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The neural basis of the egocentric and allocentric spatial frame of reference

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ABSTRACT

The present study examines the functional and anatomical underpinnings of egocentric and allocentric coding of spatial coordinates. For this purpose, we set up a functional magnet resonance imaging experiment using verbal descriptions of spatial relations either with respect to the listener (egocentric) or without any body-centered relations (allocentric) to induce the two different spatial coding strategies. We aimed to identify and distinguish the neuroanatomical correlates of egocentric and allocentric spatial coding without any possible influences by visual stimulation. Results from sixteen participants show a general involvement of a bilateral fronto-parietal network associated with spatial information processing. Furthermore, the egocentric and allocentric conditions gave rise to activations in primary visual areas in both hemispheres. Moreover, data show separate neural circuits mediating different spatial coding strategies. While egocentric spatial coding mainly recruits the precuneus, allocentric coding of space activates a network comprising the right superior and inferior parietal lobe and the ventrolateral occipito-temporal cortex bilaterally. Furthermore, bilateral hippocampal involvement was observed during allocentric, but not during egocentric spatial processing. Our results demonstrate that the processing of egocentric spatial relations is mediated by medial superior–posterior areas, whereas allocentric spatial coding requires an additional involvement of right parietal cortex, the ventral visual stream and the hippocampal formation. These data suggest that a hierarchically organized processing system exists in which the egocentric spatial coding requires only a subsystem of the processing resources of the allocentric condition.

1. Introduction

Human beings move in three-dimensional space and must be able to orient themselves and navigate within this space. The entities in space and the spatial relations between them change continuously during everyday life. In order to keep track of the position of objects we need a stable, but at the same time flexible system to code and update the representation of space that surrounds us; a *Frame of Reference* (FoR).

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The FoR can be defined as a means of representing the locations of entities in space. At least two different FoRs are distinguishable. It is possible to encode or represent the positions of each object in relation to oneself. This type of FoR is referred to as *egocentric* and is defined by subject-to-object relations. The locations of objects in space are represented with respect to a personal agent. Spatial positions can also be coded in object-centered coordinates that are independent of the observer's current position. This mode of representing spatial relations is referred to as *allocentric*. The allocentric FoR is constituted by object-to-object relations and therefore, it refers to a framework that is independent from the agent's position (Vogeley, 2003; Vogeley and Fink, 2003).

Based on a large amount of neuropsychological and neurophysiological studies in spatial cognition, anatomically and functionally separate neuronal circuits can be assumed for allocentric and egocentric spatial coding. Yet, some questions remain to be resolved. Neuropsychological investigations on unilateral spatial neglect have provided indications for distinct spatial FoRs. Viewer- or body-related neglect indicates an impairment of the egocentric FoR (Beschin et al., 1997; Calvanio et al., 1987; Chokron and Imbert, 1995; Fujii et al., 1996; Heilman et al., 1983; Hillis et al., 1998; Karnath et al., 1991; Karnath and Fetter, 1995; Ladavas, 1987) whereas stimulus- or object-related neglect concerns the contralesional side of objects, independent of their position relative to the body. The latter indicates an impairment of the allocentric FoR (Caramazza and Hillis, 1990; Driver and Halligan, 1991; Hillis and Caramazza, 1991; Walker and Young, 1996; Young et al., 1992). Two recent studies show that in fact the two FoRs can be differentially affected in patients with unilateral neglect (Hillis and Rapp, 1998; Ota et al., 2003). Both investigations presented two patients; one showing body-centered neglect while the processing of object based spatial processing remained intact, and the other patient showing object-centered neglect while there was no impairment of body-centered spatial processing. This double dissociation provides strong evidence for the existence of two at least partly separate FoRs for coding spatial coordinates in the human brain.

Moreover, Hillis et al. (2005) describe patients who exhibit left “allocentric” neglect and hypofusion of the right superior temporal gyrus, whereas patients with hypofusion of the right angular gyrus demonstrate a left “egocentric” neglect (Hillis et al., 2005). They conclude that egocentric neglect can be associated with frontal and dorsal hypofusion in right posterior inferior frontal gyrus, angular gyrus and supramarginal gyrus and the visual association cortex. Allocentric neglect can be associated with more ventral hypofusion, including right superior temporal gyrus and posterior inferior temporal gyrus. However, some studies also reported simultaneous deficits of body-centered and stimulus-centered FoRs (Arguin and Bub, 1993; Farah et al., 1990; Nyffeler et al., 2005; Walker, 1995). For example, a stroke of the right medio-temporo-occipital region including the parahippocampal cortex led to allocentric as well as egocentric spatial impairments (Nyffeler et al., 2005).

The involvement of the hippocampus in spatial memory functions is well known, especially in allocentric memory (for review see Nadel and Hardt, 2004). It has been proposed that there is parallel processing of egocentric and allocentric information in the parietal lobe and the hippocampal formation, with eventual transfer to the hippocampus for long-term storage in allocentric coordinates (Feigenbaum and Morris, 2004; Kesner, 2000; Save and Poucet, 2000).

The importance of frontal and parietal cortical regions in human spatial processing has been demonstrated by neuroimaging investigations of the FoR. Two fMRI studies investigated the neural underpinnings of FoRs using tasks in which subjects had to judge the localization of a visual stimulus with respect to either the body or to an object (Galati et al., 2000; Vallar et al., 1999). Both investigations revealed a bilateral, mostly right hemispheric parieto-frontal network related to the egocentric FoR. Galati et al. (2000) also reported posterior parietal and frontal premotor activations with a similar right-sided asymmetry associated with the allocentric FoR. A more recent fMRI study compared viewer-centered, object-centered and landmark-centered spatial coding of visually presented realistic 3D-information (Committeri et al., 2004). According to this study viewer-centered egocentric coding is mainly processed in the dorsal stream and frontal areas, whereas allocentric coding centered on external references requires both dorsal and ventral regions (Committeri et al., 2004).

The results of these investigations in combination with the conclusions based on research on spatial neglect provide strong evidence that allocentric and egocentric spatial information is processed in at least partly separate neural networks (Nadel and Hardt, 2004). Despite this wealth of knowledge there still is a lack of evidence regarding the cortical subregions involved in either egocentric or allocentric spatial transformations and in the amount of overlap in parietal regions. Furthermore, the visual stimulation used by former investigations could have interfered with the neuroanatomical correlates that underlie different spatial coding strategies. Thus, these investigations do not permit to disentangle whether the involvement of primary and secondary visual areas is due to the visual stimulation per se, or results from the task and the processing of spatial information associated with it.

Taken together, neuropsychological investigations indicate the existence of functionally and anatomically independent egocentric and allocentric spatial FoRs and point out the relevance of parietal areas. However, lesion studies do not yield precise information regarding anatomically defined neural circuits that underlie egocentric and allocentric spatial coding. Additionally, interindividual differences in lesion size and location, as well as compensatory processes during rehabilitation avoid clear and definite interpretations. Therefore data from brain-damaged patients cannot provide a definite neuroanatomical basis for the distinction between the egocentric and the allocentric FoR. Results from neuroimaging studies investigating egocentric and allocentric spatial judgment and spatial navigation are lacking essential information. In particular, questions regarding the specific involvement of different subregions in allocentric and egocentric spatial coding, the amount of overlap (predominantly in parietal regions), the possible interference due to visual stimulation and the modulating influence of interindividual strategies remain unsolved.

The aim of the present fMRI study is to investigate the core regions of human spatial processing and to identify dissociable cortical networks for the processing of egocentric and allocentric spatial coding. To rule out any possible bias due to the perception of visual stimuli, we used verbal descriptions of spatial relations either with respect to the listener to induce an egocentric spatial coding, or without any body-centered relations to induce an allocentric coding. For the experimental condition investigating the allocentric FoR [A_{FoR}], we used verbal instructions defining the spatial relations between different objects (colored triangles, quadrangles, and circles; see example below). Verbal instructions were also used in the egocentric FoR task [E_{FoR}], but the spatial positions of the objects were related to the participants. In both conditions the task for the participants was to respond by making a spatial judgment. To control for auditory input as well as additional task demands we applied a control condition [cont], in which no reference was made to spatial relations in the verbal instructions.

Based on the aforementioned evidence we hypothesize that the processing of both egocentric and allocentric spatial coding are associated with bilateral activations of a fronto-parietal cortical network. Moreover we assume that egocentric and allocentric FoRs could be considered partly unique domains, which recruit distinct brain areas. The two FoRs could be constituted by a hierarchical processing network or by widely independent neural circuits. A hierarchical processing network would predict that one of the two spatial computations requires only a subsystem of the processing resources of the other. The existence of distinct neural circuits would predict that egocentric and allocentric spatial coding require unique processing resources that are not shared by the other processes.

2. Results

2.1. Behavioral data

Behavioral data were successfully collected from all participants and subjected into a repeated measure analysis of variance (ANOVA). Analysis of the percentage of correct responses revealed no significant main effect for the factor task (egocentric, allocentric, control) ($F(2,30)=2.03$, $P=0.148$). Overall, the mean accuracy with which the subjects performed the tasks was 84% of trials. Analysis of reaction times explored a significant main effect of task ($F(2,30)=7.13$, $P=0.003$). Post-hoc paired t-tests showed no significant differences between the egocentric (4645 ± 1422 ms after onset of the given question; see Experimental procedures) and the control (4736 ± 1603 ms) condition ($t(15)=0.9$, $P=0.4$), the allocentric (5064 ± 1476 ms) and the control condition ($t(15)=-3.2$, $P=0.06$), and the allocentric and the egocentric conditions ($t(15)=-3.1$, $P=0.07$).

2.2. fMRI data

2.2.1. Activations observed for each experimental condition relative to the control condition

To reveal general differences in neural activation associated with A_{FoR} and E_{FoR}, we calculated contrasts for "*general effects*" comparing the allocentric and egocentric conditions separately with the control condition ([$A_{FoR}>$cont] and [$E_{FoR}>$cont]). Results of the analysis are shown in Fig. 1 and listed in Table 1. Both, the egocentric and allocentric conditions, revealed activation of a bilateral fronto-parietal network including the superior posterior parietal lobe, the superior occipital gyri and the superior frontal gyri. The egocentric condition revealed activations mainly within the superior posterior parietal lobe (precuneus), the bilateral superior occipital gyri, the bilateral superior frontal gyri, the anterior part of the calcarine sulcus

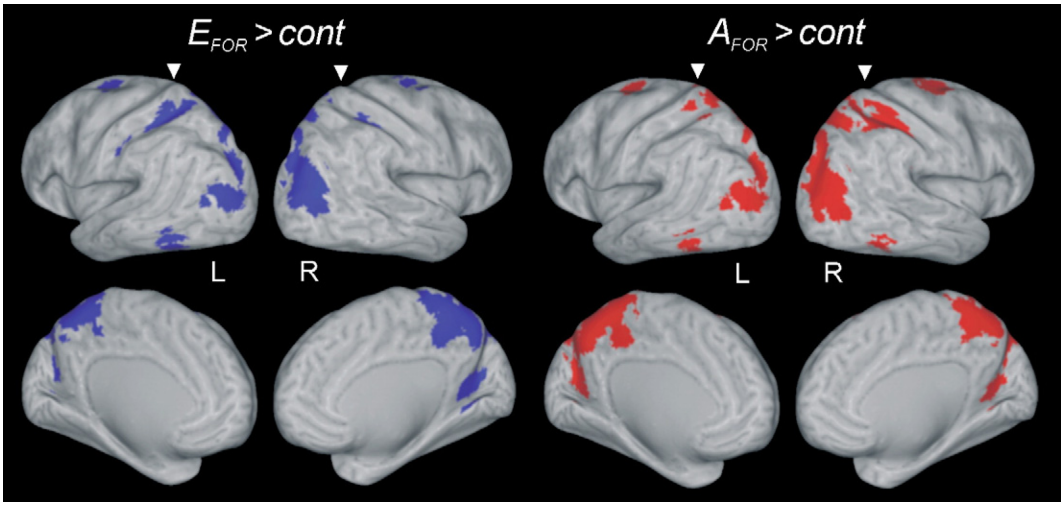

Fig. 1 – *General activation.* Activations observed for egocentric and allocentric coding in space relative to the control condition. The color labels refer to the egocentric (blue) and allocentric (red) spatial conditions. Activations are overlaid on lateral and medial three-dimensional views of an inflated standard brain. Left side of the figure shows activations for E_{FOR} relative to cont, right side of the figure shows activations for A_{FOR} relative to cont. Triangle indicates the position of the central sulcus.

Table 1 – Peak activation observed for egocentric and allocentric coding in space relative to the control condition (general effects)

Condition and anatomical area	L/R	T-value	x	y	z
E_{FOR}>cont					
Superior parietal lobe (precuneus)	L	12.15	−3	−51	51
	R	9.62	9	−69	51
Superior occipital gyrus	L	10.45	39	−81	21
	R	8.55	−39	−78	18
Calcarine sulcus	L	9.37	−15	−36	15
	R	9.11	18	−57	12
Superior frontal gyrus	L	6.9	−21	−3	54
	R	6.16	27	−3	60
Inferior temporal gyrus	L	7.03	−57	−60	−15
Inferior parietal lobe	R	5.92	36	−36	39
A_{FOR}>cont					
Superior occipital gyrus	R	10.23	39	−81	21
	L	8.48	−27	−75	24
Inferior parietal lobe	R	7.64	36	−36	39
	L	5.99	−30	−42	39
Calcarine sulcus	R	6.83	18	−54	12
	L	6.21	−18	−63	15
Superior frontal gyrus	R	8.39	30	0	57
	L	7.10	−21	0	54
Inferior temporal gyrus	L	7.22	−54	−60	−12
	R	5.49	51	−57	−15

The coordinates are given according to the MNI space together with their *T*-scores.
Height threshold: *T*=4.96 (*P*=0.05, FWE-corrected), Extent threshold: *k*=10 voxels.

bilaterally, the left inferior temporal gyrus, and the right inferior parietal lobe. The allocentric condition revealed activations of the bilateral superior occipital gyri extending into the inferior and superior parietal lobes, the bilateral calcarine sulci, the bilateral superior frontal gyri, and the bilateral inferior temporal gyri.

2.2.2. *Core regions of the egocentric and the allocentric conditions*

In order to verify the existence of concurrently activated regions, that means neuronal regions that are activated during both the egocentric [E_{FoR}] and the allocentric [A_{FoR}] condition, in a next step the minimum activation of both conditions was calculated to specifically address the issue of core regions generally involved in spatial coding. The results of the analysis are shown in Fig. 2 and listed in Table 2. Commonly shared activations were found bilaterally in the superior occipital gyri, the superior parietal lobe (precuneus), the anterior part of the calcarine sulci, the superior frontal gyri, and the left inferior temporal gyrus.

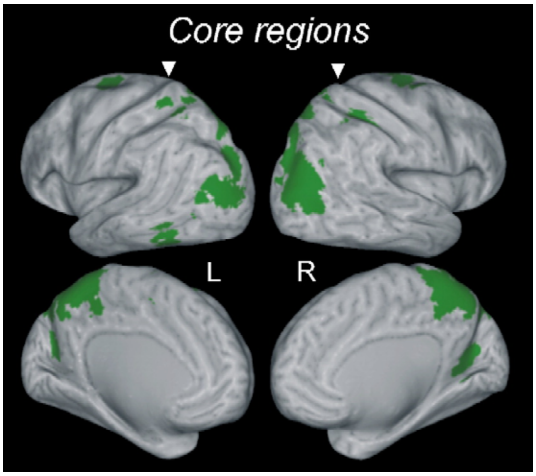

Fig. 2 – *Core regions of the egocentric and allocentric conditions.* Concurrently activated regions generally involved in spatial coding (regions that are activated during both the egocentric [E_{FOR}] and the allocentric [A_{FOR}] condition). Activations are overlaid on lateral and medial three-dimensional views of an inflated standard brain. Triangle indicates the position of the central sulcus.

2.2.3. *Differential activation between the experimental conditions*

In a next step we calculated "*differential effects*", comparing the allocentric condition with the egocentric condition [A_{FoR}>E_{FoR}] and the egocentric condition with the allocentric condition [E_{FoR}>A_{FoR}]. Results of the analysis are shown in Fig. 3 and listed in Table 3. When compared to the allocentric condition the egocentric condition revealed activations exclusively within the precuneus. The allocentric condition in comparison to the egocentric condition revealed activation of the bilateral hippocampal gyri, bilateral inferior temporal gyri, the right inferior and superior frontal gyrus, and of the right inferior and superior parietal lobe.

3. Discussion

The aim of this study was to identify and distinguish the neuroanatomical correlates of egocentric and allocentric spatial coding without any possible influences due to the processing of visual stimuli. More specifically, we examined the core regions of human spatial processing and investigated

Table 2 – Core regions of the egocentric and allocentric conditions

Anatomical area	L/R	T-value	x	y	z
Superior occipital gyrus	R	10.23	39	−81	21
	L	7.46	−30	−75	24
Superior parietal lobule (precuneus)	L	9.43	−12	−69	51
	R	9.19	9	−69	54
Calcarine sulcus	R	6.82	18	−54	12
	L	6.22	−18	−63	15
Superior frontal gyrus	L	6.9	−21	−3	54
	R	6.15	27	−3	60
Inferior temporal gyrus	L	6.67	−54	−60	−12
Inferior parietal lobe	R	5.92	36	−36	39

The coordinates are given according to the MNI space together with their *T*-scores.
Height threshold: *T*=4.96 (*P*=0.05, FWE-corrected), Extent threshold: *k*=10 voxels.

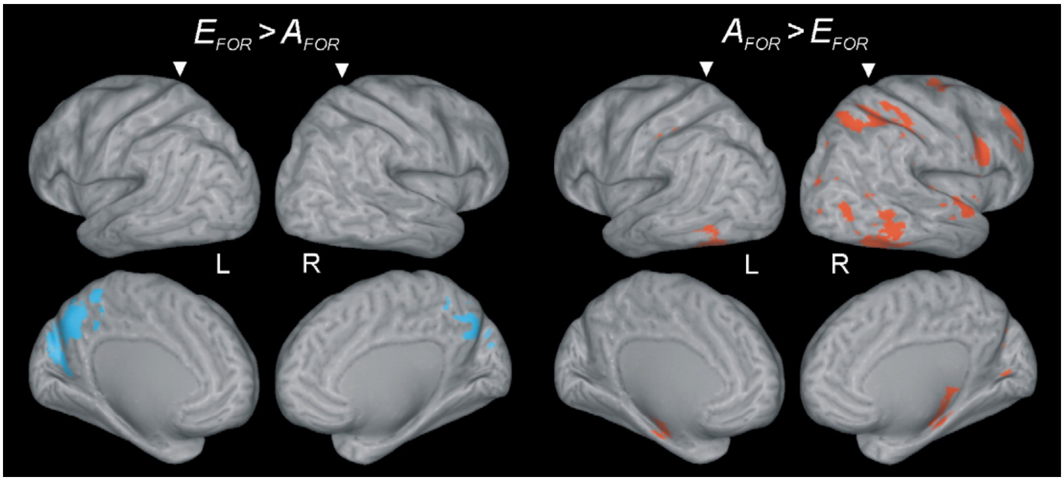

Fig. 3 – *Differential activation.* Activations observed for the comparison between allocentric and egocentric coding in space. Effects for $E_{FOR} > A_{FOR}$ are indicated in blue, effects for $A_{FOR} > E_{FOR}$ are indicated in red color. Activations are overlaid on lateral and medial three-dimensional views of an inflated standard brain. Triangle indicates the position of the central sulcus.

to what extent egocentric and allocentric coding rely on functionally and neuroanatomically dissociable mechanisms.

The results clearly indicate a bilateral fronto-parietal network associated with both spatial tasks. We identified the superior occipital gyrus, the medial parts of the superior parietal cortex (the precuneus) and the bilateral superior frontal gyri as core regions for egocentric and allocentric spatial coding. Comparing the hemodynamic response during egocentric and allocentric conditions revealed partly separate neural circuits mediating different spatial coding strategies. While egocentric spatial coding revealed activation mainly within the medial parts of the posterior superior parietal lobe, the use of the allocentric reference frame revealed activation in the right parietal lobe, the bilateral ventrolateral occipito-temporal cortex and the bilateral hippocampal formation.

Table 3 – Differential activation between the experimental conditions (direct comparison)

Condition and anatomical area	L/R	T-value	x	y	z
$E_{FOR} > A_{FOR}$ masked [incl.] by $E_{FOR} >$ cont at $P = 0.05$					
Superior parietal lobule (precuneus)	L	5.09	−6	−63	36
		4.85	−9	−72	27
		4.18	−3	−51	51
$A_{FOR} > E_{FOR}$ masked [incl.] by $A_{FOR} >$ cont at $P = 0.05$					
Hippocampus	L	5.65	−33	−18	−15
	R	5.33	30	−24	−6
Cerebellum	L	5.47	−15	−33	−45
	R	5.33	6	−33	−39
Middle temporal gyrus	R	5.29	51	−3	−9
Inferior temporal gyrus	R	4.60	45	−54	−15
	L	4.38	−45	−66	−15
Superior frontal gyrus	R	4.22	39	42	18
Inferior parietal lobe	R	4.6	24	−51	42
Superior parietal lobe	R	3.44	48	−33	45
Inferior frontal gyrus	R	4.00	54	6	18

The coordinates are given according to the MNI space together with their T-scores.
Height threshold: $T = 2.55$ ($P = 0.05$, FDR-corrected), Extent threshold: $k = 10$ voxels.

3.1. *Parietal cortex and spatial coding*

Neurophysiological studies have demonstrated the existence of both body- and object-based representations in posterior parietal cortex of the monkey brain. It has been shown that neurons coding visual information in egocentric (body- and body part-centered) coordinates are located in the parieto-occipital region (PO) (Galletti et al., 1993), lateral intraparietal area (LIP) (Andersen et al., 1990), ventral intraparietal area (VIP) (Duhamel et al., 1997), and area 7a (Andersen et al., 1985). Neurons whose firing rate is modulated by the specific location inside an object independent of the observer's position have also been found in the posterior parietal cortex (area LIP: Sereno and Maunsell, 1998). In humans, several neuroimaging studies on spatial judgment revealed a strong involvement of posterior parietal cortex during egocentric and allocentric perceptual tasks (Committeri et al., 2004; Galati et al., 2000; Vallar et al., 1999).

In the present study, only the medial superior parietal cortex (precuneus) exhibited a stronger involvement during the egocentric task. As illustrated in Fig. 3, the activation of the precuneus was specific for the processing of egocentric spatial information. Precuneus activation associated with egocentric spatial coding has also been reported in previous studies for tasks selectively requiring an egocentric spatial processing (Committeri et al., 2004; Galati et al., 2000). Based on neurophysiological and functional imaging studies in healthy humans, it has been argued that the posteromedial parietal cortex acts in concert with the lateral parietal areas in elaborating information about egocentric and allocentric spatial relations for body movement control, voluntary attention shifts and mental imagery tasks (Cavanna and Trimble, 2006). More generally, it has been suggested that the precuneus is involved in visual imagery tasks (Fletcher et al., 1995, 1996) and that the generation of a coherent image is instantiated through activation of the precuneus. However, the visual imagery process on its own cannot account for the specific activation of the precuneus during egocentric spatial coding seen in the present study. Since the "*differential effects*" also explored stronger activations of the precuneus for egocentric when compared to allocentric spatial coding, the involvement of the precuneus cannot be attributed exclusively to visual imagery processing. The role of the precuneus in egocentric coding is also demonstrated by cortical lesions of the precuneus and the superior parietal lobe which have been associated with egocentric disorders such as "optic ataxia" (Perenin and Vighetto, 1988) and neglect (Hasselback and Butter, 1997). Furthermore, it has been shown that the left precuneus is selectively involved in the mental simulation of routes when compared to pure visual imagery of landmarks (Ghaem et al., 1997).

Interestingly, an fMRI study on mental viewer rotation showed a specific involvement of the left precuneus during the egocentric transformation task (Creem et al., 2001). In this context, it is noteworthy that several studies showed an advantage for spatial updating after imagined viewer rotations when compared to array rotations (Creem-Regehr, 2003; Wraga et al., 2000). The behavioral data from our study also show a reaction time advantage for the egocentric condition when compared to the allocentric or to the control condition. Future research needs to explore more in detail whether this viewer advantage is responsible for the shorter response times we found in the egocentric condition. For example, our study did not require a mental viewer rotation and it is therefore possible that the mere use of egocentric coordinates could speed up the process.

Several studies investigating the neuronal underpinnings of allocentric spatial judgment tasks have reported activation of the posterior parietal cortex, mainly in the right hemisphere (Galati et al., 2000). In the present study, we also found a right-sided involvement of posterior parietal areas during allocentric spatial coding. The right superior parietal cortex exhibited specific activation for the coding and maintenance of allocentric spatial information. This is in line with studies on object-based neglect concerning the left side of individual objects as a consequence of right hemispheric posterior parietal lesions (Vallar et al., 2003).

3.2. *Frontal cortex and spatial processing*

For the two conditions we observed hemodynamic responses in the superior frontal gyrus. The analysis of core regions revealed hemodynamic responses in the bilateral superior frontal gyri. These areas comprise the rostral part of the dorsal premotor cortex, also called pre-PMd in the Brodmann area 6 (Picard and Strick, 2001). In contrast to the caudal part of the PMd the pre-PMd is known to be involved in spatial attention, spatial working memory and updating spatial mental operations (Boussaoud, 2001; Hanakawa et al., 2002; Picard and Strick, 2001; Tanaka et al., 2005). Boussaoud (2001) demonstrated a clear separation of the left rostral (Talairach coordinates: $x=-20$, $y=1$, $z=49$) and the left caudal part of the PMd (Talairach coordinates: $x=-33$, $y=-7$, $z=49$). While a spatial attention and memory task evoked strong hemodynamic responses in the rostral part of the PMd (pre-PMd) a motor intention task activated more the caudal part of the PMd (Boussaoud, 2001).

Using fMRI and rTMS Tanaka et al. (2005) demonstrated an interesting functional double dissociation in which the medial Brodmann Area 6 plays a critical role in updating verbal information and the lateral BA 6 plays an essential role in updating spatial information (Tanaka et al., 2005). According to our study, we assume that activity in the pre-PMd is associated with the updating of spatial information. This process was necessary in both of the tasks in order to maintain the spatial information. Furthermore, other studies examining the egocentric and allocentric frame of reference also reported a general involvement of premotor areas (Committeri et al., 2004; Galati et al., 2000).

3.3. *Hippocampus and allocentric spatial coding*

Yet another finding of the present study is the activation of the bilateral hippocampal formation during the allocentric condition. In particular the "*differential effects*" revealed stronger involvement of the bilateral hippocampi during allocentric spatial processing.

Coding of topographical space is typically associated with activations of the hippocampal formation. Neurons with allocentric properties have been found in the hippocampal formation of both rats (O'Keefe and Dostrovsky, 1971; Taube et al., 1990) and monkeys (Ono et al., 1993; Rolls and O'Mara, 1995). In humans, these spatial properties of the hippocampus neurons have led to theoretical assumptions of the cognitive map theory of hippocampal function (O'Keefe et al., 1979; O'Keefe and Nadel, 1978). The cognitive map theory proposes that the hippocampus represents the environment, locations within this environment and its content, providing the basis for spatial memory and flexible navigation (O'Keefe and Nadel, 1978). Several investigations on patients with selective lesions of the hippocampal formation provide evidence for the cognitive map theory (Bohbot et al., 2004; Burgess et al., 2002; Feigenbaum and Morris, 2004; Nadel and Hardt, 2004). Recently, Parslow et al. (2004) used fMRI to compare allocentric and egocentric spatial memory in healthy individuals. Bilateral hippocampal and parahippocampal activations were found only in the allocentric memory encoding phase (Parslow et al., 2004). Interestingly, even though our task did not require long-term spatial memory we found stronger bilateral hippocampal activation in the allocentric vs. the egocentric condition. Similarly, using a "line bisection task" with allocentric and egocentric conditions Galati et al. (2000) found a right sided hippocampal activation in the allocentric vs. the egocentric condition. Based on these findings we conclude that the hippocampal activation revealed in the present study for the allocentric task could reflect the viewer-independent coding of spatial relations.

3.4. *Ventrolateral occipital–temporal cortex and allocentric spatial coding*

Another finding revealed by the present study is the activation of the bilateral inferior temporal cortex (fusiform gyrus) extending into the inferior occipital cortex during the processing of allocentric information, also described as the ventro-lateral occipito-temporal cortex. In the present study, the features of the stimuli (verbally described objects) were constant across all experimental conditions. Therefore, the observed activational differences within the ventral visual stream must be associated with different spatial coding strategies, rather than a pure difference in processing the features of the objects.

It has been suggested that the ventral and dorsal visual streams are supposed to rely on different spatial frames of reference (Goodale and Haffenden, 1998). According to this assumption, the two streams process information about object features and about their spatial locations, but each stream uses this visual information in different ways. In the ventral stream, the processing extracts the constant characteristics of objects and their relations. The representation is object-based so that size, shape, and relative location can be maintained across different viewing conditions (Milner and Goodale, 1993). In contrast, the transformation performed by the dorsal stream deals with information about the location and disposition of objects in egocentric coordinates and supports actions directed to these objects. The underlying visuomotor transformations are viewer-centered and they mediate the visual control of skilled actions (Goodale et al., 1991; Goodale and Milner, 1992; Milner and Goodale, 1995). Our results indicate that allocentric spatial coding allocates an object-based representation within the ventrolateral occipito-temporal cortex, even if only linguistic information is processed.

As suggested by Goodale and Milner (1992), the perceptual mechanism of the ventral stream provides constant, viewer-independent, long-term representation of the surrounding world. As a matter of fact, the hippocampal formation plays a key role in human spatial processing by maintaining a cognitive map, providing a stable survey representation of the environment (O'Keefe and Nadel, 1978). Yet another aspect is the role of the hippocampus in spatial memory consolidation (Barrash et al., 2000).

The results presented in our investigation suggest that human spatial processing by means of allocentric relations depends on stable representations of constant object qualities mediated by a neurofunctional network involving both the ventral visual stream and the hippocampal formation (see also Galati et al., 2000; Nadel and Hardt, 2004).

Interestingly, a recent fMRI study on the neuronal underpinnings of different spatial judgment tasks also showed a selective involvement of bilateral ventrolateral occipito-temporal cortex for an object-centered task (Committeri et al., 2004). In this investigation visual scenes were presented and participants had to judge spatial distances between objects with respect to reference objects. Both investigations revealed an involvement of ventrolateral occipito-temporal areas during the allocentric (object-centered) condition even though in our study we used a non-visual paradigm that did not explicitly require the judgment of distance. These results provide evidence for a viewer-independent coding of objects and their spatial relations mediated by the ventral stream.

3.5. *Activation of visual areas in the absence of visual input*

For the comparison of the spatial experimental conditions with the non-spatial control task, both spatial judgment tasks revealed activations of the bilateral superior occipital cortex. The involvement of the higher visual areas in spatial coding is consistent with former investigations on spatial coding using visual stimulation (Committeri et al., 2004; Parslow et al., 2004) as well as spatial mental imagery relying on auditory instructions (Mellet et al., 1996, 2000). The activation of the higher visual areas in these tasks as well as in our study indicate that spatial imagery based on visual and on verbal stimulation can recruit regions known to be involved in high-order visual processing.

A further interesting finding of the present study is the involvement of primary visual areas in both spatial processing tasks. Despite some controversial findings (Knauff et al., 2000; Mellet et al., 2000), there is a wealth of evidence showing that mental visual imagery leads to activations in primary visual cortex and therefore recruits at least partly the same cortical areas that are also associated with visual perception (Klein et al., 2000; Kosslyn et al., 2001; Kosslyn and Thompson, 2003; Slotnick et al., 2005). The primary visual cortex is particularly involved when participants generate high-resolution mental images. Since we used a purely non-visual paradigm the observed activational increases in primary visual cortex are likely to reflect mental imagery processing. Thus, spatial reasoning can involve the generation of high-resolution mental images, which then help to solve the tasks. This is in concordance with the verbal reports made by the subjects concerning the strategies they used to maintain the spatial information and to solve the tasks. All subjects consistently reported to have mentally built up a visual–spatial map of the objects to maintain their positions.

3.6. *Summary – the neuronal networks of spatial frames of reference*

In the present study, we examined the functional and anatomical underpinnings of egocentric and allocentric coding of spatial coordinates. We found a common fronto-parietal network for the spatial mental processing, representing the core regions involved in both tasks, the egocentric frame of reference and the allocentric frame of reference coding. This network comprises primary and secondary visual areas, parietal areas, and the left premotor region. To our knowledge this is the first study using a purely non-visual task to investigate different spatial coding strategies. By using exclusively verbal descriptions we provide strong evidence that spatial processing requires primary visual cortex functions, which reflect mental imagery processing. The results of this study show that egocentric and allocentric spatial coding are partly unique domains which recruit distinct brain regions.

The egocentric spatial coding is mainly associated with precuneus activations. Even though this region is also part of the common network, it is significantly stronger involved in egocentric than in allocentric spatial coding. The allocentric condition recruits right-sided parietal areas, the bilateral ventral visual stream, and the hippocampal formation. In the context of the proposed processing networks, results of the present study do not support the existence of independent neural circuits. In particular, an independent neural processing mode would predict unique processing resources for egocentric and allocentric spatial coding. The activations in both spatial tasks overlapped widely. However, the prediction of a hierarchical network is that both spatial computations require a subsystem of the shared processing resources. The present study demonstrates that the processing of the egocentric condition involves partly the same areas (precuneus) as the processing of allocentric spatial information. Furthermore, the allocentric task involves additional cortical and subcortical areas, which are not involved during egocentric spatial coding. Thus, we suggest a hierarchical processing network, in which the egocentric spatial coding requires only a subsystem of the processing resources of the allocentric condition.

Interestingly, the activation of the precuneus was significantly stronger during the egocentric condition than during the allocentric condition, thus indicating that the relationship is not purely hierarchical. However, the hierarchical organization proposed here can be applied to explain several phenomena describing egocentrically and allocentrically spatial coding. Most animals are capable of egocentric coding, but only primates and humans are genuinely capable of allocentric spatial encoding. Additionally, in ontogenesis children firstly relate space to their own body and develop rather late the ability to encode in an allocentric spatial reference frame (Berthoz, 2002). It has been discussed that the allocentric encoding is more powerful because it “enables the mental manipulation as well as manipulation of relations between objects without having continuously relate them to the own body” and is therefore “constant with respect to a person's own movement” (Berthoz, 2002, p. 99). The allocentric coding seems to be the coding mechanism, which developed late in phylogenesis as well as in ontogenesis, probably based on egocentric coding and in consequence partly relying on the same yet also recruiting additional neural resources.

4. Experimental procedures

In the present study we investigated the computation of egocentric [E_{FoR}] and allocentric [A_{FoR}] references in the context of an fMRI setting. The experimental conditions were varied by verbal instructions defining the spatial relations either with [E_{FoR}] or with [A_{FoR}] reference to the subject.

4.1. *Participants*

Twenty-one participants (10 females) took part in this experiment. After a full explanation of the nature and risks of the research, they all gave informed consent for the study according to a protocol approved by the local Ethics Committee. None of them had any history of neurological, psychiatric or hearing impairment. All participants performed a training experiment, which included trials of each condition. We used exactly the same timing as during the MR acquisition. During debriefing after the experiment all participants were interviewed regarding the kind of strategies they applied to solve the tasks. To guarantee that BOLD-caused variance in fMRI data was related to the FoR task we defined two independent inclusion criteria: (i) subjects had to perform above than 70% correct responses in all experimental conditions and (ii) subjects had to report two clearly distinct solving strategies in debriefing, indicating that the strategies of interest were used. Out of the 21 participants, two had a performance with less than 70% correct responses in one of the experimental conditions during the fMRI session. Additionally, three participants reported not having used an egocentric spatial coding strategy during the egocentric task. We included the remaining 16 subjects (7 females), aged 20–40 years (mean 25 years) for further statistical analysis. All participants were right-handed as assessed with a standard handedness questionnaire (Annett, 1992).

4.2. *Stimulation*

We used three sets of auditory stimulation according to three different conditions that have been examined. This procedure was chosen to avoid any influences due to visual stimulation and to rule out any differences in reading speed. For the experimental condition investigating the allocentric FoR [A_{FoR}], we used verbal instructions defining the spatial relations between different objects (colored triangles, quadrangles, and circles; see example below). Verbal instructions were also used in the egocentric FoR task [E_{FoR}], but the spatial positions of the objects were related to the participants. In both conditions the task was to respond by making a spatial judgment. The egocentric task included three, the allocentric task three to four different colored objects at different spatial locations. In the egocentric condition the reference point was always the participant and the task required to spatially relate the last object to the participant. The allocentric condition always concerned the spatial relation between the last and the first object. To control for auditory input as well as additional task demands we applied a control condition [cont], in which no reference was made to spatial relations in the verbal instructions.

Examples for the allocentric FoR task (A_{FoR}):

Description “The blue triangle is to the left of the green square. The green square is above the yellow triangle. The yellow triangle is to the right of the red circle.”

Question: “Is the blue triangle above the red circle?”

Correct answer: “Yes”

Examples for the egocentric FoR task (E_{FoR}):

Description: “The blue circle is in front of you. The yellow circle is to your right. The yellow square is to the right of the yellow circle.”

Question: “Is the yellow square to your right?”

Correct answer: “Yes”

Examples for the control condition (cont):

Description: “The circle is brighter than the square. The triangle is darker than the circle.”

Question: “Is the circle brighter than the triangle?”

Correct answer: “Yes”

Binaural auditory stimulation was presented via MR compatible headphones (Resonance Technology, Northridge, USA). The participants completed 12 trials for each experimental condition (A_{FoR}, E_{FoR}, cont), balanced for questions requiring *yes* and *no* responses. They responded with the middle and index finger of their right hand by pressing one of two response buttons. The order of the 36 trials was randomized and separated into two runs. Fig. 4 describes the timing of an individual trial. As shown in Fig. 4, after the verbal presentation of the spatial information (*V*) and prior to the question (Q) and the response, there was a time window of 5000 ms during which the participants had to maintain the spatial information (maintenance, *M*). Additionally, 3000 ms after the end of each question, a stop signal (auditory square wave pulse) was presented indicating the end of each individual trial to ensure smallest possible task influences on the following baseline.

4.3. *fMRI scanning*

Functional magnetic resonance imaging was performed on a 3-T whole-body MRI system (Siemens Magnetom Trio, Erlangen, Germany), using the standard 8-channel phased array head coil. Using a midsagittal scout image, 32 axial slices (slice thickness = 4 mm) of a T2*-weighted gradient echo EPI sequence were acquired parallel to the bicommissural plane and covering the whole brain. The following acquisition parameters were used: repetition time (TR) = 2.5 s, echo time (TE) = 36 ms, field of view = 224 × 224 mm^2, flip angle = 80°, matrix size = 64 × 64, voxel size = 3.5 × 3.5 × 4 mm^3. The start of the stimulus presentation was triggered by the MR scanner and during the experiment the stimulus presentation was synchronized with the MR acquisition. Each participant underwent two consecutive imaging sessions (runs), resulting in 560 volumes. To reach the steady state of longitudinal magnetization relaxation, four dummy scans were collected before each run. During scanning the room lights were dimmed and the participants were instructed to keep their eyes closed. At the end of each session, a high-resolution T1-weighted volume (3D Turbo FLASH, TR = 1950 ms, inversion time = 1100 ms, TE = 4 ms, flip angle = 12°, 176 slices, matrix = 256 × 224, voxel size: 1 mm^3) was acquired for anatomical co-registration.

4.4. *fMRI data analysis*

Artifact elimination and image analysis was performed using MATLAB 6.5 (Mathworks Inc., Natick, MA, USA) and the SPM2 software package (Institute of Neurology, London, UK, http://www.fil.ion.ucl.ac.uk). All images were acquisition time-corrected, realigned to the first image of each session, spatially normalized into standard stereotaxic space defined by the template provided by the Montreal Neurological Institute (Evans et al., 1993) and resliced to an iso-voxel size of 3 × 3 × 3 mm^3. Finally the normalized images were spatially smoothed using a Gaussian kernel with 6 mm full-width-at-half-maximum (FWHM).

Condition and subject effects were estimated using the General Linear Model (GLM) as implemented in SPM (Friston et al., 1995a,b). The effect of global differences in scan intensity was removed by scaling each scan to the global mean of all scans. Low-frequency drifts were removed using a temporal high-pass filter (cut-off of 128 s). The remaining physiological artifacts (like respiration-induced signal modulations) were reduced by modeling the intrinsic autocorrelations.

For each subject, 9 event types were defined by crossing the three experimental conditions (A_{FoR}, E_{FoR}, cont) and the three consecutive task periods (verbal information, maintenance, and question). The six conditions of interest corresponding to the two consecutive task periods (verbal information, maintenance) of each experimental condition were modeled using the appropriate stimulus function convolved with a canonical hemodynamic response function (HRF). Similar, the three conditions of no interest corresponding to the task period of questioning for each experimental condition were modeled. After estimation of model parameters for each participant, an analysis of variance (ANOVA) was calculated for the whole group, using the individual contrast images for the main effects. To test hypotheses about regionally specific condition effects, linear contrasts were employed in the context of a random effects procedure (Friston et al., 1999).

To reveal general activational differences associated with A_{FoR} and E_{FoR}, we calculated (I) contrasts for “*general effects*” comparing the allocentric and egocentric conditions separately with the control condition ([A_{FoR} > cont] and [E_{FoR} > cont]).

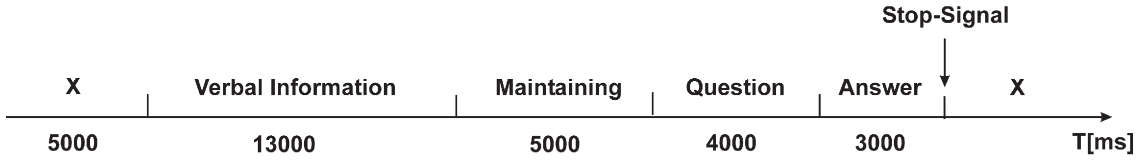

Fig. 4 – *Timing of an experimental trial.* The trial starts with a baseline period (*x*) of 5 s, followed by the verbal spatial information (*V*) for 13 s. Then, for a time of 5 s, the participants had to maintain the information about the objects and their spatial relations (*M*). After that a question (*Q*) was presented for a duration of 4 s. Then the participants had 3 s to answer the question by pressing one of two response buttons. To ensure smallest possible task influences for the following baseline, an auditory STOP signal is presented after each response period. All conditions were presented in a randomized order, resulting in 36 trials and total length of 18 min, separated into two runs.

In order to verify the existence of concurrently activated regions, that means neuronal regions that are activated during both the egocentric and the allocentric conditions, (II) the minimum activation of both conditions was calculated to specifically address the issue of core regions generally involved in spatial coding. Here the *t*-maps of the contrast $[E_{\mathrm{FoR}} > cont]$ and $[A_{\mathrm{FoR}} > cont]$ where used to calculate a map comprising for each voxel the minimal *t*-value of both contrasts. The results of these statistics were thresholded by $T = 4.96$ ($P = 0.05$ corrected for multiple comparisons (FWE)) and a spatial extent of $k = 10$ voxels.

To reveal to what extent egocentric and allocentric spatial coding are neurofunctionally dissociable, we calculated (III) "*differential effects*", directly comparing the allocentric and egocentric conditions $[A_{\mathrm{FoR}} > E_{\mathrm{FoR}}]$ and $[E_{\mathrm{FoR}} > A_{\mathrm{FoR}}]$. For this analysis a masking procedure was applied. Here the contrast $[A_{\mathrm{FoR}} > E_{\mathrm{FoR}}]$ was masked inclusively by $[A_{\mathrm{Fo}} > \mathrm{cont}]$, and the contrast $[E_{\mathrm{FoR}} > A_{\mathrm{FoR}}]$ was masked inclusively by $[E_{\mathrm{FoR}} > \mathrm{cont}]$ using an uncorrected masked *P*-value of 0.05. In this procedure the voxels reaching the significance level in the contrast which serves as the mask form a region of interest. Due to this procedure only areas that have proven to be functionally significant for the condition of interest in comparison to the control condition were included into this analysis. The results of these statistics were thresholded by $T = 2.55$ ($P = 0.05$ corrected for multiple comparisons (FDR)) and a spatial extent of $k = 10$ voxels.

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