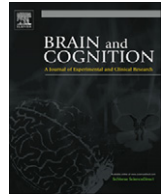


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## Brain activation during spatial updating and attentive tracking of moving targets

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## ABSTRACT

Keeping aware of the locations of objects while one is moving requires the updating of spatial representations. As long as the objects are visible, attentional tracking is sufficient, but knowing where objects out of view went in relation to one's own body involves an updating of spatial working memory. Here, multiple object tracking was employed to study spatial updating and its neural correlates. In a dynamic 3D-scene, targets moved among visually indistinguishable distractors. The targets and distractors either stayed visible during continuous viewpoint changes or they turned invisible. The parametric variation of tracking load revealed load-dependent activations of the intraparietal sulcus, the superior parietal lobule, and the lateral occipital cortex in response to the attentive tracking task. Viewpoint changes with invisible objects that demanded retention and updating produced load-dependent activation only in the precuneus in line with its presumed involvement in updating spatial working memory.

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## 1. Introduction

As you move in dynamic environments such as in traffic, team sports, or – nowadays less common – while hunting or escaping predators, the suspected locations of other actors in relation to yourself change. Despite your self-motion you keep aware of where to look for them and you can point to their suspected locations. Keeping track of invisible objects as targets of motor actions (e.g., hand or eye movements) during self-motion is a case of spatial updating (Wang et al., 2006). Spatial updating denotes the processing of changes in spatial relations relative to one's own body on small and large scales. On a large scale, one's own location in relation to remote landmarks has to be updated during wayfinding and navigation (Waller & Greenauer, 2007). On a small scale, the egocentric relations to objects in the immediate surroundings need updating during self-motion (Wruga, Creem-Regehr, & Proffitt, 2004). In search for the neural correlates of spatial updating, the neural representation of object locations provides an indicative starting point: Perceptually encoded object locations are represented in multiple body-centered reference frames in the posterior parietal cortex (PPC), where they are also updated based on information about self-motion (Colby & Goldberg, 1999; Knudsen, 2007).

When the eyes move, object locations in relation to the retina need updating but object locations in relation to the head and body remain unchanged. Mechanisms that compensate for eye movements based on corollary discharge update object locations in the PPC in relation to the retina (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Merriam, Genovese, & Colby, 2007). Much less is known, however, about how the brain performs spatial updating when the whole body moves and turns or when the impression of observer motion and perspective changes are achieved by camera movements in films and video games. Recently, a connectionist model of spatial memory was suggested that specifies the coupling of egocentric and allocentric representations in spatial updating (Byrne, Becker, & Burgess, 2007). The model components are identified with neuronal structures. A head-centered egocentric representation located in the precuneus (medial parietal cortex) is assumed to provide spatial information tied to a specific view. It interacts with an allocentric representation in the medial temporal cortex that integrates across views. Observer movements including changes in head direction are monitored to connect input from various views in the construction of an allocentric representation. Real and imagined observer motion can alter the “viewpoint” in the allocentric representation and consequently the expected view in the egocentric representation. Thus, the egocentric representation in the precuneus is updated.

The precuneus is widely interconnected with higher cortical areas (including lateral PPC) and subcortical structures, but no direct connections with primary sensory regions have been observed (Cavanna & Trimble, 2006). In the neural model of spatial

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memory (Byrne et al., 2007), the head-centered representation in the precuneus is assumed to be less dependent on perpetual visual input than the salience maps in lateral PPC. It can retain the locations of invisible objects and of objects in remembered and imagined scenes. Nonetheless, activation in the precuneus is thought to be strongly modulated by attentional processes.

Consistent with this model of spatial memory and updating, an fMRI-study of spatial updating found that the precuneus was the only brain area in which activation increased with the number of object locations that had to be updated during visually signaled forward motion (Wolbers, Hegarty, Büchel, & Loomis, 2008). In this study, objects in a simulated 3D scene turned invisible by sinking into the ground and optic flow produced by a moving dot pattern suggested forward self-motion, after which observers had to indicate the novel object locations.

A second type of actual or signaled self-motion that is common in studies of spatial updating is a change of viewpoint achieved by moving around a scene (e.g., Wang et al., 2006). The fMRI study that we report here employed such a visually signaled rotational viewpoint change in a tracking task. Our goal was to investigate brain activation in response to spatial updating demands, but with rotational viewpoint changes that aim at the core of the postulated interplay of head-centered and allocentric representations in Byrne et al.'s model of spatial memory. In the present study, observers had to update the locations of invisible objects across continuous changes of camera viewpoint around a 3D scene. The implied observer motion combines translation and rotation and is common in movies and video games. To motivate the participants to keep track of object locations we applied a dynamic object tracking task.

The multiple object tracking task is a common paradigm to investigate the tracking of object locations (Pylyshyn & Storm, 1988; Scholl, 2009). In the basic task, visually indistinguishable and independently moving objects are presented and the observer tracks a subset of the objects as targets. At the beginning of a trial, the targets are briefly highlighted and at the end, the observer has to indicate the targets or to decide for a single highlighted object whether it is one of the targets or not. Multiple object tracking (MOT) has repeatedly been examined with fMRI (Culham, Cavanagh, & Kanwisher, 2001; Culham et al., 1998; Howe, Horowitz, Morocz, Wolfe, & Livingstone, 2009; Jovicich et al., 2001; Tomasi, Ernst, Caparelli, & Chang, 2004) and reliably activates areas associated with motion and object processing (area MT+ and lateral occipital cortex), visuo-spatial attention, and the programming and suppression of eye movements (PPC and the frontal eye fields).

The PPC and the frontal eye fields (FEFs) are core parts of a fronto-parietal network subserving spatial attention, spatial working memory and visuomotor behavior (Corbetta & Shulman, 2002; Curtis, 2006). Multiple areas in the PPC are topographically organized as are the FEF (Hagler, Riecke, & Sereno, 2007; Silver & Kastner, 2009). The FEF code for saccade targets, and they are involved in suppressing saccades (Corbetta, 1998; Kelley, Serences, Giesbrecht, & Yantis, 2008). Both FEF functions contribute to shifts of attention without shifts of fixation (covert attention) because saccade targets receive spatial attention even if saccades are suppressed (Moore & Fallah, 2004).

When the objects in a tracking task are shown as moving within a 3D-scene, the processing of viewpoint changes can be studied by introducing camera movements. Previous studies have shown that continuous camera movements do not affect tracking performance at all as long as the tracked objects remain visible (Huff, Meyerhoff, Papenmeier, & Jahn, 2010; Liu et al., 2005; Thomas & Seiffert, 2010). Tracking is impaired but still possible if objects turn invisible during the viewpoint change and their locations have to be updated based on continuous visual information about the surrounding scene (Huff et al., 2010). Continuous visual information about viewpoint changes indicates changes of the observer's location within a

spatial layout and changes of the direction, in which the observer faces. Purely visually signaled viewpoint changes as in the case of camera movements in films or video games are not accompanied by proprioceptive and vestibular cues. Still, camera movements seldom cause disorientation. Successful spatial updating while processing continuous changes in camera viewpoint demonstrates that spatial updating in the sense of updating egocentrically represented object locations is possible without proprioceptive and vestibular cues. However, spatial updating based on purely visual input is not equivalent to spatial updating resulting from actual self-motion. For example, actual self-motion interferes with MOT whereas continuous viewpoint changes as a result of camera movements do not (Thomas & Seiffert, 2010).

In the present study, viewpoint changes were indicated by continuous rotations of a rectangular floor plane in a simulated 3D-scene resulting from camera movement around the scene (see Fig. 1). Observers tracked 2, 3, or 4 out of 12 green balls moving on the rectangular floor plane. In no-tracking trials, observers passively viewed the movement without tracking. In all trials, the viewpoint on the scene continuously changed by 30° after 4 s. The balls either stayed visible throughout the whole trial or they turned invisible for the 1.5 s, in which the viewpoint change took place. Thus, in the tracking trials with temporarily invisible balls, the target locations had to be updated based on the visual information about the viewpoint change that the rotating floor plane provided. The variation of tracking load allowed us to detect increasing brain activation in response to a higher number of attended and updated object locations.

The activation in response to the MOT task and tracking load should reveal networks encompassing occipital, frontal, and parietal cortical areas contributing to motion processing, visuo-spatial attention, and working memory that have been observed in previous studies of MOT (Culham et al., 1998, 2001; Howe et al., 2009; Jovicich et al., 2001; Tomasi et al., 2004). We were particularly interested in the effect of viewpoint changes during which objects turn invisible. Following the logic of Wolbers et al. (2008), we increased the number of object locations that needed updating in the invisibility interval and took correspondingly increasing activation as an indicator of brain areas that contribute to spatial updating.

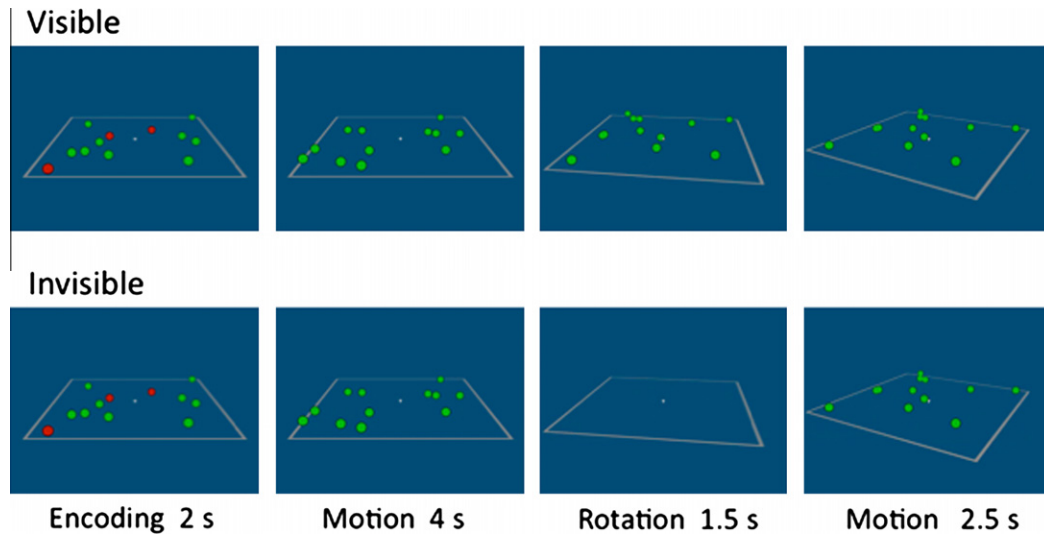
## 2. Methods

### 2.1. Participants

Twenty-one right-handed neurologically healthy volunteers (14 male, 7 female, mean age 25.7 years,  $SD = 5.2$ ) gave informed consent (the study was approved by the Ethics committee of the University of Greifswald) and participated in return for monetary compensation. All reported normal or corrected-to-normal visual acuity. The data of two additional participants were not included in the reported analyses. One exceeded the limit for head movement during image acquisition (more than 2 mm in the  $x$ ,  $y$ , or  $z$ -direction) and the other showed exceptionally low tracking performance (more than 3  $SD$  below the average even at low tracking load).

### 2.2. Stimulus presentation

Visual stimuli were back-projected onto a translucent screen, which participants viewed through a mirror mounted on the head coil. The display consisted of a dark blue background covering 13.9° × 18.4° of visual angle, on which a dark gray line was drawn to indicate the border of a rectangle floor plane as viewed from a camera angle elevated 20° above the  $x$ - $y$  plane (see Fig. 1). The floor rectangle subtended 4.8° of visual angle vertically and 10–17.5° horizontally. To minimize eye movements during scanning,



**Fig. 1.** A schematic illustration of the stimulus material in tracking trials. On a static display, 2, 3, or 4 balls were marked as targets (Encoding). Then, all balls started to move on the floor plane (Motion). At the end of the first motion interval, all objects stopped and the scene was rotated continuously by 30° clockwise or counter-clockwise (Rotation). The objects either were visible during rotation or invisible. When the rotation was completed, all objects started to move again until they finally stopped (Motion). Then, one object turned red and participants indicated whether they thought it was one of the targets or not (Response, not shown). In addition to tracking trials there were passive viewing trials also with objects visible or invisible during rotation, however, no objects were drawn in red, neither at the beginning, nor at the end. Tracking trials started with a “!” and the fixation dot on an empty floor plane; passive viewing trials started with an “X” and the fixation dot on an empty floor plane. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

participants were instructed to fixate a white point that was shown in the center and remained visible in the foreground of the display throughout stimulus presentation.

At the beginning of each trial, the floor plane rectangle appeared and participants first saw a symbol for 0.5 s indicating whether their task in the upcoming trial would be active tracking (“!”) or passive viewing (“X”). Next, the symbol was replaced by 12 balls that remained static for 2 s at random positions on the floor plane (see Fig. 1). The balls subtended 0.5–0.8° of visual angle depending on their position in the 3D-scene. They were drawn in green with a black border. In active tracking trials, two, three, or four of the balls were initially drawn in red during this 2 s interval indicating the targets to be tracked. Subsequently, they turned green and thus were indistinguishable from the remaining balls. Then all balls started to move in random directions at  $\sim 2^\circ/\text{s}$  on linear trajectories. They bounced off the border of the floor plane in the manner of billiard balls and their trajectories were allowed to intersect. After 4 s of motion, the balls stopped and the viewpoint on the 3D-scene changed continuously by 30° clockwise or counter-clockwise within 1.5 s. This viewpoint change resembled a rotational camera movement around a vertical axis through the center of the floor plane. In *visible* trials, the balls remained visible during the viewpoint change; in *invisible* trials, all balls vanished at the beginning of the viewpoint change and reappeared when the viewpoint change was completed (see Fig. 1). Then, all balls started to move again continuing their trajectories in the 3D-scene. At the end of this second motion interval of 2.5 s, all balls stopped. In active tracking trials, one of the balls turned red and participants were instructed to respond with the index finger of their right hand on a response pad if the probed ball was one of the targets or with the middle finger of their right hand if the ball was a distractor. Half of the probed balls in active tracking trials were targets resulting in a chance level of .5 for tracking performance. The interval with static balls at the end of a trial was always 1.5 s. Finally, the display was erased and only the fixation point remained visible until the following trial started.

The participants were scanned during three runs, each of which lasted 650 s and consisted of 32 trials (12 s each) interleaved with fixation intervals lasting 6, 8, or 10 s. The 32 trials in each run

encompassed equal numbers of track 2, track 3, track 4, and passive viewing trials. In half of each trial kind the balls remained visible and in the other half the balls were invisible during the viewpoint change. This resulted in 96 trials in total, which were rendered in advance. Thus, each participant was presented with the same tracking sequences, which homogenized visual stimulation across participants at the expense of an even sampling of trial difficulty (see Section 3.1). The order of presentation was pseudo-random within each run and the order of runs was balanced across participants. Prior to the scanning session, each participant was acquainted with the task while completing at least 32 training trials including all trial types.

### 2.3. Data acquisition

Magnetic resonance imaging was carried out at 3 T with a Siemens Magnetom Verio scanner using a 12-channel head coil. At the beginning of each scanning session, field homogeneity was optimized by a shimming sequence and a GRE field map was acquired for the unwarping procedure. Then the experimental trials were presented in three runs, each consisting of 32 trials. During each run, 325 volumes with 34 slices (1 mm gap) were acquired using echo-planar imaging (TR 2000 ms, TE 30 ms, flip angle 90°, FoV 192 mm, matrix 64 × 64, voxel size 3 × 3 × 3 mm). The first two volumes in each run were discarded to allow for T1 equilibration effect. Finally, a T1-weighted anatomical volume was recorded (MPRage, TR 1900 ms, TE 2.52 ms, flip angle 90°, matrix 256 × 256, voxel size 1 × 1 × 1 mm).

### 2.4. Data preprocessing

Preprocessing and statistical analysis of fMRI data was performed using SPM8 (Wellcome Department of Imaging Neuroscience, London) implemented in MATLAB (MathWorks, Inc., Natick, MA). Unwarping of geometrically distorted EPIs was performed in the phase encoding direction using the FieldMap Toolbox. Each time-series was realigned to the first image of each run and resliced. EPIs were coregistered to the T1-weighted anatomical image and T1-weighted images were segmented to localize gray and

white matter as well as the cerebro-spinal fluid. This segmentation was the basis for spatial normalization to the Montreal Neurological Institute (MNI) template, which was then resliced and smoothed with a  $8 \times 8 \times 8$  mm full-width at half maximum (FWHM) Gaussian kernel filter to increase the signal-to-noise ratio. To correct for low-frequency components, a high-pass filter with a cut off of 128 s was applied.

## 2.5. Statistical analysis

For each participant a design matrix was created. The event intervals within each trial (instruction 0.5 s, encoding 2 s, motion 4 s, rotation 1.5 s, motion 2.5 s, response 1.5 s) were modeled as boxcar functions convolved with a canonical hemodynamic response function. Individual statistical maps were calculated for the contrasts of interest: (1) activation elicited by performing MOT: tracking > passive viewing, (2) activation increasing with tracking load: tracking 4 > tracking 2 (equivalent to the linear contrast with weights 1, 0, and  $-1$  for load levels 4, 3, and 2, respectively), and (3) activation increasing with demands on updating: tracking 4 invisible objects > tracking 2 invisible objects in the rotation interval. Contrast images of each participant were then used for group statistics calculated as random effects analyses at the 2nd level, which take variance between participants into account.

The manipulation of visibility during rotation occurred late in the tracking interval and thus, tracking and tracking load activations could build up in visible and in invisible rotation trials. As a consequence, possible effects of visibility on tracking activations would be reduced. They were not the focus of this study, but we tested for them by paired *t*-tests comparing tracking and tracking load contrast images computed separately for visible and invisible rotation. The significance levels for these tests were the same as for the tracking and tracking load contrasts.

The significance level for the tracking > passive viewing contrast was  $p < .05$  corrected for the whole brain volume (familywise error rate, FWE; Brown & Russell, 1997). For the linear contrasts testing for the effect of tracking load and for the effect of updating demands in the rotation interval, regions of interest (ROIs) were defined by anatomical masks. The regions of interest for the effect of tracking load were the parietal, occipital, and frontal regions consistently identified in previous studies (Culham et al., 2001; Jovicich et al., 2001; Tomasi et al., 2004): superior parietal lobe, inferior parietal lobe, and intraparietal sulcus; MT+ and lateral occipital cortex; inferior precentral sulcus. The region of interest for the effect of updating demands was the precuneus (Wolbers et al., 2008). To determine the ROI peak voxels, we employed anatomical masks from the SPM Anatomy Toolbox Version 1.8 (Eickhoff et al., 2005) and, for the inferior precentral sulcus and the precuneus that were not defined by ANATOMY, using anatomical masks from the Automated Anatomical Labeling Toolbox (Tzourio-Mazoyer et al., 2002). ROIs varied in size, thus, a uniform small volume correction was used: The significance level was  $p < .05$  FWE corrected for spherical volumes with 12 mm radius (257 voxels) centered on group peak voxels within regions of interest. To visualize the load effects, we used rfxplot (Gläscher, 2009) to prepare plots of average regression coefficients at peak voxels of load and updating demand activations.

## 3. Results

### 3.1. Behavioral results

Mean proportions of correctly identified targets are shown in Fig. 2A. Five of the 72 tracking sequences (7%) were not included in the calculation of the shown means and the analysis of behav-

ioral data because disproportionately few participants responded correctly to the probed object in these sequences. The reason for this was that the finally probed object intersected with a target earlier in the sequence and participants likely continued to track the wrong object. Four of these five particularly difficult sequences cumulated in the three targets-visible condition. With these sequences included, the mean proportion correct for the three targets-visible condition was .70 (*SE* .03), which would not reflect the relative difficulties of the conditions as we confirmed in an additional experiment reported below that used novel sequences for each participant.

An overall ANOVA including the within-subjects variables visibility (visible vs. invisible) and tracking load (2, 3, or 4 targets) confirmed that tracking was more difficult when the objects were temporarily invisible,  $F(1,20) = 37.34$ ,  $MSe = 0.018$ ,  $p < .001$ , and when more objects had to be tracked,  $F(2,40) = 6.84$ ,  $MSe = 0.013$ ,  $p = .003$ . The interaction was not significant,  $F(2,40) = 1.39$ ,  $MSe = 0.012$ ,  $p = .26$ .

To determine the differences in tracking difficulty between the conditions more precisely, we conducted an additional behavioral experiment with the same design of materials and the same parameters, but novel sequences for each participant. Twenty-four new participants (21 female, 3 male, mean age 21.3, *SD* 2.4) were presented with 144 trials (24 trials in each condition). The mean proportions of correctly identified objects are shown in Fig. 2B. An overall ANOVA including the within-subjects variables visibility and tracking load confirmed the effect of visibility,  $F(1,23) = 44.98$ ,  $MSe = 0.010$ ,  $p < .001$ , and the effect of tracking load,  $F(2,46) = 15.15$ ,  $MSe = 0.012$ ,  $p < .001$ . The interaction was not significant ( $F < 1$ ). Pairwise comparisons confirmed the visibility effect at each level of tracking load with effect sizes *d* of 0.82, 1.02, and 0.83 for 2, 3, and 4 targets, respectively. When objects remained visible, tracking 2 targets was significantly easier than tracking 3,  $d = 0.57$ , and tracking 3 was easier than tracking 4,  $d = 0.60$ . When objects turned invisible during the viewpoint change, tracking 2 targets was significantly easier than tracking 3,  $d = 0.55$ , the difference between tracking 3 and tracking 4 was not statistically significant,  $t(23) = 1.38$ , two-tailed  $p = .18$ ,  $d = 0.34$ .

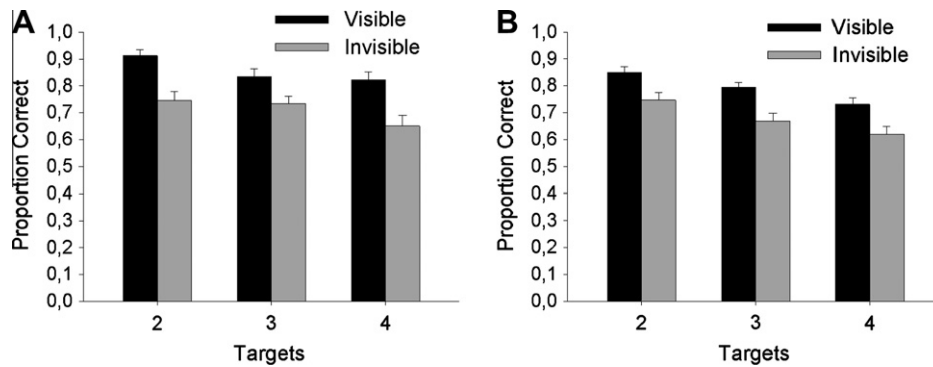
### 3.2. Functional magnetic resonance imaging

Functional imaging data are presented for three analyses. First, we report the activation resulting from performing the MOT task. Second, we identify areas that responded to an increasing tracking load. Third, we focus on spatial updating and report activation triggered by viewpoint changes during which objects were invisible. We identify areas showing an increase in activation when the number of targets increased, for which egocentric self-object relations had to be updated.

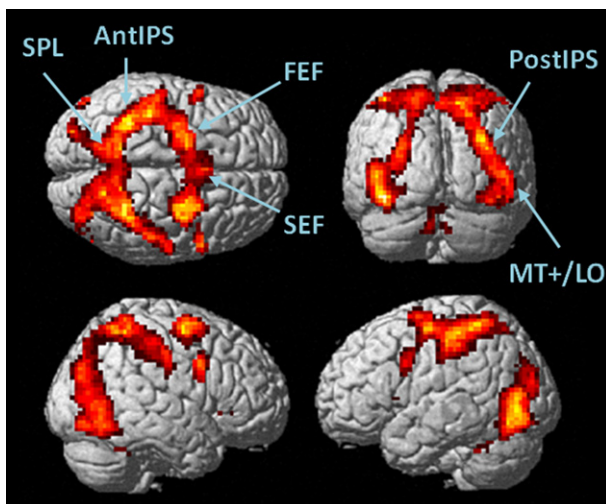
#### 3.2.1. Effects of tracking

The activation resulting from performing the tracking task was determined by the contrast between tracking and passive viewing. The regressors that were included in the contrast covered the interval from the encoding of the targets to the end of the second motion sequence (shown in Fig. 1). The 1.5 s rotation interval was included because the tracking activation was not captured well if a novel tracking onset after the brief rotation was modeled. This was true even when objects turned briefly invisible. In passive viewing trials, the optical stimulation in the respective interval was equivalent except that no objects were marked as targets.

Tracking as opposed to passive viewing was associated with strong bilateral activation of parietal, frontal and occipital cortex (see Fig. 3 and Table 1). The activation of PPC encompassed the superior parietal lobule (SPL) and medially parts of the precuneus. It extended along the intraparietal sulcus (IPS) and further towards



**Fig. 2.** (A) Tracking performance in the scanner. (B) Tracking performance of a new sample of participants outside the scanner, when a new set of stimulus materials for each participant improved the control of random variations in trial difficulty. The bars show the mean proportion correct in identifying the probed ball as a target or a distractor (error bars indicate the standard error of the mean).



**Fig. 3.** Surface rendered statistical maps of the tracking vs. passive viewing contrast showing brain areas more strongly activated by multiple object tracking than by passive viewing. The results of the random effects analysis were thresholded at  $p < .05$  corrected for the entire brain (FWE). Left top: superior view, right top: posterior view, left bottom: right hemisphere; right bottom: left hemisphere. SPL: superior parietal lobule; AntIPS: anterior intraparietal sulcus; FEF: frontal eye field; SEF: supplementary eye field; PostIPS: posterior intraparietal sulcus; MT+: human motion complex; LO: lateral occipital cortex.

occipital and occipitotemporal cortex (MT+ and lateral occipital cortex). The precentral frontal cortex was activated with strong foci in premotor cortex (FEF) and weaker medial activation of supplementary motor cortex (SEF). Separate clusters of activation were located more laterally in or close to the precentral sulcus. Additional foci of activation were observed bilaterally in the cerebellum, thalamus, and the insular cortices. This pattern of activation was similar whether objects were visible or invisible during the brief rotation interval. Visibility during rotation had no significant effect on tracking activation as explored by paired  $t$ -tests comparing tracking > passive viewing contrast images computed separately for visible and invisible rotation. Neither the invisible > visible, nor the visible > invisible comparison yielded significant visibility effects.

### 3.2.2. Effects of tracking load

Tracking load was varied in three levels (2, 3, and 4 targets). This parametric variation was used to identify brain regions, in which activation increased with the number of targets. The linear contrast for the three levels of tracking load was computed for

the same interval as in the analysis of tracking effects (from encoding to the end of the second motion interval). Three clusters showed increasing activation with an increase of tracking load from 2 to 4: the anterior IPS and SPL in the right hemisphere, the posterior IPS in the left hemisphere and occipitotemporal and lateral occipital cortex (MT+ and LO) in the right hemisphere (Table 2 and Fig. 4). For peak voxels of each of these clusters of activation, regression coefficients are plotted in Fig. 5 separately for trials with objects visible and invisible during rotation and the three levels of tracking load. The increase in activation with tracking load in these areas was observed irrespective of object visibility during rotation. Visibility had no significant effect on load activations as explored by paired  $t$ -tests comparing tracking 4 > tracking 2 contrast images computed separately for visible and invisible rotation. Neither the invisible > visible, nor the visible > invisible comparison yielded significant visibility effects.

### 3.2.3. Effects of tracking across invisible rotation

Tracking targets that were temporarily invisible during a rotation of the 3D scene required the spatial updating of retained target locations based on continuous visual information. The more targets were tracked, the more locations had to be retained and updated. Thus, areas that show increased activation when more target locations have to be retained and updated probably do have a role in spatial updating. The parametric variation of tracking load within invisible rotation conditions lets us determine areas that show increased activation when more target locations have to be retained and updated. Again, we computed the linear contrast for the variation of tracking load, however, this time using only the regressors for the rotation interval (1.5 s) in the invisible condition (see Fig. 1 invisible rotation). The only significant cluster, in which activation increased with the number of updated target locations was located in the precuneus (Fig. 6A). For the activated bilateral cluster (peak voxels at  $-3 -51 33$  and  $3 -48 30$  with  $t$ -values of 4.44 and 4.43, respectively), the regression coefficients for the invisible rotation event are plotted in Fig. 6B. The regression coefficients for the conditions with visible objects are plotted as well. Only the conditions with invisible objects produced a linear increase in precuneus activation with increasing demands of spatial updating. With visible objects, the precuneus activation was similar across load levels. Note that the invisible activation is lower than the visible activation for two and three targets, which is consistent with the involvement of the precuneus in tracking visible targets (see Table 1).

For comparison, we computed the same linear contrast for the rotation interval in the visible condition. This contrast revealed no significant activations at all. A paired  $t$ -test comparing tracking 4 > tracking 2 contrast images computed separately for visible and invisible rotation further confirmed that the rotation interval

**Table 1**  
Spatial coordinates of the brain areas showing significant activation in the group contrast tracking vs. passive viewing ( $p < .05$ ; FWE corrected).

Brain areas	MNI coordinates [xyz]		t-Value
	Left hemisphere	Right hemisphere	
<i>Parietal</i>			
Superior parietal lobule	[-36 -48 57]	[27 -54 57]	14.84 17.11
Anterior IPS	[-18 -57 54]	[18 -63 54]	12.16 16.37
Posterior IPS	[-24 -72 27]	[33 -78 33]	10.51 12.33
Precuneus	[-12 -60 60]	[9 -51 54]	11.94 12.94
<i>Frontal</i>			
Frontal eye fields	[-27 -9 57]	[27 -6 54]	17.56 14.12
Supplementary eye fields/SMA	[-9 0 63]	[9 0 57]	9.74 10.77
Inferior precentral sulcus	[-57 6 30]	[57 9 36]	11.73 11.00
Insula	[-30 15 9]	[30 24 6]	7.97 7.67
<i>Occipitotemporal</i>			
MT+/LO	[-45 -72 3]	[48 -69 3]	14.90 11.86
<i>Subcortical</i>			
Thalamus	[-15 -21 9]	[15 -21 3]	9.03 7.23
Cerebellum	[-24 -57 -27]	[27 -54 -27]	9.34 9.88

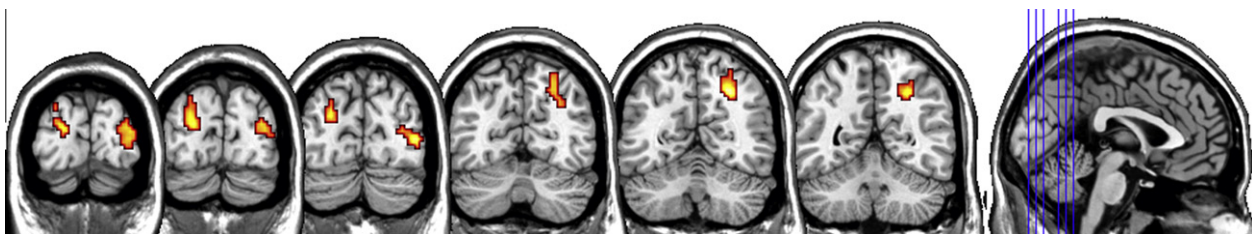
Note: IPS: intraparietal sulcus; SMA: supplementary motor area; MT+: human motion complex; LO: lateral occipital cortex.

**Table 2**  
Spatial coordinates of the brain areas showing significant load-dependent activation in the group analysis (tracking 4 vs. tracking 2;  $p < .05$ , FWE corrected for spheres of 12 mm radius).

Brain areas	MNI coordinates [xyz]		t-Value
	Left hemisphere	Right hemisphere	
Anterior IPS		[27 -57 42]	6.87
Superior parietal lobule		[24 -60 48]	5.60
Posterior IPS	[-21 -84 18]		5.88
Occipitotemporal (MT+/LO)		[45 -78 6]	6.07

Note: IPS: intraparietal sulcus; MT+: human motion complex; LO: lateral occipital cortex.

caused load-dependent precuneus activation in the invisible condition but not in the visible condition. The peak voxel for this contrast was located in the precuneus at  $-3 -57 39$ ,  $t(20) = 6.29$ .



**Fig. 4.** Statistical maps of the contrast revealing effects of tracking load (tracking 4 vs. tracking 2 targets) drawn on coronal sections. In the right parietal cortex (right anterior IPS) and in middle occipital cortex bilaterally, activation increased with an increasing number of targets. For visualizing the load activations that were significant at  $p < .05$  (FWE corrected for spheres of 12 mm radius), a threshold of  $p < .001$  (uncorrected) and a cluster threshold of 50 voxels were applied.

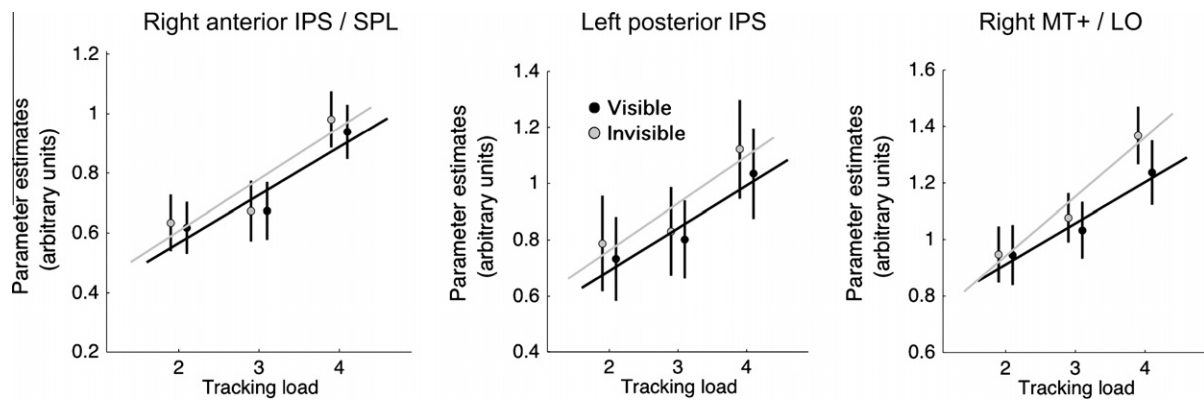
#### 4. Discussion

We employed multiple object tracking (MOT) in a 3D scene to study the neural correlates of attentive tracking and spatial updating across continuous rotational viewpoint changes. When objects remained visible during scene rotation (a continuous viewpoint change), observers could track targets with the same mechanisms as in ordinary MOT displays. Previous studies have shown that tracking performance is not impaired if the whole scene undergoes motion (Huff et al., 2010; Liu et al., 2005; Thomas & Seiffert, 2010). However, when objects turned invisible for the duration of the scene rotation, observers had to retain and update the locations of the targets in order to continue tracking when they reappeared. The visual information that was available during the scene rotation signaled a viewpoint change and thus provided cues to the changes in egocentrically encoded target locations.

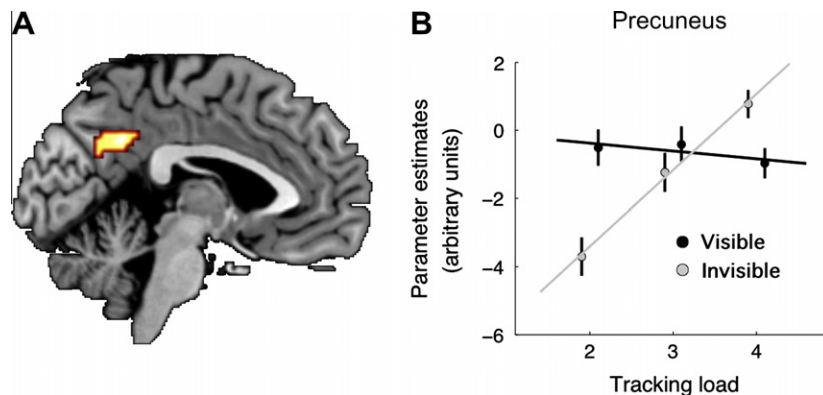
The only significant increase in brain activation in response to increased load in retaining and updating locations of invisible targets was observed in the precuneus. From our results alone, we cannot discern whether the load-dependent precuneus activation in the invisible rotation condition was the result of updating or merely of retaining an increasing number of object locations. If targets turn invisible, their locations have to be retained in spatial working memory and spatial working memory has to be accessed to continue tracking when the targets reappear. Increasing demands of selecting object locations in a static spatial working memory representation increases precuneus activation (Bledowski, Rahm, & Rowe, 2009). Thus, the precuneus activation in response to invisible rotation may just reflect spatial working memory demands. Yet, invisible rotation clearly called for updating in addition to accessing spatial working memory. Importantly, updating increased load-dependent precuneus activation compared to accessing spatial working memory in Wolbers et al. (2008).

This previous study employed a spatial memory task with a static array of objects that turned invisible before visual cues signaled forward ego-motion. In a control condition without signaled forward motion, the objects just turned invisible. The condition with motion required updating and accessing spatial working memory, the control condition without motion required only accessing spatial working memory. In both conditions, Wolbers et al. observed increasing precuneus activation with an increasing number of objects, however, the precuneus activation was significantly higher in the updating condition. Thus, because the invisible rotation condition in the present study clearly required spatial updating, the load-dependent precuneus activation likely indicates involvement of the precuneus in updating, not just in accessing spatial working memory.

In turn, the load-dependent precuneus activation restricted to the invisible rotation condition in the present study strengthens Wolbers et al.'s conclusions. Wolbers et al.'s static condition did not require updating and did not induce self-motion processing. In the present study, the condition not requiring updating instead of being static contained motion interpretable as self-motion as



**Fig. 5.** Diagrams of tracking load effects showing regression coefficients of the regressors specifying the tracking interval (from encoding to the end of the second motion interval) for the three clusters, in which activation increased with tracking load (error indicators show the standard error of the mean). Plotted are averages of individual peak voxels within spherical search volumes of 6 mm radius centered on the group peak voxels listed in Table 2. IPS: intraparietal sulcus; SPL: superior parietal lobule; MT+: human motion complex; LO: lateral occipital cortex.



**Fig. 6.** (A) Statistical map of the contrast revealing effects of spatial updating (tracking 4 vs. tracking 2 targets in the rotation interval when objects were invisible). Activation of the precuneus increased bilaterally when the number of objects increased, for which spatial updating had to be performed. For visualizing the updating load activation that was significant at  $p < .05$  (FWE corrected for a sphere of 12 mm radius), a threshold of  $p < .001$  (uncorrected) and a cluster threshold of 50 voxels were applied. (B) Diagram showing the spatial updating effect: average regression coefficients of the regressor specifying the rotation interval for the cluster of voxels in the precuneus, in which activation increased with an increasing number of object locations that had to be updated (error indicators show the standard error of the mean). Plotted are averages of individual peak voxels within a search volume of 6 mm radius centered on the group peak voxel (MNI coordinates:  $-3 -51 33$ ).

well. Thus, updating demands are manipulated at similar levels of self-motion processing.

Both our results on tracking invisible objects across scene rotation and the results of Wolbers et al. (2008) support the neural model of spatial memory and imagery of Byrne et al. (2007), which assigns the precuneus a central role in spatial updating. In this model, the precuneus is assumed to provide egocentric representations of locations (supported by perceptual input, retained in spatial working memory, or remembered from long-term memory) and can be modulated by directed attention. The egocentric representation in the precuneus is assumed to be updated based on information about ego-motion and it can be detached from perceptual input and represent imagined and remembered scenes as well as imagined ego-motion. These functions assigned to the precuneus are consistent with earlier findings suggesting that the precuneus is involved in self-centered mental imagery and episodic memory retrieval (for a review see Cavanna & Trimble, 2006).

While we have provided evidence that the precuneus is involved in spatial updating across visually signaled viewpoint changes and Wolbers et al. obtained similar results with visually signaled forward self-motion, it is unclear whether the illusion of self-motion is a prerequisite for finding increasing precuneus activation with increasing demands of spatial updating. For obvious reasons, we did not study actual whole-body movements and

therefore, our results pertain only to spatial updating as it occurs in response to visually signaled changes in self-object relations. Actual self-motion induces automatic spatial updating based on vestibular and proprioceptive cues, which differs from spatial updating in response to merely visual cues even if these are as rich as optic flow in virtual reality (e.g., Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Thomas & Seiffert, 2010; but see Riecke, Cunningham, & Bühlhoff, 2007). It is possible that Wolbers et al. (2008) succeeded in inducing automatic spatial updating equivalent to actual self-motion by presenting an expanding dot pattern simulating forward motion. A cautious interpretation would be that both the present study and Wolbers et al. (2008) induced spatial updating of egocentric representations as it occurs when observers process camera movements in films and video games.

Tracking temporarily invisible targets among identical distractors was a difficult task as evident from behavioral performance. Performance in the scanner was similar to performance of another sample of observers outside the scanner and the performance in a previous study that employed a similar task (Huff et al., 2010). Performance showed the common decrease with tracking load in MOT (Franconeri, Lin, Pylyshyn, Fisher, & Enns, 2008) and an impairment due to temporal invisibility, which also replicates previous results (Huff et al., 2010). Although updating the locations of multiple invisible targets is difficult, it demonstrates that observers can

retain the locations of invisible targets and use visible scene motion to update the self-object relations to continue tracking after the targets reappear at changed retinocentric coordinates. Either target locations have to be retained with respect to the reference frame that the visible scene provides (allocentric) or they are retained as egocentric self-target relations and are linked to the visible scene via the observer's viewpoint (cf. Jahn, Papenmeier, Meyerhoff, & Huff, in press). With actual self-motion, spatial updating seems to rely on egocentric representations (Wang et al., 2006), but we cannot exclude with certainty that observers might have processed the floor plane as an object rotating in front of them and the targets and distractors as parts of the rotating object (allocentric). Such object-centered updating is unlikely in the case of the extended floor pattern used by Wolbers et al. (2008). Thus, either both fMRI results pertain to egocentric updating or both egocentric and allocentric updating involve the precuneus.

The precuneus is also activated by the basic MOT task as has been shown previously (e.g., Culham et al., 1998) and in the present study. This confirms that the precuneus contributes to spatial attention even if targets remain visible (Cavanna & Trimble, 2006; Nobre et al., 2004). With visible objects, objects are attentionally selected and tracking requires retaining the selection. With invisible objects, locations have to be retained without perceptual support and updated indirectly by processing cues to observer motion. The precuneus seems to be involved in both attentive tracking of visible targets and tracking and updating of invisible targets. The latter seems to cause stronger load-dependent activation. The basic MOT task encompasses the encoding of target locations, attentive tracking of moving targets and the retention of a task set. Part of the task set in the present study was to keep fixation during tracking. We did not monitor fixation and according to participants comments in the post-session interviews they did not succeed in suppressing eye movements completely. Even so, suppressing eye movements was a task component, which contributed to the activations observed in the tracking vs. passive viewing contrast.

These tracking vs. passive viewing activations matched closely the patterns of activation observed in previous studies that monitored fixation during tracking inside (Culham et al., 1998) or outside the scanner (Culham et al., 2001; Howe et al., 2009; Jovicich et al., 2001). Particularly areas in posterior parietal cortex in and around the intraparietal sulcus, the frontal eye fields (Paus, 1996), supplementary eye fields (Grosbras, Lobel, Van de Moortele, Lebihan, & Berthoz, 1999), MT+ (Wilms et al., 2005) and adjacent lateral occipital cortex (Larsson & Heeger, 2006) reliably show higher activation during multiple object tracking than during passive viewing. The frontoparietal network is also activated by other tasks that demand shifts of covert attention (e.g., Kelley et al., 2008) and spatial working memory (Curtis, 2006), and is the source of top-down attention signals (Kanwisher & Wojciulik, 2000; Knudsen, 2007). Higher visual areas, to which MT+ and LO belong, are more strongly modulated by attention than early visual areas. MT+ is the main area for motion processing and thus its activation by attended motion stimuli is expected. The activation in adjacent LO is consistent with task demands as well. The lateral occipital cortex contains topographically organized areas that contribute to form and object processing (Larsson & Heeger, 2006) and is modulated by attention (Tootell et al., 1998).

The areas showing increased activation with increasing tracking load were consistent with load-dependent areas that were previously reported (Culham et al., 2001; Jovicich et al., 2001; Tomasi et al., 2004). They overlap with areas showing task-dependent activation and encompass the left posterior IPS and the anterior IPS, the SPL and MT+/LO in the right hemisphere. Previous studies observed bilateral load-dependent activation in these areas and additional frontal activations most consistently in inferior precentral

cortex. The reason for fewer load-dependent activations observed in the present study probably was that our design was not optimized for identifying load effects in basic MOT. Tracking load was restricted to a maximum of four targets to keep the invisible rotation trials manageable and tracking intervals were brief.

Nonetheless, the observed load-dependent areas are consistent with areas identified as responding to visuo-spatial short-term memory load. For instance, Xu and Chun (2006) found activation in posterior IPS to increase with the number of objects held in memory up to a limit of four, whereas activation in anterior IPS increased with feature complexity. Activation in LO increased with the number and complexity of objects held in short-term memory as well. The conclusion that an area in the posterior IPS provides pointers to discrete objects was confirmed in studies of visual attention (Cusack, Mitchell, & Duncan, 2010). Such spatial pointers or indices are necessary for the parallel tracking of multiple targets that are visually indistinguishable from distractors. They correspond to proposed mechanisms of MOT: to visual indices following targets preattentively that are postulated in the FINST ("fingers of instantiation") theory (Pylyshyn, 2001) and to object files (Kaheman, Treisman, & Gibbs, 1992; Xu & Chun, 2009) that store object locations and are updated while multifocal attention follows targets (Cavanagh & Alvarez, 2005).

These updating mechanisms work as long as the targets are in view, however, they hit their limits if the observer moves and the objects turn invisible. Then, spatial updating that processes cues to observer motion and modifies egocentric spatial relations becomes necessary. The recently suggested neural mechanisms for this kind of spatial updating assign a central role to the precuneus, which is assumed to hold the egocentric representations that are updated (Byrne et al., 2007). In direct support of these ideas, the present findings provide strong evidence for an important role of the precuneus in dynamic spatial attention, spatial working memory, and spatial updating.

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