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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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BRAIN and

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 (Wraga, 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).

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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 3Dscene 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 $13.9^{\circ} \times 18.4^{\circ}$ 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,

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