

Interactions between ego- and allocentric neuronal representations of space

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In the primate brain, visual spatial representations express distances of objects with regard to different references. In the parietal cortex, distances are thought to be represented with respect to the body (egocentric representation) and in superior temporal cortices with respect to other objects, independent of the observer (allocentric representation). However, these representations of space are interdependent, complicating such distinctions. Specifically, an object's position within a background frame strongly biases egocentric position location judgments. This bias, however, is absent for pointing movements towards that same object. More recent theories state that dorsal parietal spatial representations subservise visuomotor processing, whereas temporal lobe representations subservise memory and cognition. Therefore, it may be hypothesized that parietal egocentric representations, responsible for movement control, are not influenced by irrelevant allocentric cues, whereas ventral representations are.

In an event-related functional magnetic resonance imaging study, subjects judged target bar locations relative to their body (egocentric task) or a background bar (allocentric task). Activity in the superior parietal lobule (SPL) was shown to increase during egocentric judgments, but not during allocentric judgments. The superior temporal gyrus (STG) shows a negative BOLD response during allocentric judgments and no activation during egocentric judgments. During egocentric judgments, the irrelevant background influenced activity in the posterior commissure and the medial temporal gyrus. SPL activity was unaffected by the irrelevant background during egocentric judgments. Sensitivity to spatial perceptual biases is apparently limited to occipito-temporal areas, subserving the observed biased cognitive reports of location, and is not found in parietal areas, subserving unbiased goal-directed actions.

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Introduction

In the primate central nervous system, a variety of neuronal maps or representations of the outside world can be found. These representations often code locations of objects with respect to particular references: relative to the observers' body or body parts (egocentric representation) or relative to another object or a background independent of the observer (allocentric representation).

Egocentric representations can be found in dorsal stream brain areas subserving goal-directed actions (Goodale and Milner, 1992; Milner and Goodale, 1995). Using single cell recordings in monkeys or functional imaging techniques in humans, it has been demonstrated that the coding of space in parietal (Andersen, 1995; Carey, 2000; Connolly et al., 2003; Medendorp et al., 2005), subcortical (Meredith and Stein, 1986a,b) and (pre)motor structures (Kalaska and Crammond, 1992; Cisek and Kalaska, 2002) takes place relative to a particular effector. Space in the above studies was found to be coded relative to either current gaze axis (retinotopic), head orientation, or even body (or trunk) orientation.

Areas holding allocentric representations of space are thought to subservise the conscious perception of objects, or memory functions, and are found mainly along the ventral processing stream (Goodale and Milner, 1992; Milner and Goodale, 1995). Neurons in the rat hippocampus, the so-called 'place cells', have been reported to code the position of the animal within a particular environment, similar to the coordinates of a map (O'Keefe, 1976; O'Keefe and Dostrovsky, 1971). Comparable neurons coding allocentric space have been found in nonhuman primates (Georges-Francois et al., 1999; Rolls, 1999). In humans, the lateral occipital complex (LOC) is considered to be the homologue to the monkey ventral stream and activated during object recognition, as has been demonstrated in several neuroimaging studies (Malach et al., 1995; Faillenot et al., 1997; James et al., 2002).

Interestingly, the findings of a recent fMRI study on human subjects revealed that different mainly right hemispheric networks are involved when egocentric (fronto-parietal) or allocentric spatial judgments (frontal and hippocampus) on intersecting horizontal and vertical bars were given (Galati et al., 2000).

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The way the brain codes space in neural reference frames can have implications for behavior. For example, it has been reported that the endpoint distributions of goal-directed arm movements, starting immediately after target presentation, are not influenced by other objects in the environment. Delayed movements to these targets, however, do show such a dependence (Rossetti, 1999). In a recent psychophysical study (Neggers et al., 2005), we observed that when a larger background stimulus, irrelevant for the task at hand, is placed behind a target, the judgments of the target's position with respect to the body are biased. The relative position of the irrelevant horizontal background bar systematically influenced the perceived location of the vertical target bar. Since there was no effect from egocentric target location on position judgments with respect to the background, it was concluded that a unidirectional influence from allocentric spatial coding on egocentric space representations must exist in the central nervous system (Neggers et al., 2005). It has to be noted that a modulation of allocentric displacement judgments by egocentric target position has also been reported (Sterken et al., 1999), although displacement perception is probably mediated by a different perceptual system.

Comparable effects (the induced Roelofs effect) have been reported when a large background frame was presented behind a target object (Roelofs, 1935; Bridgeman et al., 1997, 2000). Interestingly, in case of pointing towards these targets, the induced Roelofs effect was no longer present. In the light of these findings, it may be argued that egocentric representations subserving goal-directed actions are unaffected by task-irrelevant allocentric coordinates, whereas possible egocentric representations allowing us to report locations would be susceptible to task-irrelevant allocentric target coordinates.

When assuming that indeed ventral stream areas, or areas in the LOC in humans, are mediating information processing for memory and cognition and dorsal stream areas for visuomotor control (Goodale and Milner, 1992; Milner and Goodale, 1995), one can predict that mainly egocentric representations in the ventral stream or LOC would show an influence of irrelevant allocentric cues.

The findings discussed above (Bridgeman et al., 1997, 2000; Neggers et al., 2005) indicate that functional imaging studies using reference frame judgments (Galati et al., 2000) might erroneously attribute egocentric processing to regions actually processing allocentric spatial information, since allocentric information is apparently used when making egocentric judgments. Regions coding space for cognitive/memory purposes in the ventral processing stream are more likely to be affected by such 'cross-talk' than dorsal stream regions responsible for movement-related visual processing, since the behavioral effects such as the induced Roelofs effect do not occur for pointing movement endpoints.

To test this prediction, we conducted a rapid event-related fMRI study in which allocentric and egocentric stimulus coordinates were varied independently to disentangle the involvement of ego- and allocentric reference frames in making spatial judgments. This approach allows us to separate regions that code visual information in a purely egocentric manner, from regions that show an influence of irrelevant allocentric stimulus coordinates on egocentric coding. The stimuli and general aspects of the design were motivated by the work of Galati et al. (2000), since they were able to activate a large right hemispheric network during ego- and allocentric judgments, parts of which might be affected by dependence between reference frames. However, important changes were introduced to the design and analysis to be able to reveal this interdependence and

to enable a probabilistic analysis of the responses given by the subjects.

Subjects had to judge the position of a vertical bar that could appear at 4 positions left and right of the center of the projection screen. A larger horizontal background bar was drawn behind the vertical target bar. Each of the possible vertical target bar positions on the screen was combined with 4 different relative placements of the background bar. A stimulus could therefore have 4 egocentric coordinate values (with respect to the body midline), as well as 4 allocentric coordinate values (with respect to the center of the horizontal background bar). The design of the present fMRI study is largely identical to our previous psychophysical study (Neggers et al., 2005). Subjects were required to judge either the position of the vertical bar with respect to the body midline in egocentric task blocks or the position of the vertical bar with respect to the center of the horizontal background bar in allocentric task blocks. It was expected that the parietal lobule is more active during egocentric spatial judgments (Andersen, 1995; Carey, 2000; Connolly et al., 2003; Medendorp et al., 2005), whereas superior temporal cortex and areas around the hippocampus/hippocampal formation might be more active during allocentric judgments (Rolls, 1999; Galati et al., 2000). The influence of task-irrelevant allocentric coordinates on responses during egocentric judgments is expected to be present in ventral stream areas/LOC, since these areas reportedly are responsible for cognitive spatial judgments (Milner and Goodale, 1995), prone to such biases. Since goal-directed movements do not show an induced Roelofs effect on a behavioral level (Bridgeman et al., 1997, 2000), egocentric representations in dorsal visuomotor areas are expected not to show an influence of the placing of the background during egocentric judgments.

Methods

Participants

Twelve healthy participants (6 male and 6 female, age range 22–29 years, right-handed) with no history of neurological disorders and normal or corrected to normal vision took part in the experiment. Participants gave written informed consent. The applied procedure was approved by the Medical Ethical Committee of the Utrecht University Medical Center.

Apparatus

Functional imaging was performed with a Philips ACSNT 1.5-T clinical scanner, using the blood oxygen level-dependent (BOLD) sensitive, navigated 3D PRESTO pulse sequence (Liu et al., 1993; van Gelderen et al., 1995; Ramsey et al., 1998) with the following parameter settings: TE/TR 35/24 ms, flip angle 9°, FOV 256 × 192 × 96 mm, voxel size 4 mm isotropic, scan-time per fMRI volume 1.49 s, 864 scans per experimental session (21 min 45 s). Navigated PRESTO minimizes the contribution of blood inflow effects and of draining veins by using extra gradients, thereby improving the accuracy of localizing activity. Furthermore, due to short echo-times, the spatial integrity of images is preserved, and susceptibility artifacts near air–tissue interfaces are minimized (Ramsey et al., 1998). During an experimental session, the task described below was performed by a subject, and changes in the BOLD signal were analyzed as described in the Data analysis section. After the functional sequence, an anatomical scan was

acquired (TE/TR 4.6/30 ms, flip angle 30°, FOV 256×180×208 mm, voxel size 1 × 1× 1.2 mm).

Subjects were holding an MR-compatible air-pressure response box with four buttons in their right hand, of which they pressed the left or right button depending on the task at hand.

The head of a subject was positioned in the receive coil within a box-shaped container (the front and top sides were open). Foam bars were positioned between the head of the subject and the side surfaces of the container to prevent head movements.

Stimuli

Stimuli were projected on a large transparent screen (1 m wide) placed in front of the participant using a projector that was placed outside the scanner room. Participants viewed the screen through a mirror placed on the head coil, with an effective screen distance of 2.5 m, thus realizing a viewing angle of 22.6°. Stimuli were displayed on a black background and were generated by custom made scripts for the Presentation Software package by Neurobehavioral Systems Inc. The scanner room was almost completely darkened by switching off all the lights, closing the curtains to the

control room, and strongly dimming the light in the control room, making it unlikely that the subjects could see the edges of the screen and use them for relative position judgments. The stimuli were presented around the vertical meridian of the screen (0° reference). 32 different visual stimuli were created to test the hypotheses described in the Introduction. Each stimulus consisted of a vertically oriented green bar (width × height = 0.77 × 2.7°; 24 bits RGB color coding: 0, 255, 0) placed in front of a darker (2 possible luminances) green horizontal background bar (width × height = 10.7 × 0.77°; 24 bits RGB color coding: 0, 128, 0 or 0, 64, 0).

The vertical bar could intersect the horizontal background bar at 4 different locations with respect to the center of the horizontal background bar: −0.78, −0.26, 0.26, 0.78°, forming 4 different combined horizontal and vertical bar stimuli, differing in their levels of allocentric positions of the vertical bar (see Fig. 1A). In the experiment, the vertical bars could be located at 4 different positions relative to 0° (the center of the screen): −1.54, −0.51, 0.51, 1.54° forming 4 different levels of egocentric (relative to the body) positions. Each egocentric position of the vertical bar on the screen was combined with each of the 4 possible relative (with respect to that vertical bar) horizontal background bar placements, as well as

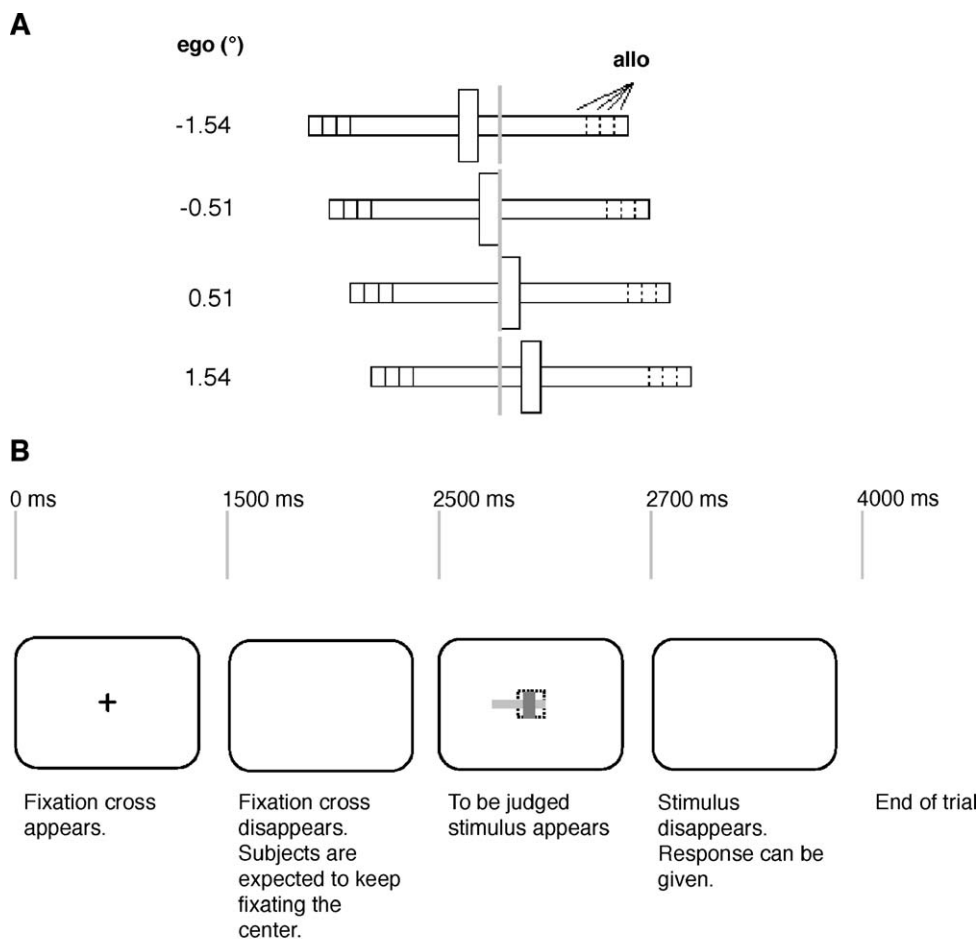


Fig. 1. (A) This figure depicts the 4 possible configurations of the to be judged stimulus (a vertical target bar intersecting a horizontal background bar) at 4 possible locations on the screen. The vertical bar was chosen at one of the depicted 4 screen positions, the location of the horizontal background bar was varied independently around that vertical bar position. The visual angles of the eccentricities of the vertical target bar positions are also given. (B) A schematic overview of one trial. At $t = 0$, the fixation cross is displayed, at $t = 1500$, the screen is blanked, at $t = 2500$, the to be judged stimulus is displayed for 200 ms, after which the subjects had 1300 ms to give their response. After this, a new trial starts. Note that before each trial a blank screen with a random duration (between 0 and 500 ms) was inserted.

two luminances for the horizontal background bar, creating $4 \times 4 \times 2 = 32$ different visual stimulus types.

Procedure

Stimuli were presented in short task sequences of 8 trials, followed by a rest period of 18 s. There were 24 sequences of 8 trials. A trial started ($t = 0$) with a small fixation cross. The screen was cleared after 1500 ms, but subjects were instructed to keep fixating the center of the screen for the remainder of the trial (until after the target disappeared again). In our previous psychophysical study (Neggers et al., 2005), we used an infrared eyetracker to control fixation outside the scanner, and trials where subjects could not maintain fixation were aborted and repeated later during the session. For trials where central fixation was guaranteed in our previous study, we found the same behavioral effects as in the present study (see Results, ‘Behavior’ section). From this, one can conclude that subjects were able to keep fixation on the screen’s center in the scanner as well, for a large majority of the trials. 1000 ms later, a target stimulus (vertical target and horizontal background bar) was presented for 200 ms after which the screen was cleared again, and subjects had 1300 ms to respond (see Fig. 1B). After a blank screen with a random duration varying between 0 and 500 ms, the next trial started. During each sequence of 8 trials, subjects performed one of three different tasks. In the egocentric judgment task (EGO), they had to press a button on the left or right side of the response box corresponding to the position of the vertical bar relative to their body midline. In the allocentric judgment task (ALLO), they had to judge whether they perceived the vertical bar to be at the left or right of the center of the horizontal background bar, and in a nonspatial control task (COLOR), they had to indicate whether the background bar had a high or low luminance (the 2 possible luminances were shown to the subjects before the experiment) by pressing right or left, respectively. The latter task was intended as a nonspatial control task, contrasting both spatial tasks with the control task might allow one to indicate which areas are involved in spatial judgments in general. The task instructions were given in advance of each sequence of 8 trials (during the 18-s rest period in between the sequences) by displaying the word ‘EGO’, ‘OBJECT’, or ‘COLOR’ in the center of the screen. The ego- and allocentric target coordinates as well as the background bar luminance were randomized from trial to trial over the entire session. The order of the task sequences of 8 trials was randomized at the beginning of each fMRI experiment. The 32 stimulus types ($4 \times$ ego, $4 \times$ allo, 2 luminances) combined with 3 judgment tasks result in 96 conditions, each of which was repeated twice, resulting in 192 trials altogether (yielding 24 task sequences of 8 trials). Most analyses, both on behavioral and fMRI data, lump together certain conditions (stimulus coordinate, task, etc.) ensuring sufficient repetitions for each comparison, see the ‘Data analysis’ section.

The time and identity of all events were registered for use in image analysis. Before the experiment started, the subjects were able to practice the task outside the scanner room.

Data analysis

Behavioral

The response probability P of pressing the LEFT key for a certain stimulus type was calculated as a function of the judged stimulus coordinate X ($4 \times$ ego- and 4 times allocentric positions),

for each session. This was achieved by simply counting the number of LEFT responses for a particular stimulus type and dividing it by the number of repetitions. For example, when a stimulus was always reported to be left of the center, the probability P was 1, when it was always reported to be on the right, it was 0, and when it was ambiguous, it was around 0.5. Such bifold decisions can be accurately described by a PROBIT curve (1) (see Fig. 2 for a graph of (1) and some possible data points), with values varying between 1 and 0.

$$P(X) = \frac{1}{1 + e^{-a(X-\theta)}} \quad (1)$$

a reflects the steepness of the transition of the probability plot between 0 and 1 when traversing along the X -axis. θ is the value of the independent variable X where the $P(X) = 0.5$, implying that both choices are equally likely (see dashed line in Fig. 2), or, in this experiment, where the stimulus would be perceived to be at the center (0° with respect to the required reference position). The estimation of θ is most important for the analysis of the probabilities observed in the present study and should reflect the hypothesized effects on spatial judgments. Please note that in the following actually the function $1-P(X)$ was fitted (probability of pressing left, decreasing for larger horizontal coordinate X). For example, when a perceptual bias causes a target stimulus to be perceived more to the right, the function P would start decreasing for smaller values of X , and hence, θ decreases, or vice versa. This description of response probabilities and the subsequent analysis of θ values are quite common in psychophysics (McKee et al., 1985).

The estimated θ 's for each participant in each task condition (ego- and allocentric judgment: TASK) and for each level of irrelevant coordinates ($4 \times$ in experiment 1: IRR) were analyzed in a 4×2 repeated measures ANOVA in order to test a linear model of the spatial interdependencies (linear contrast). Separate ANOVAs per task were performed when the TASK*IRR interaction was significant. The behavioral results were not directly incorporated in the fMRI analysis. They are however important to

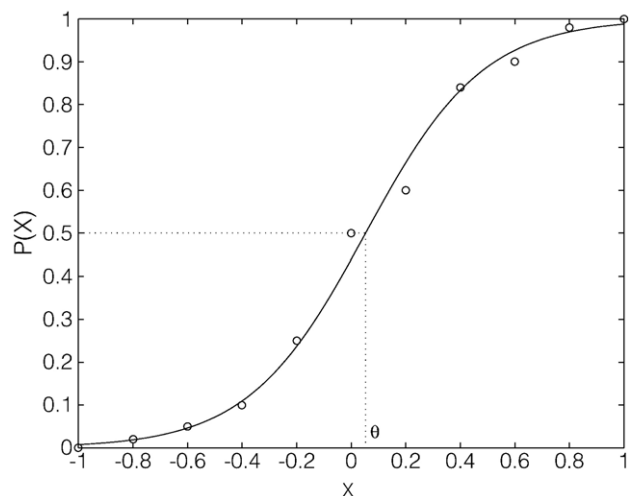


Fig. 2. Example of a fit of a binomial probit function (solid line) to possible data points (open circles) representing response probabilities as a function of a dependent variable X . The value on the x -axis yielding a probability of 0.5, or guessing, correspond to the θ in the probit function Eq. (1). In our experiments, θ denotes the position of the vertical bar where subjects would perceive it at the center (i.e., the probability of pressing left (and right) is 0.5), and can be used to investigate spatial perceptual biases.

ensure that for subjects performing in an fMRI setting, the interaction between allocentric target coordinates and egocentric judgments, for which the present fMRI study intends to detect neural correlates, is comparable to previous psychophysical experiments (Neggers et al., 2005).

Image analysis

Preprocessing

The fMRI time series data were analyzed using SPM2 (<http://www.fil.ion.ucl.ac.uk/spm/spm2.html>). Functional scans were realigned (without reslicing) to the first scan to correct for slight movements of the head and were then coregistered with the T_1 -weighted anatomical image using full affine transformations (no reslicing). The anatomical T_1 -weighted image was normalized to MNI space (Montreal Neurological Institute). The same normalization parameters were applied to the functional scans, which were then resliced at $4 \times 4 \times 4$ mm. Finally, the normalized functional scans were smoothed with a 8-mm (FWHM) Gaussian kernel.

Statistical analysis

The preprocessed functional scans were statistically modeled using the general linear model (GLM, see Friston et al., 1995b) as implemented in SPM2, in an event-related manner. The design of the experiment can be referred to as a rapid event-related, or rER-fMRI design, where modeled events follow each other on a shorter timescale (here ~ 4 s) than the duration of the BOLD signal. It has been demonstrated that overlapping hemodynamic responses (HRs) evoked by events in a rER-fMRI design as closely spaced as 2 s can still be separated, since the BOLD signal behaves roughly linear and hence the individual responses superimpose (Burock et al., 1998; Rosen et al., 1998). In a first stage analysis, the time series data of each individual subject's voxel (Y) is analyzed using the general linear model containing a series of predictors (regressors, functions of time) and weights (regression coefficients) β . 6 trial types (the different conditions) were defined and modeled separately with event-related regressors. For the EGO, ALLO, and COLOR task condition, there were targets with a low and high background

luminance, resulting in six event types: EGO-high, EGO-low, ALLO-high, ALLO-low, COLOR-high, and COLOR low. Six functions of time (not used directly as regressors) representing these event types were constructed using Dirac delta functions (1 for times where the modeled event type occurred, and 0 otherwise). 12 regressors were constructed by convolving these 6 functions of time with the canonical HR function (HRF) as implemented in SPM2 (two gamma functions) and, creating a second regressor per event type, with its temporal derivative. The latter is done in order to make a better fit of HRs, known to slightly vary between regions and subjects, using a first-order Taylor expansion (Henson et al., 2002). To model HR responses during egocentric judgments that can vary in height depending on the position of the irrelevant background bar, four more regressors were added to the model (leading to a total of 16 regressors for the effects of interest), 2 for the EGO-high stimulus events and 2 for the EGO-low stimulus events: both the original HRF and dHRF/dt regressors multiplied by the allocentric (task-irrelevant) coordinate of the stimulus. By doing so, one can model egocentric task responses that vary in response amplitude for the irrelevant allocentric stimulus coordinates, possibly reflecting the process underlying the reported influence of background frames on egocentric judgments. See Fig. 3 for an example of these four regressors per egocentric stimulus type. In analyzing such parametrically modulated responses, it is common to model the average response and the amount of parametric modulation of the response around that average with different regressors, constituting a first (or higher)-order polynomial expansion, that will then be fitted to the data (Friston et al., 1995a; Buchel et al., 1998). Subsequently, the fitted amount of modulation can be tested for statistical significance.

Additionally, the moment of written instruction was modeled (using again HRF and dHRF/dt) as a so-called 'nuisance regressor' that can correct the time series data for the HRs caused by instruction. In total, the model therefore had 19 regressors, 16 regressors of interest, 2 nuisance regressors, and a regressor with only 1 s modeling the baseline activation (which is common practice).

The contrasts discussed in the Results section are a weighted sum of the regression coefficients β . In a subsequent second level group

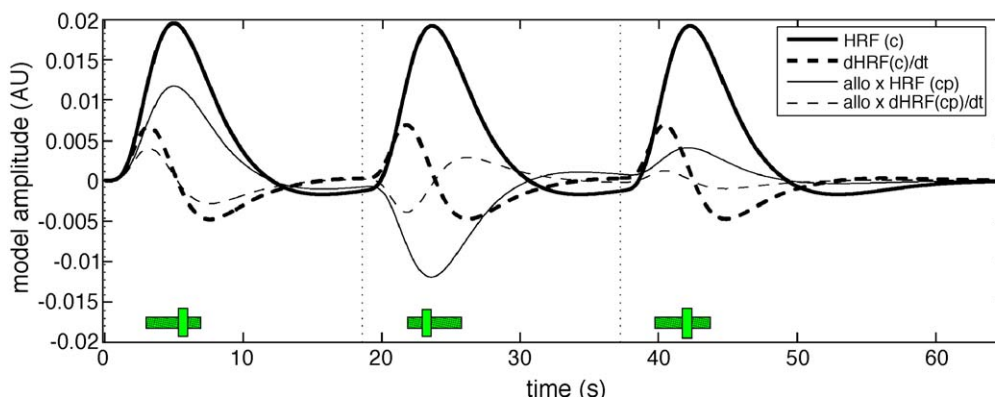


Fig. 3. An example of the four regressors that were used to model stimulus events during the egocentric judgment task using parametric modulation, for 3 subsequent events. The onset times (dashed black vertical lines) are arbitrary and chosen only to demonstrate this concept. The canonical hemodynamic response function HRF(c) and its temporal derivative dHRF(c)/dt (thick solid and dashed lines) can be distinguished, as well as their parametrically modulated counterparts HRF(cp) and dHRF(cp)/dt (thin solid and dashed lines). The regressors for HRF(cp) were obtained by scaling HRF(c) with a factor that linearly relates to the allocentric stimulus coordinates of each stimulus (the amount of horizontal offset of the vertical target bar with respect to the irrelevant background bar), see inlays of the stimuli below the regressors. The sum of the HRF(c) and HRF(cp) regressors in a general linear model can model response amplitudes that vary in amplitude depending on the allocentric stimulus coordinates.

analysis ('random effects analysis'), these β contrasts for all subjects were then tested per voxel in a Z test against zero. We list all voxels in Table 1 with $P < 0.001$ uncorrected and marked clusters with asterisk that were significant on a cluster-level with $P < 0.05$ corrected for a search volume, using Gaussian random field theory thresholds. The search volumes are described in the corresponding results section and are based on the Talairach Daemon neuroimaging database (Lancaster et al., 1997, 2000) used by the "WFU_pick-atlas" tools (Maldjian et al., 2003).

We considered the following contrasts:

$$\beta(c)_{\text{EGO,HIGH}} - \beta(c)_{\text{ALLO,HIGH}} + \beta(c)_{\text{EGO,LOW}} - \beta(c)_{\text{ALLO,LOW}} \quad (2)$$

$$\beta(cp)_{\text{EGO,HIGH}} + \beta(cp)_{\text{EGO,LOW}} \quad (3)$$

$$\beta(c)_{\text{EGO,HIGH}} + \beta(c)_{\text{EGO,LOW}} + \beta(c)_{\text{ALLO,HIGH}} + \beta(c)_{\text{ALLO,LOW}} - 2 \times (\beta(c)_{\text{COLOR,HIGH}} + \beta(c)_{\text{COLOR,LOW}}) \quad (4)$$

Here, c stands for the regressor containing canonical HRFs per event, cp for its parametrically modulated counterpart (see above and in Fig. 3).

Contrast Eq. (2) should be significant for voxels with different activation magnitudes for the EGO and ALLO type tasks and contrast Eq. (3) is assumed to reflect an influence of the irrelevant allocentric coordinate on egocentric judgments. Contrast Eq. (4) should reflect areas that are more active for spatial judgments (of either type) in general than for intensity judgments.

Results

Behavior

Performance was analyzed using a PROBIT analysis of response probabilities. The probability of pressing the LEFT key was calculated for all subjects and for each trial type. For the average response probabilities, see Fig. 4.

Through the probabilities as a function of stimulus coordinate, a PROBIT function was fitted, and the interpolated stimulus coordinate that would lead to 50% ($P = 0.5$) chance of pressing the LEFT button (the θ value from the PROBIT Eq. (1)) was considered for further analysis, with probabilities for high an low luminance background bar trial types pooled. Subjects were quite able to distinguish the small differences in position of the vertical bar. As in our previous paper using identical stimulus configurations (Neggers et al., 2005), it can be seen in the upper panels of Fig. 4 that the task-irrelevant placement of the target bar with respect to the horizontal background bar influences the egocentric spatial judgments (θ values) in a linear fashion (IRR: $F(1,11) = 7.3$, $P < 0.05$, linear contrast, separate ANOVA for egocentric task). In the lower panels of Fig. 4, it can be seen that the task-irrelevant egocentric target placement had no effect on allocentric spatial judgments ($F(1,11) = 3.14$; $P = 0.12$), linear contrast, separate ANOVA for allocentric task), also similar to our previous paper. The observation that task-irrelevant allocentric coordinates have an effect on egocentric judgments, and that on the other hand task-irrelevant egocentric coordinates do not have an effect during allocentric judgments, is significant when all the θ values are analyzed in one ANOVA, as indicated by the interaction between

Table 1

An overview of the clusters that were significant for the contrasts considered, the coordinates of the maximum Z value and the number of voxels

Area	MNI coordinates of Z_{max}			Z_{max}	No. of voxels $Z > 3.09$ ($Z > 2.58$)	Brodman area
<i>Ego > Allo (contrast [1], positive Z)</i>						
Right STG	48	-20	-8	3.53*	6 (18)	22/48
Right SPL	28	-60	64	3.23*	2 (8)	5/7
Middle FG	28	-4	48	3.19	1(4)	6
Right SOG	40	-84	24	3.17	1(3)	19
Left LN	-28	-8	-8	3.09	1(3)	
<i>Allo > Ego (contrast [1], negative Z)</i>						
Medial FG	0	-24	52	-2.94	(4)	4
Right CN	8	12	12	-2.64	(2)	
<i>Parametric influence of allocentric coordinate on egocentric judgements (contrast [2])</i>						
Left/Right PC	0	-64	8	-4.61*	25 (61)	30
Right MTG	52	-56	12	-3.91*	8 (23)	21
Left MTG	-44	-72	16	-3.19	1(8)	39
Left MFG	-40	28	36	2.99	(3)	44
Midbrain	8	-20	-12	2.84	(4)	
<i>Ego + Allo-2x Control (contrast [3])</i>						
Right MFG	40	48	20	3.94	10	45/46
Search areas	right SPL				104	
	right STG + MTG + MOG				1595	

All areas significant at $Z > 3.09$ ($P < 0.001$ uncorrected) are listed, and some trends ($Z > 2.58$, $P < 0.01$ uncorrected). Areas that were significant at a cluster level in one of the search areas at $P < 0.05$ corrected were marked with an asterisk. The search areas and their sizes counted in voxels of $4 \times 4 \times 4$ mm are listed in the table. All labels and volumes used here were derived from the Talairach Daemon (see Methods). Abbreviations: LN: lentiform nucleus (putamen), FG: frontal gyrus, STG: superior temporal gyrus, SPL: superior parietal lobule, SOG: superior occipital gyrus, MOG: middle occipital gyrus, FG: frontal gyrus, CN: caudate nucleus, PC: posterior commissure, MTG: medial temporal gyrus.

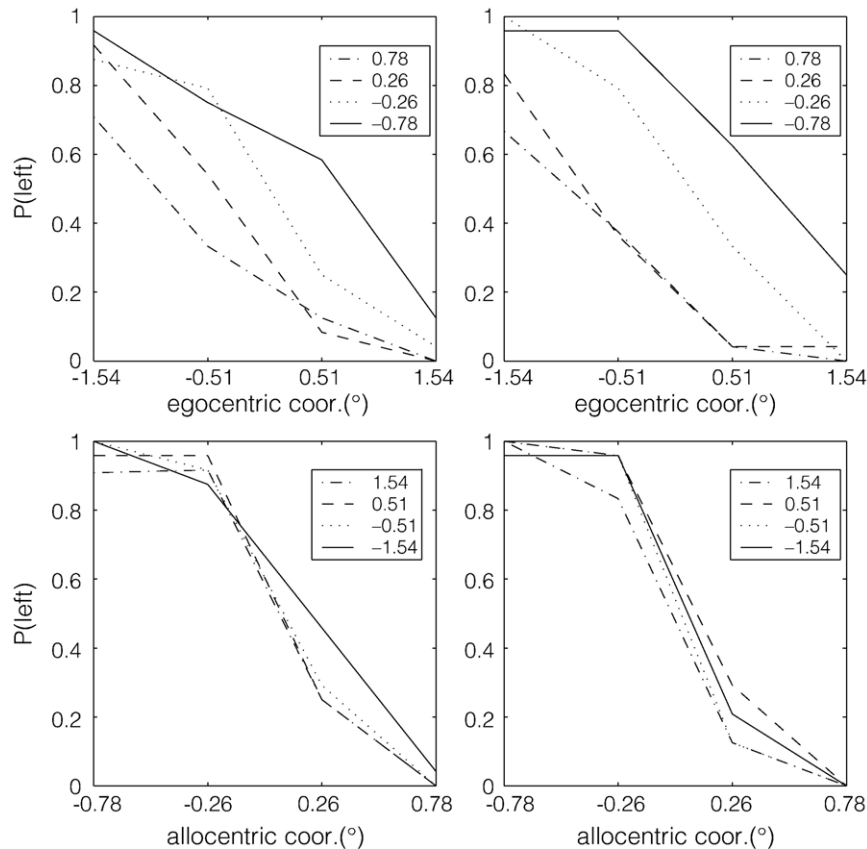


Fig. 4. Response probabilities of pressing the left key for the egocentric task, averaged over all subjects. A separate curve is plotted for each irrelevant allocentric coordinate (background position) indicated by dashed line types and for high panel a and low panel b background luminance. Response probabilities of pressing the left key for the allocentric task, a separate curve is plotted for each irrelevant egocentric coordinate (background position), and for high panel c and low panel d background luminance.

task and irrelevant coordinate ($TASK*IRR: F(1,11) = 5.16, P < 0.05$).

The response probabilities from this fMRI experiment did not allow reliable PROBIT fits when the data were analyzed separately for each trial type (e.g., no grouping of high–low luminance), due to the reduced number of repetitions per trial type (2) that were possible in this fMRI experiment. Nevertheless, in Fig. 4, one can observe a trend of a stronger bias of irrelevant allocentric target placement on egocentric judgments for high luminance backgrounds. This interaction did become significant in our previous paper (Neggers et al., 2005).

The reaction times of the ego- and allocentric and color judgments for the 2 luminance levels were compared to see whether conditions were comparable with respect to processing speed. It appeared that reaction times for egocentric (523 ms), allocentric (542 ms), and color judgments (499 ms) were not significantly different in a repeated measures ANOVA ($TASK: F(2,11) = 2.8, P = 0.082$) nor was the interaction with luminance ($TASK*LUM: F = 2.99, P = 0.072$).

To compare the number of responses that was actually made in each task condition or luminance level, an ANOVA was ran on the number of key presses per task and luminance level. Overall, subjects failed to give a response in less than 1% of the trials. No differences in total number of responses were observed between tasks ($F(2,22) = 1.49, P = 0.25$) nor was there an interaction with luminance ($F(2,22) < 1$). The lack of significant differences in processing speed and actual number of responses demonstrate that

it is valid to make a direct comparison between the evoked BOLD responses for ego- and allocentric task conditions.

fMRI results

Egocentric versus allocentric task conditions

For egocentric judgments, we hypothesized that mainly right dorsal areas (most notably the parietal reach region in the superior parietal lobule) and for allocentric judgments mainly right ventral areas would be activated. Therefore, we limited our search area to the superior parietal lobule (SPL) and to areas along the ventral stream (superior temporal gyrus (STG), medial temporal gyrus (MTG), medial–occipital gyrus (MOG)) respectively, as defined in the Talairach Daemon atlas. For the definition and sizes of the search areas, see Table 1.

Several cortical areas exhibited activations in an event-related manner with different magnitudes during ego- or allocentric task sequences, although identical stimuli were presented in either task. This was analyzed by determining the contrast between the average magnitudes of responses for ego- with allocentric task sequences, contrast Eq. (2) (see Methods). Most notably, an area within the right SPL showed significantly ($P < 0.05$ corrected for the search area) increased responses during the egocentric task as compared to the allocentric task (see Fig. 5A). Secondly, the most posterior part of the right hippocampal formation and a bordering more lateral area in the STG were also found to have a significant ($P < 0.05$ corrected for the search area) positive contrast for ego versus allocentric task

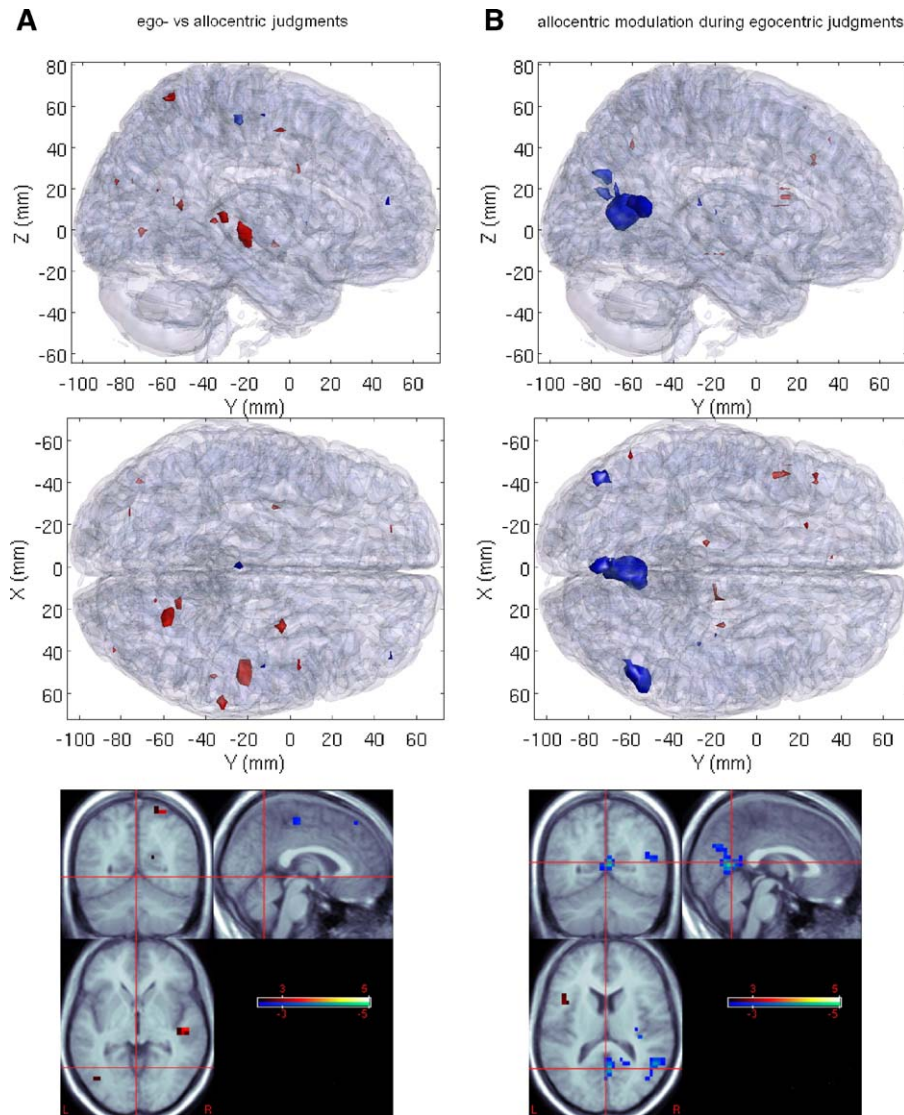


Fig. 5. (A) (left panels) Sagittal and transversal view of a MNI glass brain (gray matter rendering of normalized single subject) with the average activation patterns (group Z-maps) of the 12 subjects for contrast Eq. (1) (thresholded at $Z > 2.58$ in red or $Z < -2.58$ in blue). The main findings are all visible: contrast Eq. (1) activates parts of the superior parietal lobule and around the superior temporal gyrus. Below the glass brain, the same Z-map is projected as color codes on 3 orthogonal slices through the average normalized T_1 -weighted scans of all 12 participants. See Table 1 for all results. (B) (right panels) Sagittal and transversal view of contrast Eq. (2). The main findings are all visible at this intersection: contrast Eq. (2) activates parts of the medial temporal gyrus and around the posterior commissure. Below the glass brain, the same Z-map is projected as color codes on 3 orthogonal slices through the average normalized T_1 -weighted scans of all 12 participants. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

activations. See Table 1 for a complete list of activated areas, their MNI coordinates, and associated Brodmann areas.

The average activity magnitudes (%signal change) of the regions that showed significantly different activity in a direct ego versus allocentric comparison were calculated per task condition separately in order to obtain more insights in how such differences could arise. To do so, the event-related response amplitude following ego- or allocentric position judgments (regression coefficients associated with the canonical HRFs in the statistical model) were averaged for those voxels in the SPL and STG that reached a statistical threshold $Z > 3.09$ ($P < 0.001$ uncorrected) for contrast Eq. (2). See Fig. 6. The positive contrast for the SPL seems to have arisen from a clear positive activation around egocentric judgments and a small or absent activation around

allocentric judgments. The positive contrast for the STG voxels though seems to be caused by a clear negative response amplitude (deactivation) during allocentric judgments and hardly any response during egocentric judgments.

Furthermore, allocentric position judgments seemed to evoke larger responses than egocentric judgments in the medial frontal gyrus and right caudate nucleus (trend).

Spatial versus nonspatial judgments

The right middle frontal cortex showed increased activity ($P < 0.001$ uncorrected) for spatial judgment tasks as compared to the control tasks (i.e., contrast Eq. (4)). This implies that for both ego- as well as allocentric spatial judgments, this area is apparently activated, as compared to the intensity judgment task.

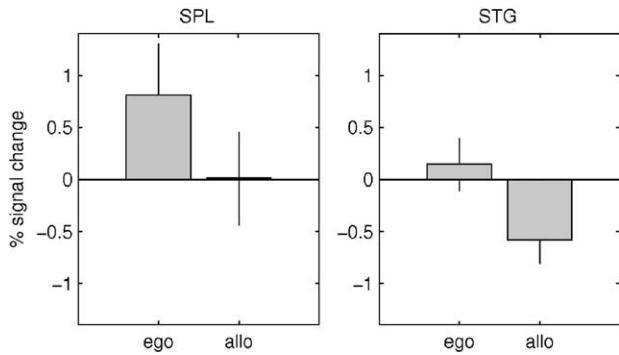


Fig. 6. For the superior parietal lobule (SPL) and the superior temporal gyrus (STG) separately, average activation amplitudes (regression coefficients or β s for canonical HRFs) are plotted as bar graphs for voxels that were significant at $Z > 3.09$ ($P < 0.001$ uncorrected) for contrast Eq. (1), for ego- and allocentric judgments. In SPL, the contrast ego- versus allocentric judgments (Eq. (1)) are positive due to positive activation for egocentric judgments and hardly any activation during allocentric judgments. In STG, however, this contrast is positive due to a deactivation for allocentric and no activation for egocentric responses.

Parametric influence of irrelevant allocentric stimulus coordinates

Areas that might be involved in generating the influence of the allocentric stimulus coordinate on egocentric judgments are detected using contrast Eq. (3). We hypothesized that occipito-temporal areas along the ventral processing stream could show such a task-irrelevant bias.

Most notably, large areas comprising the posterior commissure (PC; whole brain significant) and the medial temporal gyrus (MTG, search area significant) showed a strong negative influence of task-irrelevant allocentric stimulus coordinates during egocentric judgments. In the left MTG, a small area exhibited the same influence. See Fig. 5B and Table 1.

There were some trends for a positive modulation of response amplitude with irrelevant stimulus coordinates, in the middle frontal gyrus (MFG) and in the midbrain (thalamus).

Discussion

In the present experiment, subjects had to judge the position of a target bar with respect to either their body midline (egocentric task) or a horizontal background bar behind the target bar (allocentric task). In a nonspatial control task, they had to judge the intensity of the background bar. It was demonstrated that different, mainly right hemispheric brain areas were recruited depending on the reference frame relative to which spatial judgments were made, although identical stimuli were used for all judgment tasks. Egocentric position judgments resulted in larger activations within the right SPL and STG when compared to judgments of allocentric target position. In the SPL, egocentric judgments resulted in clear activation, whereas for allocentric judgments, no activation was observed. The parietal cortex is located within the dorsal stream of visual processing and is thought to subserve action coordination and control (Goodale and Milner, 1992; Milner and Goodale, 1995). Based on single cell recordings and neuroimaging techniques, many subsystems coding the egocentric spatial location of objects have been identified in the parietal cortex, albeit with respect to different effectors (Andersen, 1995; Carey, 2000; Connolly et al., 2003; Medendorp et al., 2005).

The right hemispheric involvement in spatial judgments is also congruent with findings from patients with right parietal lobule damage suffering from spatial unilateral neglect. Spatial neglect can be “egocentric” (visual defects in a contralesional region of space) or “allocentric” (visual defects at one side of an object) in nature (Humphreys and Riddoch, 1994), or both (Gainotti et al., 1972).

The present findings suggest that spatial coding within the parietal cortex is not only involved in guiding our actions but also for mentally judging spatial locations from an egocentric perspective. This seems not completely in agreement with the ventral/dorsal stream hypotheses proposed by Milner and Goodale (1995). According to them, areas in the dorsal stream are involved with visuomotor processes that we are largely unaware of, whereas judging locations implies the involvement of awareness.

The larger event-related activation in the hippocampal formation/STG during egocentric judgements as compared to allocentric judgements is somewhat puzzling at first sight, since in many animals these areas are associated with allocentric coding, irrespective of the perspective of the observer (O’Keefe, 1976; O’Keefe and Dostrovsky, 1971; Georges-Francois et al., 1999; Rolls, 1999). Furthermore, Galati et al. (2000) observed larger activation in the hippocampus during allocentric judgments in a block design. Another fMRI study (James et al., 2002) on humans demonstrated that neural activation in response to a 3D object increased due to a 3D prime irrespective of the viewing angle of the prime in the lateral occipital complex (LOC), whereas in the intraparietal sulcus, this priming effect was only present with identical viewing angles of the prime and target object. This also suggests that information processed along the ventral stream is coded largely in an allocentric fashion.

However, the positive contrast between ego- and allocentric judgments in the STG is mainly due to a negative HR amplitude during allocentric judgments and a slightly positive or absent amplitude for egocentric judgments. Recent investigations regarding the neurophysiological nature of the BOLD response showed that negative BOLD responses are realistic phenomena (Shmuel et al., 2002; Pfeuffer et al., 2004) observed in various brain regions and very likely to be caused by a short decrease in neuronal activity, instead of ‘blood stealing’ by positively activated regions (Smith et al., 2004). Short decreases in electrical neuronal activity are a widespread phenomenon in the central nervous system (Duffy and Burchfiel, 1975; Ojemann et al., 1988; Munoz and Wurtz, 1993; Raemaekers et al., 2005). Decreases in neuronal activity can reflect meaningful neuronal processing, for example, because processes are inhibited, or by releasing inhibition of areas to which the region with decreased activity is connected. The latter demonstrates that direct subtraction of event-related BOLD response amplitudes between conditions can be misleading when the sign of the activation is not taken into account. The positive sign of the direct subtraction of neuronal responses during allo- from egocentric judgments, as expressed in contrast Eq. (2), might merely reflect allocentric information processing expressed as a decrease in neuronal activity, which would be congruent with the putative ventral stream processing of allocentric information (Malach et al., 1995; James et al., 2002). At the very least, it would not be correct to conclude that the positive contrast between ego- and allocentric judgment conditions in STG implies an involvement in egocentric processing, when there actually is no activation during egocentric judgments and a clear negative response during allocentric judgments.

Interestingly, activity in the present study in areas around the posterior commissure and the right medial temporal gyrus was modulated by the position of the background bar during the egocentric task. The latter activations, which are located within the LOC that is supposedly subserving object recognition (Malach et al., 1995; James et al., 2002), might be responsible for the influence of an irrelevant background bar on egocentric judgments of targets (Bridgeman et al., 1997, 2000; Neggers et al., 2005). This is intriguing, since it has been demonstrated that goal-directed pointing movements are not affected by an irrelevant background, whereas perceptual spatial judgments are (Bridgeman et al., 1997, 2000). The fact that during egocentric judgments mainly neuronal responses in occipito-temporal areas are affected by a task-irrelevant background whereas neuronal responses in the parietal lobe are not might be the neuronal correlate of the behavioral dissociation mentioned above. It was indeed argued by Bridgeman and colleagues that dorsal processing for movement control might be insensitive to this bias and that ventral stream areas are. Our finding on allocentric influences on responses in occipito-temporal areas is therefore congruent with the two visual processing stream theory proposed by Milner and Goodale (1995).

Whereas the induced Roelofs effect itself has been replicated several times, the source of the induced Roelofs effect, however, is subject to considerable debate (de Grave et al., 2002; Dassonville et al., 2004; Neggers et al., 2005). Mainly, the effect could, besides an interaction between neuronal representations of space, also simply be attributed to a shift in the perceived egocentric 'straight ahead'. Subjects were usually told to judge egocentric positions with respect to where they felt their body midline was. Some studies showed that the 'perceived straight ahead' shift seems to have a different origin than the induced Roelofs effect (de Grave et al., 2002), leading to the rejection of this hypothesis. Others, however, showed by having subjects point to the mirror location of a target surrounded by a frame that actually the midline shift hypothesis can explain both the induced Roelofs effect for judgments as well as for goal-directed actions (Dassonville et al., 2004), since errors usually cancel out for the action control system. It was therefore correctly claimed that the dissociation between the Roelofs effect for judgments as compared to pointing movement endpoints by itself does not prove the two visual stream hypothesis as put forward by Milner and Goodale (1995), since this behavioral dissociation might be explained by both the midline shift idea (Dassonville and Bala, 2004) and the two visual streams theory. The present findings are therefore helpful in providing additional support for the assumption that the separate dorsal and ventral stream visual processing cause the induced Roelofs effect to be present in location judgments and not in pointing movements, since the conclusions are based directly on measurements in the human cortex rather than indirectly inferred from psychophysical findings.

The allocentric judgment task did not clearly give rise to larger activation than during egocentric position judgments, apart from some trends. Spatial judgments in general, i.e., allocentric and egocentric judgments as compared to the nonspatial control task, clearly activate a frontal area, which might indicate that this area is involved in general aspects of making spatial judgments. Interestingly, the right MFG has been indicated as a crucial node in the spatial working memory network in several neuroimaging studies (McCarthy et al., 1996; Kessels et al., 2000; Leung et al., 2002) as well as MFG lesion studies on

monkeys (Goldman et al., 1971). Galati et al. (2000) also observed an overlap in egocentric and allocentric involvement in the frontal cortex.

Notice that the task used here and in the studies by Galati et al. (2000) might be related to the classical neuropsychological line bisection test, which is used as a standard to diagnose the presence of spatial unilateral neglect (Vallar, 1998). Typically, neglect patients fail to explore the space contralateral to the lesion and ignore stimuli presented in that half of space, which could be interpreted as an egocentric disorder (Bisiach et al., 1985; Karnath et al., 1991). Spatial neglect may also apply to the contralesional side of objects, independent of their position relative to the observer (Walker, 1995; Driver, 1999). Object based neglect can be seen as a basically allocentric disorder. The present study provides further insights in the implementation of ego- and allocentric processing mechanisms in the healthy human brain.

Importantly, we were able to disentangle ego- and allocentric neuronal representations in the brain, by taking into account the influence of irrelevant allocentric stimulus coordinates on egocentric judgments with parametric modulation analyses. The results seem to be congruent with behavioral experiments where goal-directed movements (Bridgeman et al., 1997, 2000), presumably relying on parietal egocentric representations of space, are not influenced by allocentric cues, whereas location judgments, probably relying on ventral stream processing, are influenced by the position of a background.

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