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Research Report

The neural basis of ego- and allocentric reference frames in spatial navigation: Evidence from spatio-temporal coupled current density reconstruction

K. Gramann[a,*], H.J. Müller[a], B. Schönebeck[b,1], G. Debus[b,1]

[a]Department Psychology, Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität München, Leopoldstr. 13, D-80802 München, Germany
[b]Rheinisch-Westfälisch-Technische Hochschule Aachen, Germany

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ABSTRACT

Different strategies in spatial navigation during passages through computer-simulated tunnels were investigated by means of EEG source reconstruction. The tunnels consisted of straight and curved segments and provided only visual flow, but no landmark, information. At the end of each tunnel passage, subjects had to indicate their end position relative to the starting point of the tunnel. Even though the visual information was identical for all subjects, two different strategy groups were identified: one group using an egocentric and the other group an allocentric reference frame. The current density reconstruction revealed the use of one or the other reference frame to be associated with distinct cortical activation patterns during critical stages of the task. For both strategy groups, an occipito-temporal network was dominantly active during the initial, straight tunnel segment. With turns in the tunnel, however, the activation patterns started to diverge, reflecting translational and/or rotational changes in the underlying coordinate systems. Computation of an egocentric reference frame was associated with prevailing activity within a posterior parietal-premotor network, with additional activity in frontal areas. In contrast, computation of an allocentric reference frame was associated with dominant activity within an occipito-temporal network, confirming right-temporal structures to play a crucial role for an allocentric representation of space.

1. Introduction

The ability to orient within our environment is crucial for everyday life. Maintaining orientation during navigation requires the uptake and integration of polymodal sensory information, the further processing of the spatial information within different frames of reference, and the computation of a spatial representation of the environment traversed. Various methods can be used when navigating in the environment, for example, piloting and path integration (Loomis et al., 1999). In piloting, or position-based navigation, the navigator updates his or her current position and orients within the environment by using *external* cues, such as significant landmarks (church towers, intersections, etc.), in conjunction with a map. Path integration or velocity-based navigation, by contrast, refer to the updating of position and orientation

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* *Corresponding author.* Fax: +49 89 21805211.
E-mail address: gramann@psy.uni-muenchen.de (K. Gramann).
[1] Institut für Psychologie, RWTH Aachen, Jägerstraβe 17-19D-52066 Aachen, Germany.

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within an environment using *internal* (*ideothetic*) or *external* (*allothetic*) information (Mittelstaedt and Mittelstaedt, 1982). Both methods rely on different sensory inputs, with piloting using primarily visual information and path integration information from the visual, vestibular, kinesthetic, and motor systems.

Path integration and piloting are based on representations of the environment with distinct underlying reference frames. Piloting involves an allocentric frame, with entities in space represented in terms of a coordinate system that lies outside the navigator. Path integration, by contrast, is based on an egocentric reference frame, with the underlying coordinate system referring to the body axes of the navigator. Although the use of the ego- and allocentric reference frames gives rise to distinct spatial representations conveying different types of information (Klatzky, 1998), it remains an open question whether these representations differ with respect to the underlying neural networks. The present study was designed to isolate the neural networks that subserve the computation of ego- and allocentric reference frames, with the navigator passing through a virtual tunnel environment that provided only sparse visual information.

Neuropsychological studies support the idea of a functional dissociation between allo- and egocentric reference frames (Vallar et al., 1999; Ota et al., 2001; Fink et al., 2003). Furthermore, neurophysiological studies in the monkey have demonstrated the existence of body- and object-based representations in the brain (Graziano et al., 1994; Olson and Gettner, 1995; Duhamel et al., 1997; Breznen et al., 1999). In humans, the use of an egocentric reference frame has been shown to involve a fronto-parietal network including posterior parietal cortex and premotor cortex, more extensively in the right hemisphere (Vallar et al., 1999; Galati et al., 2000). In contrast, the use of an allocentric frame involves activity within only a subset of the same areas (Galati et al., 2000). Despite their contributions to uncovering the cortical networks underlying the two frames of reference, the studies reviewed above used only static stimuli, in particular, the line bisection paradigm. This represents a critical limitation for understanding the use of different reference frames in spatial orientation under ecological conditions.

Virtual environments (VE) or desktop-based simulations present a convenient and sufficient means to investigate spatial navigation behavior within a more realistic environment (Christou and Bülthoff, 2000; Höll et al., 2003; Steck et al., 2003; Jansen-Osmann, 2002; Wolbers et al., 2004). For example, in an fMRI study using a desktop-generated virtual reality, Shelton and Gabrieli (2002, 2004) found differences in brain activation during the encoding of route information, as compared to the encoding of survey information. Survey encoding activated a subset of the same regions that were activated during route encoding, including inferior temporal cortex and posterior superior parietal cortex. Route encoding, relative to survey encoding, led to additional activations in medial temporal, anterior superior parietal, and postcentral regions. Another recent study by Iaria et al. (2003) used VE to investigate the neural correlates of differential navigational strategies in virtual maze learning: a spatial strategy (based on the use of landmarks for spatial inferences) versus a nonspatial strategy (verbal coding of the number of arms within the maze). Iaria et al. observed that over one third of the subjects who preferred a spatial strategy changed their strategy when landmarks were eliminated. With respect to the brain regions involved in navigation, Iaria et al. identified a network consistent with other studies (Aguirre et al., 1998; Maguire et al., 1998; Mellet et al., 2000), with increased activity in posterior parietal regions, motor–premotor areas, as well as dorsolateral premotor cortex, for both strategy groups. When participants' brain activity was analyzed with respect to the strategy employed, only the spatial strategy was found to be associated with increased activity within the right hippocampus proper. Importantly, the cited studies presented VEs with visual flow information plus a large number of visual landmarks during the encoding of the environment. Thus, it may well have been the use of landmarks that was critical for the finding of overlapping networks, since landmarks can be represented within both an ego- and an allocentric spatial representation.

The present study was designed to differentiate the use of distinct spatial representations and their underlying electrocortical correlates using visual flow information only. Spatial information processing was investigated by analyzing electroencephalographic activity (in particular, using spatio-temporal coupled Current Density Reconstruction, stCDR) recorded while participants 'traversed' a route through simulated tunnels (Gramann et al., 2005). Tunnel routes consisted of a set of straight and curved segments, providing the navigator with visual information about translational and rotational changes solely through changes in the rate of optic flow (see Fig. 1A for an example of a turn to the left). The navigators' task was to indicate the location reached at the end of the tunnel passage relative to the origin of the route. Since there were no reference points at the end of the passage, the navigator could solve this task only by building up an internal spatial representation of the eccentricity of the end position, the relative heading during the last as compared to the initial tunnel segment, and the distance of the end position from the origin. In principle, this representation could be based on an ego- and, respectively, an allocentric reference frame. With this tunnel task, participants can be divided into two groups according to the particular reference frame they prefer to use: the first group, referred to as 'turners', use an egocentric frame, the second group, 'nonturners', an allocentric frame[2].

The tunnel task makes it possible to distinguish between the use of ego- and allocentric reference frames during spatial navigation, while keeping the visual flow information constant. Therefore, any differences in cortical activation patterns cannot be attributed to differences in the visual input or the use of nonspatial strategies, such as verbal encoding of route information. Rather, distinct activation patterns would be

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[2] In the present study, no further distinction between head-based and body-based egocentric frames of reference is made. During navigation heading direction is mainly defined by the orientation of the navigators' body axes. Since the head-frame and the body-frame were aligned throughout the experiment with subjects sitting in front of the screen we assume that no differences in the representation of both reference frames occurred. However, it might be possible that both strategy groups use an egocentric frame of reference but that this reference frame is aligned to the head or the body.