV plus 1PP-AV relative to 3PP-GV plus 3PP-AV), at the principally activated voxels for the key contrasts (Figure 3).

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The data reported in this experiment have been deposited in the fMRI Data Center (http://www.fmridc.org). The accession number is 2-2004-115YN.

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