Behavioral and electrocortical evidence of distinct reference frames supporting path integration

Inaugural-Dissertation

zur Erlangung des Doktorgrades der Philosophie

and der Ludwig-Maximilians-Universität

München

vorgelegt von

Davide Riccobon

aus

Triest

München, November 2007

Referent:	PD Dr. Klaus Gramann
Korreferent:	Prof. Dr. Hermann J. Müller
Tag der mündlichen Prüfung:	**19. Dezember 2007**

CONTENTS

ACKNOWLEDGMENTS

A number of people have contributed to the successful completion of this doctoral thesis. First of all, I am particularly grateful to Klaus Gramann. He did not only support and supervise my work on this dissertation throughout the last years but also guided my first steps into the world of the 'Electroencephalography', from the electrodes application to the interpretation of EEG-data. In addition, I would like to thank Hermann Müller who gave me the possibility to pursue my scientific interest at the Psychology Department of the Ludwig-Maximilians-University. Moreover, I would like to thank my friends and colleagues Manuela Laws, Markus Müller, and Thomas Töllner for their useful collaboration as well as Lena Burbulla, Isabel Rätzel, Laura Voß, and Beate Killian for their help in running the experiments.

Last but not least, I would like to thank my wife Ingrida, my parents Roberto and Sara, and my sister Elisa for accompanying and supporting me during the past years.

CHAPTER I

General Introduction

Spatial navigation

Spatial cognition enables us to deal effectively with spatial relations, visual spatial tasks and orientation of objects in space, including the ability to orient oneself in space relative to objects and events and the awareness of self-location (Reber, 1985). The manifold environmental knowledge is acquired by different modalities (vision, audition, vestibular system, etc.) and then integrated into higher order representations (Bryant, 1992; Kerkhoff, 2000; Tversky, 1993). A simple example is a walk to the workplace. Here, we use different sources of information to navigate. A cognitive map of the environment, including information about environmental features or objects (landmarks) and their spatial relations (Golledge, 1999) is available. The relative change of landmark positions supplies information about self-motion and allows for the updating of one's own position and orientation within a larger reference system (Loomis, Klatzky, Golledge, & Philbeck, 1999). This form of navigation is commonly referred to as "position-based navigation" or "piloting". "Path integration", by contrast, refers to the updating of position and orientation by means of internal or external information on acceleration and velocity (Mittelstaedt & Mittelstaedt, 1982) provided by vestibular signals (Chance, Gaunet, Beall, & Loomis, 1998; Klatzky, Loomis, Beall, Chance, & Golledge, 1998), kinesthetic feedback from muscles, tendons, and joints (Bakker, Werkhoven, & Passenier, 1999; Chance et al., 1998), as well as optic flow (Kirschen, Kahana, Sekuler, & Burack, 2000; Koenderink, 1986). These distinct sources of input information all contribute to the updating process.

In recent years, virtual environments (VR) became a powerful tool to further investigate the selective influence of different input information on the resultant spatial representation, because they permit a selection and a precise control regarding the type and the time-course of the information provided. Using VR, several investigations showed that visual input is sufficient for building up a mental representation of the environment (Richardson, Montello, & Hegarty, 1999; Witmer, Bailey, Knerr, & Parsons, 1996) and that virtual spatial learning can be transferred into real world settings (for limitations see Bakker et al., 1999). Moreover, it was shown that optic flow alone is sufficient to support path integration (Gramann, Muller, Eick, & Schonebeck, 2005; Riecke, van Veen, & Bulthoff, 2002). To successfully update one's own position and orientation in VR, visual flow information on both translation and rotation has to be integrated over time with respect to a frame of reference (Klatzky, 1998; Postma, Jager, Kessels, Koppeschaar, & Honka, 2004). However, there is a lack of consensus in the literature regarding the nature of the reference frame subserving this updating process: either an egocentric frame of reference, or an allocentric frame of reference might be used for the updating process or, alternatively, both frames of reference might be active in parallel.

Frames of Reference in Spatial Navigation. Wang & Spelke (2000) provided strong evidence that path integration relies on the processing of spatial information within an egocentric reference frame. The authors tested their subjects' pointing accuracy to an array of objects either when they were disoriented or when they remained oriented. In case subjects encoded the spatial layout allocentrically, the disorientation would have been expected to influence the localization of each object the same way: the perceiver was disoriented but the relationships among objects remained intact. Alternatively, if only the relationships of single objects to the perceiver, and not among themselves were represented, the disorientation would have effected the localization of objects to a different extent. The results showed that the represented angular relationships among objects were distorted, thus supplying evidence that only an egocentric representation was used. Consequently, the authors proposed egocentric updating as the underlying mechanism for path integration. This concept was endorsed in a later paper (Wang & Spelke, 2002), where the authors stated that the navigational system in humans was egocentric rather than allocentric in nature. This hypothesis was also corroborated in further studies (Diwadkar & McNamara, 1997; Roskos-Ewoldsen, McNamara, Shelton, & Carr, 1998; Shelton & McNamara, 1997; Wang & Simons, 1999).

Other investigations showed that updating of heading changes is severely impaired when no vestibular information on rotational changes is given (Farrell & Robertson, 1998; Klatzky et al., 1998; Loomis, Klatzky, Golledge, and Philbeck, 1993; May, 1996; Presson & Montello, 1994). Klatzky and colleagues (1998) demonstrated this in a triangulation task. The computation of an egocentric spatial representation, which entails egocentric bearing from objects (in this study of starting-point) failed whenever vestibular input was absent: in this case only translational changes were incorporated into the final spatial representation. On the other hand, when physical rotation accompanied the turn, translation and rotation were updated successfully. The authors argued that vestibular input was necessary to compute bearing within an egocentric reference frame. Wraga (2003) supplied an alternative explanation to Klatzky's findings, implying that visual stimulation alone is sufficient for the updating of heading changes but whether or not this information is used for a response depends on the response modality. If a response requires pointing movements, the reference frame for reaction is body-centered. In contrast, when a different response modality is given (e.g., arrow adjustment on a screen or verbal response), the reaction might be based on a body-free reference frame. Therefore, erroneous responses in Klatzky's experiments might have been due to a conflict between the reference system induced by the visual stimulation and the reference system used for the physical response. In a replication of the triangulation task by Klatzky and colleagues (1998), Avraamides, Klatzky, Loomis, and Golledge (2004) tested this claim by asking subjects to respond either verbally or by body rotation.

The results revealed better performances when subjects responded verbally, thus supporting Wraga's conflict hypothesis.

However, it is important to mention that subjects in Klatzky's and Avraamides' triangle completion task were not completely wrong in the imagined rotation condition: they systematically overturned the homing vector corresponding to the magnitude of the angle between the segments. Thus, the responses corresponded to some kind of spatial updating within an allocentric reference frame, where only translational changes with respect to reference axes external to the perceiver were taken into account. By using an allocentric frame of reference rather than an egocentric reference frame, subjects could solve the task of updating their own position within the environment. Several theories assume that two or more spatial representations can co-exist in parallel (Aguirre & D'Esposito, 1999; Burgess, 2006; Burgess, Spiers, & Paleologou, 2004; Sholl, 2001). The existence of different forms of spatial knowledge organized with respect to different reference frames and processed by distinct neural networks was confirmed in several brain imaging studies (Galati, Lobel, Vallar, Berthoz, Pizzamiglio, & Le Bihan, 2000; Jordan, Schadow, Wuestenberg, Heinze, & Jaencke, 2004; Mellet, Bricogne, Tzourio-Mazoyer, Ghaem, Petit, Zago, Etard, Berthoz, Mazoyer, & Denis, 2000; Shelton & Gabrieli, 2002, 2004) and supported by neuropsychological findings in brain-damaged patients (Farrell & Robertson, 2000; Kessels, de Haan, Kappelle, & Postma, 2001).

Spatial Strategies. An alternative explanation for the use of distinct frames of reference in the experiments described above is the individual preference to use one or the other reference frame. Several studies identified individual preferences in spatial tasks (Denis, Pazzaglia, Cornoldi, & Bertolo, 1999; Lawton, 1996; Pazzaglia & Beni, 2001). Lawton (1996) differentiated between subjects preferring a route based strategy and an orientation strategy. The preference for one or the other strategy was consistent for indoor and outdoor environments. Individual differences with respect to the strategy applied in spatial tasks were also reported by Denis (et al., 1999) and Pazzaglia and Beni (2001), who distinguished between the preferential use of a survey representation or the preference to use visual memory of landmarks. Common to both distinctions is the assumption that an allocentric reference frame subserves orientation and survey strategy whereas an egocentric reference frame is associated with route based strategy and visual memory for landmarks.

Importantly, in a simulated tunnel task that closely resembles the triangulation task described above (Avraamides et al., 2004; Klatzky et al., 1998), Gramann (et al., 2005) identified a stable individual preference for the use of an egocentric or an allocentric frame of reference for reactions in a pointing task after passages through virtual tunnels. One group of subjects, referred to as “Turner”, preferentially used an egocentric reference frame in which egocentric bearing from the starting-point was updated during stimulus turns and subsequent translations even though no vestibular input was given. A second group of subjects, referred to as “Nonturner”, did not integrate heading changes in the resultant spatial representation that was used for the response. As a result, this strategy group systematically overturned the homing vector by the amount of the angle of turns during the passage (Gramann et al., 2005; Gramann, Muller, Schonebeck, & Debus, 2006).

Independent of subject’s strategy, an egocentric reference frame had to be active in order to process the ongoing egocentric information supplied in a first person perspective. During the tunnel passage, the Turner group was supposed to update a spatial representation based on this egocentric frame of reference. Less clear was the underlying process for Nonturners. This group might transfer the ongoing egocentric information into an allocentric reference frame already during the passage and thus update an allocentric spatial representation. Alternatively, the

Nonturner group might update only an egocentric spatial representation and further process the available information in order to derive allocentric spatial parameters at the end of the path. For a better understanding of the processes underlying spatial navigation, Gramann and colleagues (2005, 2006) analyzed Turners' and Nonturners' response accuracy in a series of three experiments, which supplied first evidences that a path integration process can rely on different reference frames for the updating of a spatial representation.

In order to further elaborate on earlier findings, additional investigations were conducted focusing on the encoding of spatial information as well as on the retrieval and possible further computational steps applied to the information included in the mental representations constructed by path integration. On the basis of behavioral parameters alone, inferences about the cognitive processes accompanying navigation and related spatial tasks are possible only with limitations. The additional measurement of the underlying neural activity supplies further insight into the type and time-course of the cognitive processes involved. In the following sections, two methods will be presented referring to different aspects of the electroencephalogram (EEG): induced oscillatory activity and event related potentials.

Electroencephalographic oscillations

The analysis of EEG-oscillatory behavior is based on the assumption that rhythmic, coherent oscillations of neuronal assemblies are related to different forms of sensory and cognitive processes (Basar, Basar Eroglu, Karakas, & Schurmann, 2001). According to the experimental paradigm and to the perceptual or cognitive process of interest, different forms of brain oscillations can be observed. The occurrence of oscillations in direct temporal relation to a particular stimulus is referred to as 'evoked activity'. This kind of activity is time-locked to a discrete stimulus, which usually presents a clear-cut onset and is identifiable from a background. The term 'induced activity' has been chosen to refer to brain rhythms, which are only weakly time-locked to a stimulus (Bullock, 1992) and vary with respect to their onset. This kind of activity is present under different conditions, e.g. in case of a continuous visual stimulation during virtual navigation, and is associated to a broad range of mental processes. The coherent electrical activity arising from large amounts of neuronal populations usually results in high amplitude, low frequency oscillation (Pfurtscheller, 2003) like the alpha and theta band. These two frequency bands in particular were shown to play an important role in the top-down control and processing of ongoing information (e.g., von Stein & Sarnthein, 2000).

Theta band. Theta activity is supposed to allow for a functional communication among large neural assemblies over distant brain regions in order to support cognitive functions (Mizuhara, Wang, Kobayashi, & Yamaguchi, 2004; von Stein & Sarnthein, 2000) and thus to be distributed over the whole scalp and in particular over prefrontal, central and parietal regions, as indicated by several working memory-investigations (Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005; Schack, Klimesch, & Sauseng, 2005).

The theta rhythm has often been associated with cognitive processes in general (Kahana, Seelig, & Madsen, 2001) and with different aspects of working memory in particular (Klimesch, 1996; Klimesch, Schack, & Sauseng, 2005; O'Keefe & Burgess, 1999). Gevins, Smith, McEovy, and Yu (1997), Jensen and Tesche (2002), and Onton, Delorme, and Makeig (2005) showed that theta activity relates to memory maintenance and increases for increasing task difficulty. Moreover, in several studies Klimesch supplied evidence that theta activity does not only reflect memory storage but also encoding processes (Klimesch, 1999; Klimesch, Doppelmayr, Russegger, & Pachinger, 1996; Klimesch, Doppelmayr, Schimke, & Ripper, 1997). Recent studies linked theta oscillations also to the encoding of spatial information in virtual navigation tasks (e.g., Caplan, Kahana, Sekuler, Kirschen, & Madsen, 2000; Caplan, Madsen, Raghavachari, & Kahana, 2001). During virtual maze navigation, Bischof and Boulanger (2003) proved not only that theta activity reflects spatial encoding but also that theta is associated to critical stages during navigation in virtual environments.

Alpha band. A second frequency band relevant for top-down processes is the alpha band. Since Hans Berger (1929) identified the alpha rhythm as an essential kind of brain oscillations, numerous investigations were conducted focusing on the physiological and functional meaning of alpha activity. Başar offered a short review of the main contributions to alpha research (Basar & Schurmann, 1996) and later proposed an integrative theory of alpha oscillations for brain functioning (Basar & Schurmann, 1997). The author proposed the existence of a distributed alpha system within which alpha waves have several different functional correlates reflecting sensory, motor, and memory functions. Niedermeyer (1987) listed the most important criteria for defining EEG alpha rhythms, including the fact that i) high alpha activity occurs during mental and physical relaxation and ii) it is blocked or reduced by attention and mental effort. An immediate consequence of the two prior assertions is that a reduction in alpha band power during a task compared to a rest interval reflects a state of mental activity (Pfurtscheller & Aranibar, 1977). This reduction in alpha band power or desynchronization (Klimesch, 1996) can be used for the identification of those brain areas that are more active during a task as compared to a rest period. It remains to clarify which functional meaning can be ascribed to alpha desynchronization.

Moreover, it is necessary to distinguish between two distinct alpha sub-bands. A principal component analysis on EEG data (Mecklinger, Kramer, & Strayer, 1992) indicated the existence of two different and functionally independent alpha bands with a lower (7-11 Hz) and an upper (10-13 Hz) band. This distinction was also supported in further studies (Klimesch, Schimke, & Pfurtscheller, 1993; Pfurtscheller & Lopes da Silva, 1999).

The lower alpha band usually has a widespread topography (e.g., Pfurtscheller & Lopez Da Silva, 1999). Several studies assume this band to reflect attentional processes under different experimental condition (Klimesch, 1996; Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998; Klimesch, Russegger, Doppelmayr, & Pachinger, 1998). Furthermore, Klimesch (1997) suggested that lower alpha desynchronization might support the allocation of processing resources for searching and retrieval processes but not encoding in long-term memory tasks. Nevertheless, a more recent study showed that the lower alpha band is also prevailing during the encoding of information in a spatial navigation task (de Araujo, Baffa, & Wakai, 2002).

Event-related potentials

Like electrocortical oscillatory activity, scalp-recorded event-related potentials (ERPs) have been the matter of research for a long time since they are supposed to reflect brain correlates of mental functions. An ERP, presumed to be generated by the synchronous post-synaptic activity of large neuronal populations (e.g., Allison, Wood, & McCarthy, 1986), is defined as a voltage fluctuation in the electroencephalogram time-locked to an external (i.e., stimulus presentation) or internal (i.e., cognitive process) event. Event-related voltage changes are quite small (on the order of microvolts) compared to the ongoing, spontaneous EEG-activity (on the order tens of microvolts) to which they are superimposed. Therefore, the ERPs are usually not evident in the spontaneous EEG. For an identification of event related changes it is thus necessary to extract the signal from the background EEG. This is possible, if several time-intervals (epochs) embedding the signal of interest are averaged over a sufficient number of repetitions. The background EEG-activity, assumed to be random and to vary across intervals, tends to average out whereas the time-locked event-related activity remains unaffected. The result of the averaging process is an event-related 'series of positive and negative deflections, which are thought to be the manifestation of underlying ERP components' (van Boxtel, 1998, p. 87). Whereas the term 'deflection' refers to wave features (i.e., sequence, polarity, latency) determined by a visual inspection of the waveform, 'ERP-components' are rather a theoretical construct assumed to represent psychological and physiological properties of the event under study (Donchin, Callaway, Cooper, Desmedt, Goff, Hillyard, and Sutton, 1977). Donchin, Ritter, and McCallum (1978) suggested to define a deflection (peak, waveform, etc.) as component if it presents a constancy in its polarity, latency and distribution.

The investigation of ERP-components delivers important contributions to psychological research as it allows for an evaluation of information-processing models as well as for insights into mental processes that do not influence the subject's behavior evidently (van Boxtel, 1998). In the next part, two ERP-components playing an important role in the present research will be briefly presented.

<u>N1</u>. According to Luck (2005), several visual N1-subcomponents exist. The earliest component appears over anterior regions with a post-stimulus peak in the range between 100 and 150 ms. This component is assumed to be associated with response-related or preparatory mechanisms (Vogel & Luck, 2000). Moreover, two

further posterior N1-subcomponents with a maximal deflection between 140 and 200 ms (Hillyard & Anllo-Vento, 1998) are supposed to arise from the parietal cortex and from lateral occipital cortex. Hillyard and Anllo-Vento (1998) reviewed several studies showing the posterior components to reflect spatial attention processes whereas other investigations (e.g., Hillyard, Mangun, Woldorff, & Luck, 1995) assumed that these components are associated with selective attention mechanisms. However, another line of research (e.g., Vogel & Luck, 2000) supplied evidences that the lateral occipital N1 reflects a generalized discrimination process between different stimuli when they are related to distinct responses rather than attentional functions.

P3. The P3-component is one of the most studied ERP-components. It appears in many different paradigms (Rösler, 1992) with highly variable latencies and different topography. A first general distinction between an anterior and a posterior component with maximal activity respectively over frontal and parietal electrodes was given by Squires, Squires, and Hillyard (1975). Several studies have further investigated the characteristics of the two components and have supplied evidences for their different functional meaning (see a recent theoretical overview by Polich, 2004). However, despite of the large amount of P3 experiments conducted, relative little is known about the exact psychophysiological correlates of this component (Luck, 2005). Duncan-Johnson (1981) and Polich (1987) supposed the P3 to be related to cognitive processes initiated after the signal has been completely analyzed. Further studies (e.g., Neumann, Ullsperger, Gille, Pietschmann, & Erdmann, 1986; Ullsperger, Gille, Pietschmann, & Neumann, 1986) proposed this component as possible indicator of processing difficulty. Importantly, Mollison (2005) identified a posterior P3-component reflecting attentional processes in a spatial navigation task using a virtual environment.

CHAPTER II

Synopsis

Overview of the current study

The experiments presented in the next chapters of this dissertation aimed at investigating the influence of different reference frames on the processing of spatial information in a desktop-based virtual tunnel paradigm. To this end, both behavioral and electroencephalographic methods were used. First of all, in Chapter III the behavioral data from two subsequent experiments were employed to verify whether more than one reference frame supports spatial updating and furthermore, whether more reference frames can be computed and used for the processing of distinct spatial representations in parallel. The behavioral data analyzed in Chapter III were supported by electrocortical data presented in the subsequent sections. In Chapter IV, the analyses of lower EEG frequency bands were expected to reveal important insights into processes subserving spatial updating during passages through virtual tunnels. Reaction times and event-related potentials were investigated in Chapter V in order to supply further insights into the time-course of the processing and retrieval of spatial information with onset of a response arrow requiring subjects to react. Chapter VI presents a preliminary investigation to a study combining EEG and fMRI methods. The present study was designed to determine the influence of subject's body position on navigation performance. In fact, one of the problems of this combined study might be the body orientation of subjects during the experiment. Whereas in the EEG-experiment subjects are sitting, in the fMRI-experiment subjects are lying.

Chapter III. Previous investigations (Gramann et al., 2005) supplied first evidences that sparse visual flow information is sufficient to update a spatial representation based on different reference frames (an allocentric or an egocentric one). In order to deliver additional proof to previous results, two different reaction formats were used in the present research. These were either presented in a blocked order (Experiment 1) or, alternatively, in a random sequence with reaction unpredictable on a trial (Experiment 2). Whereas the blocked order allowed subjects to update one spatial representation at a time, the random order induced the updating of more than one representation. The first reaction format allowed two groups of subjects, the Turner and the Nonturner group, to react based on different reference frames, respectively an egocentric and an allocentric one. A second reaction format forced all subjects to adopt allocentric coordinates for their reactions. The central issue was to determine whether both reference frames or only the egocentric one (i.e., Wang and Spelke, 2000) could support the updating of spatial representations during path integration. If different representations can be updated according to the task, the information needed for the reactions would be immediately available at the end of the passage. Otherwise, reactions based on allocentric parameters should be derived from the egocentric representation after the passage. Furthermore, dependent on the number of reference frames underlying navigation, a different influence of the presentation order of reaction formats (Experiment 1 vs. Experiment 2) on subjects' performances was expected. The experiment corroborated earlier findings (Gramann et al., 2005) that different reference frames can subserve path integration. More specifically, the analysis of behavioral data revealed the Turner group to employ different reference frames for the updating of distinct spatial representations in the two tasks. Moreover, the comparison of the two experiments showed this group to be able to update distinct representations in parallel if required by the task. The Nonturner group seemed to update the same allocentric representation in both tasks.

Chapter IV. The intention of the experiments in Chapter IV was to corroborate the results presented in the previous chapter focusing on the encoding of spatial information. To this end, the oscillatory behavior of low frequency bands (alpha and theta band) induced by the visual stimulation during the tunnel passage was analyzed. Oscillations within the two frequency bands were expected to allow for the monitoring of changes in mental effort with respect to material and task requirements (Bischof and Boulanger, 2003; Caplan et al., 2001) and to reveal the allocation of attentional resources with respect to different stimulus features (Klimesch, 1997). The experimental results did not supply direct insights into the mechanisms of egocentric and allocentric spatial updating, since no differences between strategy groups nor reaction formats were found. However, important evidences were gained from the comparison between the first and the second experiment. Increased mental effort in Experiment 2 compared to Experiment 1 did not reinforce the hypothesis of a unique reference system underlying path integration independent of the task to solve and consequently independent of the reaction format order. It is more likely that distinct reference systems subserved path integration during the computation of egocentric and allocentric representations. This result is in line with the hypothesis for Turners (Chapter III), showing this group to update a single representation according to the task in Experiment 1 but to update two separate representations for the two tasks in Experiment 2. On the contrary, the Nonturner group was not expected to demonstrate increased mental effort in the second as compared to the first experiment. The lack of any difference between strategy groups might suggest that Nonturners also updated different representations in the two reaction formats. At the end of the chapter, the possibility that reference frames different from the egocentric and allocentric ones exist was taken into consideration.

Chapter V. Whereas Chapter IV analyzed encoding features on the basis of induced EEG-oscillations, the present section focused on the processing and retrieval of spatial information at the end of the tunnel passage. By means of reaction times and event-related potentials, it was investigated whether subject’s reactions were based on parameters inherent to the spatial representation updated during the navigation or, alternatively, whether the reaction required the further processing of spatial information. The reaction time data revealed that the information needed for a reaction was directly retrieved from an allocentric or an egocentric representation updated during the passage, thus corroborating results from the behavioral data analysis. However, it was not possible to find convincing psychophysiological correlates for a direct retrieval of information from an egocentric or allocentric representation. One major problem for the analysis of the event-related potentials was the lack of prior knowledge relative to early phases of spatial information retrieval. However, a first contribution was provided with the present results identifying the P3-component as the first indicator of cortical activity associated with the retrieval of spatial information.

Chapter VI. The investigation presented in this chapter was designed in order to test the influence of subject's body position on navigation performance before a further study combining EEG and fMRI methods could be conducted. A major problem of this combined study might be the body orientation of subjects during the experiments: subjects are sitting in the EEG-experiment, whereas they are lying in the fMRI-experiment. Although Vidal and colleagues (2003, 2004) showed the subject's body position (sitting vs. lying) to affect path integration performance, the analyses of several behavioral measures in the present study did not reveal any influence of body position on subjects' performances and thus justified the use of the tunnel paradigm for fMRI measurements.

Conclusions

The investigations presented in this doctoral thesis supplied further evidence that both egocentric and allocentric reference frames support path integration for the updating of spatial representations. The particular reference frame employed depends on the nature of the task as well as on an individual preference.

One group of subjects, the Turner group, was able to adopt distinct reference frames for the computation of egocentric and allocentric representations. The spatial representation computed during the navigation included all the information needed for a reaction (Chapter III and Chapter V). When Turners knew the task to solve, they updated only a single representation according to the task (Chapter III: Experiment 1). Otherwise, more representations were updated in parallel as revealed by Turners' performances (Chapter III: Experiment 2) as well as by the increased mental effort in Experiment 2 as compared to Experiment 1 (Chapter IV).

Behavioral evidence (Chapter III and V) corroborated the hypothesis that the Nonturner group updated an allocentric representation to react in both tasks during navigation. The spatial information necessary to solve the tasks was directly retrieved from this representation and no further information-processing steps were required. However, the analysis of the oscillatory patterns during the encoding of spatial information (Chapter IV) did not confirm the use of the same reference frame independent of the task. Similarly to the Turners, this strategy group revealed increased cognitive effort in Experiment 2 compared to Experiment 1. The increased effort in Experiment 2 might indicate that also Nonturners adopted distinct reference frames in the different tasks and furthermore, that the two reference frames could be employed for the parallel updating of distinct representations. However, the existence of an additional reference frame cannot be demonstrated but only inferred on the basis of the current data. With this respect it can merely be argued that this reference frame supports the construction of an allocentric-like representation, where information about cognitive heading changes is not included.

In order to investigate the influence of distinct reference frames on spatial updating, the present research adopted some innovations with respect to earlier studies using the tunnel paradigm (Gramann et al., 2005, 2006). Firstly, a new reaction format requiring angular judgments within an allocentric reference frame was introduced. This task together with the homing-vector task previously employed by Gramann and colleagues (2005) allowed to compare spatial processing based on different reference frames not only using distinct groups of subjects (Turners and Nonturners) but also within the same subject group. With respect to this reaction format, there are several possible future developments. For example, it would be interesting to investigate allocentric information processing of naïve subjects that were not previously confronted with the elaboration of egocentric information in the homing vector format. In fact, in the present research the presentation order of the reaction formats was unbalanced: subjects were always trained with the homing vector format before they began with the actual experiment. Therefore, an influence of egocentric encoding on allocentric information processing cannot be excluded. Moreover, different reaction formats requiring the updating of allocentric information might be compared. Gramann (et al., 2005, 2006) already employed a reaction format forcing subjects to process allocentric information, the map-like reaction format. The main difference between the allocentric format presented here and the map-like format is that the latter format does not require angular adjustments only but also distance statements.

A further innovation of the present research was the adoption of instruction that allowed for the measurement of reaction times. This behavioral parameter was discovered to be very useful for gaining additional information about spatial processes taking place at the end of the passage. In particular, the reaction time analysis allowed to test whether subject's reactions were based on primitive parameter present in the spatial representation updated during the travel or, alternatively, a further processing of the information available was necessary.

Besides the paradigm changes reported above, this research introduced two EEG-methods for monitoring different cognitive processes. The analysis of induced oscillatory activity showed to be related to different aspects of spatial encoding. The theta band (4-6 Hz) proved to be a valid indicator of cognitive effort. Future study might corroborate the current evidence analyzing for example power modulations with respect not only to varying number of turns but also to varying tunnel length. The direction of the turns might also have an influence on task difficulty: the encoding of turns bending in the same direction might be less demanding as compared to the encoding of turns that run in opposite directions. The lower alpha band (8-10 Hz) reflects attentional processes with respect to the amount of information supplied by a stimulus. Thus, further studies might investigate in which way alpha desynchronization is related to the encoding of rotational and translational information, for instance, monitoring alpha modulation in relation to the curvature of a turn.

The analysis of event-related potential was supposed to supply insights into the neural processes supporting the retrieval of spatial information. However, this line of research did not prove to be very promising. There were two main obstacles. On the one side, the lack of prior knowledge about the retrieval of spatial information did not allow to define clear hypothesis. On the other side, the ERPs could be calculated only for a relative small number of epochs as compared to other ERP-studies, because of the quite long duration of each single trial without transient stimulus onsets. Furthermore, due to the long time of traversing through a tunnel passage only a relatively small number of trials could be recorded. This in turn led to a low signal-to-noise ratio for the resultant ERPs with uncertainties in the identification of

ERP-components on an individual level. Consequently, the ERP-based data-analyses (i.e., detection of peak latencies or peak-to-peak amplitudes) as well as the explanatory power of the data were severely restricted. Whereas the first issue can be overcome in future researches focusing on different aspects of the information to be retrieved (i.e., task difficulty, response accuracy, etc.), the second issue is inherent to the experimental paradigm and cannot be avoided.

Finally, the present thesis showed that the body position of a subject during the tunnel task does not influence his performance. This result justifies a combination of EEG and fMRI methods that require subjects to assume different positions. An EEG-fMRI study combines the high temporal resolution of the electroencephalography to the high spatial resolution of the functional magnetic resonance and could supply important insights into the dynamics of the neural networks underlying spatial navigation.

CHAPTER III

Evidence of different reference frames subserving path integration

Abstract

The present study investigated information processing underlying spatial navigation. After the passage through virtual tunnels subjects were asked to indicate their momentary position by adjusting one of two reaction formats. The 'homing vector format' allowed subjects to react based on an ego- or alternatively allocentric reference frame. Two groups of subjects performed this task differently: 'Turners' adjusted the homing vector as if they had updated their cognitive heading during turns, whereas 'Nonturners' did not. The second reaction format, the 'start-to-end format' required subjects to react based on an allocentric reference frame. Whereas in a first experiment the reaction formats were blocked, in a second experiment they were randomized and unpredictable on a trial. The behavioral-data analysis revealed Turners to adopt an egocentric perspective for reactions with the homing vector format. In the same format, Nonturners reacted based on an allocentric reference frame. In the start-to-end format, both strategy groups adopted an allocentric reference frame for their reactions. In the first experiment, only one reference frame was active at one time according to subject's preference. In the second experiment, Turners adopted more reference frames in parallel whereas Nonturners used an allocentric frame of reference only.

Introduction

Loomis, Klatzky, Golledge, and Philbeck (1999) described path integration as a navigation process by which traveler's translations and rotations are integrated over time in order to update position and orientation within a larger spatial framework. The sensory information required by path integration for the updating of a coherent environmental representation is gained from different sensory systems (Chance, Gaunet, Beall, & Loomis, 1998; Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Bakker, Werkhoven, & Passenier, 1999; Kirschen, Kahana, Sekuler, & Burack, 2000) and is more generally categorized into internal and external information (Mittelstaedt & Mittelstaedt, 1982). During navigation in real environments, both kinds of information are usually present and contribute to path integration. However, single information sources can also be sufficient for spatial updating, e.g. studies showed that optic flow alone can support path integration (Gramann, Muller, Eick, & Schonebeck, 2005; Riecke, van Veen, & Bulthoff, 2002).

Frames of reference. Successful updating of a spatial representation requires the integration of sensory information with respect to a reference system (Loomis et al., 1999; Kerkhoff, 2000). Klatzky (1998) defined a reference frame as 'a means of representing the locations of entities in space' (p. 1). In the literature about spatial behavior, two distinct reference frames are usually supposed to underlay human navigation, the allocentric and the egocentric reference frame. An allocentric frame of reference consists of an origin and a reference direction external to the navigator. In the egocentric reference frame, the navigator represents the origin of the system and his axis of orientation defines the reference axis. The use of one or the other reference frame determines the nature of the parameters – values associated to individual entities in space – conveyed in the spatial representation (Klatzky, 1998).

As all the information processed by path integration is perceived from a first person perspective, an egocentric reference system has to be active for the processing of incoming information. However, the same reference frame is not necessarily employed for the further integration of information into a spatial representation. In fact, during navigation the egocentric information might be transferred into an allocentric frame of reference for the updating of an allocentric representation. With this respect, there is a lack of consensus in the literature. Several studies supposed path integration to rely exclusively on an egocentric reference frame (Shelton & McNamara, 1997; Wang & Simons, 1999; Wang & Spelke, 2000). However, other investigations showed an influence of allocentric information supplied during the task on subject's reactions (Burgess, Spiers, & Paleologou, 2004; Mou, McNamara, Valiquette, & Rump, 2004) indicating that also an allocentric reference system might be employed for the updating of a spatial representation. Burgess (2006) supposed egocentric and allocentric spatial representations to exist in parallel within a two-system spatial model.

Several studies focusing on individual differences in spatial tasks (Denis, Pazzaglia, Cornoldi, & Bertolo, 1999; Jordan, Schadow, Wuestenberg, Heinze, & Jaencke, 2004; Lawton, 1996; Pazzaglia & Beni, 2001) revealed the spatial representations to be influenced by the spatial strategy that subjects preferred. Common to the cited papers is the distinction between an egocentric and an allocentric reference system. In these investigations the presence of landmarks in the environment allowed for the employment of alternative navigation strategies different of path-integration (i.e., piloting).

Importantly, in a pointing task after passages through virtual tunnels, Gramann and colleagues (2005) showed two groups of subjects to prefer the use of either an egocentric or an allocentric reference frame for their reactions. As no landmark information was given during the tunnel passage, the only suitable spatial process in this case was path-integration. One group of subjects, referred to as ‘Turner’, preferentially used an egocentric reference frame in which egocentric bearing from the origin of the tunnel was updated during stimulus turns and following translations (Figure 3.1). A second group of subjects, ‘Nonturner’, did not integrate heading changes in the resultant spatial representation that was used for the response and thus systematically overturned the homing vector by the amount of the angle of turns during the passage (Gramann et al., 2005; Gramann, Müller, Schonebeck, & Debus, 2006). The Nonturner group was supposed to employ an allocentric reference frame.

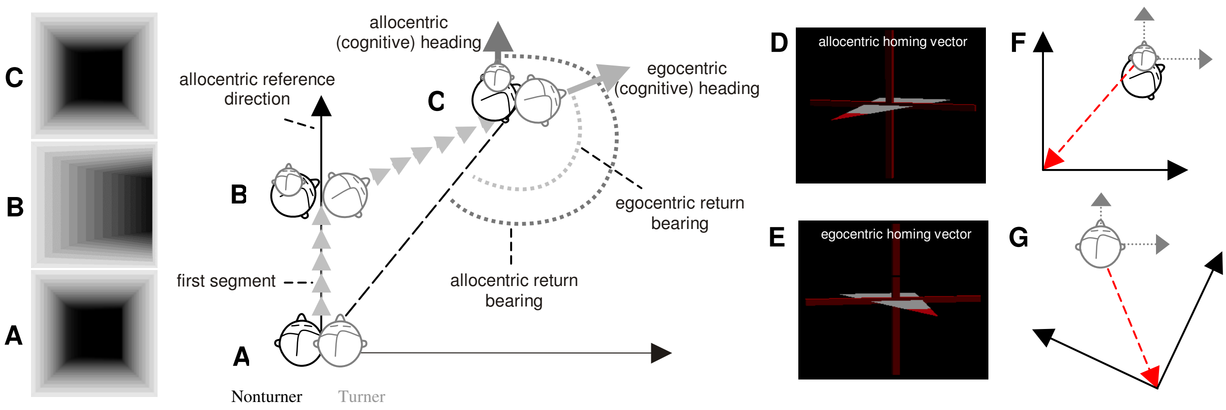

Figure 3.1. Depiction of a passage through a tunnel with a turn to the right. The most left column displays the navigator’s view into (A) the first straight segment, (B) a segment with a turn to the right, and (C) a straight segment after the turn. The second left column displays a Nonturner (dark grey head representing the perceived heading and the small light grey head representing the cognitive heading) using an allocentric frame of reference, with the navigator's heading during (A) the first straight segment, during (B) the turn, and during (C) the straight segment after the turn. Note that the perceived and the cognitive heading diverge during the turn. On the right, a Turner (light grey head representing the perceived cognitive heading which is assumed to be identical to the cognitive heading) is displayed who uses an egocentric frame of reference. During the first segment (A), the Turner's heading is the same as that of a Nonturner. During the turn (B), the axis of orientation changes. At the end of the tunnel, the Turner's cognitive heading is different from that of a Nonturner. Note that Turner builds up an additional allocentric frame of reference if they are forced to react based on an allocentric frame of reference. There is no depiction of an additional allocentric reference frame for Turner to emphasize the preferred use of an egocentric frame of reference by this strategy group. To the right-side of the figure, examples of homing vectors are displayed with the correct angular adjustment for a tunnel with one turn of 60° to the right, with panel D depicting the correct homing vector for Nonturner, and panel E that for Turner. The most right column displays (F) the coordinate system underlying the allocentric cognitive heading (grey dotted arrows) and the coordinate system of the video display (black solid arrows) and (G) the coordinate system underlying the egocentric cognitive heading (grey dotted arrows) and the coordinate system of the video display (black solid arrows).

Configural or history-free representation. Despite the kind of reference frame applied to update the navigator's position, the question remains what kind of information is included in a spatial representation built up by path integration. May and Klatzky (2000) compared two different kinds of representation. The first describes a "history-free" representation (Fujita, Klatzky, Loomis, & Golledge, 1993) in which only the turn and the distance necessary to point back to the origin were present. In this case path features (i.e., length, number of segments, etc.) should have little influence on the accuracy of the representation and no effect on reaction times. Alternatively, the "configural model" assumes that the whole path is implemented in the spatial representation and the response in a path completion task would be computed only at the end of the path (May & Klatzky, 2000). In this case, path complexity would be expected to influence accuracy as well as RTs. Previous results by Gramann (et al., 2005) supported the configural coding model at least for Turners, using an egocentric frame of reference: Turners were influenced by tunnel complexity (number of turns). By contrast, Nonturners' performance, based on an allocentric frame of reference, did not supply enough evidence to refuse the history-free model; the latter strategy group was affected only marginally by the number of turns.

Aims of the present study. The present study tested whether distinct reference frames can be used for path integration and, further, whether only one or more than one reference frame can be used in parallel. The use of a reference frame determines the type of the information (primitive parameters) implemented in the spatial representation employed to react (Klatzky, 1998). If only one of the two reference frames can be adopted during path integration and the reaction format requires the subject to react based on a different frame of reference, the parameters necessary for the reaction have to be re-computed. This process of re-computation requires time and processing resources and thus leads to prolonged RTs and reduced reaction accuracy.

To test the hypotheses, the tunnel paradigm (Gramann et al., 2005) was adopted using two different reaction formats. In a homing vector format (HVF) subjects had to indicate the starting position of the passage relative to their current position at the end of the tunnel. In this reaction format, Nonturners were expected to adopt an allocentric reference frame whereas Turners were expected to use an egocentric frame of reference (Gramann et al., 2005). In a second reaction format, the start-to-end format (SEF), subjects had to adjust the arrow so that it pointed from the starting point of the tunnel to their current position at the end of the passage. For both reaction formats identical tunnel trials were used. In contrast to the HVF, the SEF required subjects to update their own position with respect to an external reference axis and thus could be solved only based on an allocentric frame of reference. RTs and pointing accuracy for the two reaction formats were compared across and within the strategy groups. In the case that only an egocentric spatial representation was computed during path integration (Wang & Spelke, 2000), Turners were expected to react faster and more accurately in the HVF, because this is solvable by means of the preferred egocentric representation, as compared to the SEF that requires an allocentric reference frame. Similarly, since Nonturners always react based on an allocentric reference frame, they are supposed to react slower and less accurate than Turners in the HVF, independent from the reaction format.

In the first experiment, distinct spatial representations were investigated by means of blocked reaction formats. In a second experiment, the issue was addressed whether or not more spatial representations can be processed in parallel. For this purposes, the two reaction formats (HVF and SEF) were presented in a random order with reaction format unpredictable on a trial. Whereas in the first experiment Turners could process only an ego- or an allocentric representation according to the task to solve, the random sequence in Experiment 2 forced Turners to process ego- and allocentric information at the same time. Nonturners, by contrast, were supposed to update both reaction formats based on the same allocentric reference frame and, consequently, were not expected to be affected by the experimental modification.

Finally, the analyses allowed for a test of the configural vs. history free model assumptions, i.e., whether the whole outbound of the traversed path (configural model) or, alternatively, only length and direction of a homing vector (history-free model) is represented. Turners were supposed to adopt a configural model (See Gramann et al., 2005) when employing an egocentric reference frame. Since Turners were not adequately tested in an allocentric reference frame before, it is not possible to formulate any hypothesis. With respect to the Nonturner group there is not enough evidence to refuse the history-free model.

EXPERIMENT 1

Method

Subjects

19 healthy volunteers aged between 21 and 33 years (X=23.8, SD=3.6 years) were selected to take part in the experiment. All subjects with normal or corrected-to-normal vision were financially compensated for their participation. Three participants were left-handed. Due to prior findings in the literature, handedness was not considered a decisive factor (Postma et al., 2004). Due to gender-specific differences in performing way-finding task (Lawton & Morrin, 1999), only male participants were included. Out of 27 participants that were categorized, nine Nonturners and ten Turners were selected.

Task, Material, and Procedure

Subjects were seated in a darkened room in order to eliminate additional reference information. The task was presented with a beamer (Sanyo PLCXU-47) on a screen positioned at a 1,5 meter distance from the subject. Prior to the main experiment, subjects were categorized with respect to their preferential use of an allo- or egocentric reference frame, respectively (Gramann et al., 2005). In a subsequent training, participants became familiar with the task: the tunnels used in the training session were the same as in the main task but subjects always received strategy-specific feedback about their pointing accuracy.

In the main experimental session, subjects had to maintain orientation during the simulation of passages through virtual tunnels. The first and the last segment of each passage were always straight, all tunnels were of constant length (5 segments), and included one or two turns of varying angles (between 10° and 90°). Each tunnel had a turn in the second segment. Half of the tunnels had one additional turn prior to the last segment. Tunnels ended at eccentricities of 15°, 30°, 45°, and 60° on either side of the starting point. Overall, a total number of 160 trials were tested with 40 additional tunnels consisting of 3 straight segments serving as baseline trials for electrophysiological measures not reported here.

Trials started with a fixation cross shown for 500 ms followed by a picture of the tunnel entrance shown for 500 ms. Then the virtual journey began. At the end of each tunnel, the view out of the last segment was shown for 500 ms followed by the reaction format. Subjects' performance was tested in two reaction formats, the HVF and the SEF. In the HVF, subjects were asked to adjust an arrow from the tunnel end-position back to the origin of the passage. In the SEF, subjects were required to adjust a response arrow pointing from the origin of the tunnel passage to the end point of the passage. In the first experimental block, only the HVF was used whereas in the second experimental block the SEF was employed. The same material was used in both experimental blocks.

Performance measure

Side errors. Similar to previous works (Gramann et al., 2005), an important criterion regarding correct reactions were valid indications of the side of the tunnel's start position (left or right) relative to the tunnel's end-point (HVF) or, alternatively, by correctly indicating the side of the tunnel's end point relative to the starting point in the SEF. Side errors might reflect random errors due to a lack of attention or a total loss of orientation. However, previous experiments showed that the amount of side-errors systematically varied with specific tunnel features dependent on the strategy used. Side errors were analyzed separately and eliminated from further analysis.

Format errors. This measure was used for the first time due to the necessity of distinguishing errors that resulted from a confusion of the two reaction formats. Given that the eccentricity of tunnel's end positions varied between 15° and 60° on each side relative to the origin, any reaction corresponding to end positions greater than 90° was considered to be a format error. Format errors might either reveal a complete loss of orientation, as in the case of the side errors, or confusion between reaction formats. Format errors were analyzed separately and eliminated from further analysis.

Angular fit. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions provided a measure of the subject's ability to discriminate among varying eccentricities.

Absolute error. The absolute error was defined as the absolute difference between the subject's adjustment and the expected reaction. It supplied a valid measure of reaction accuracy.

Reaction times. To measure reaction times (RTs), the delay between the onset of the response arrow and the subject's response was computed.

Results

Side errors

Overall, the percentage of side errors was 6.09% with Turners demonstrating a higher percentage of side errors (7.31% and 4.72% for Turners and Nonturners, respectively). To further analyze the influence of the reaction format and the number of turns on the strategy groups' performance, a mixed design ANOVA was conducted with 'preferred strategy' (Turner vs. Nonturner) as between-subject factor and 'reaction format' (HVF vs. SEF) as well as 'number of turns' (1 or 2 turns) as repeated measures. The percentage of side errors was used as dependent variable.

The results revealed the main effects of 'number of turns' and 'reaction format' to reach significance ([$F(1,17)=26.075$; $p<.001$; $eta^2 =.605$] and [$F(1,17)=29.502$; $p<.001$; $eta^2 =.634$], respectively). These main effects were qualified by (tendentially significant) interactions of the factors 'number of turns' x 'strategy' [$F(1,17)=4.1704$; $p<.057$; $eta^2 =.197$] and the higher order interaction of all three factors [$F(1,17)=3.4100$ $p<.082$; $eta^2 =.167$] (Figure 3.2).

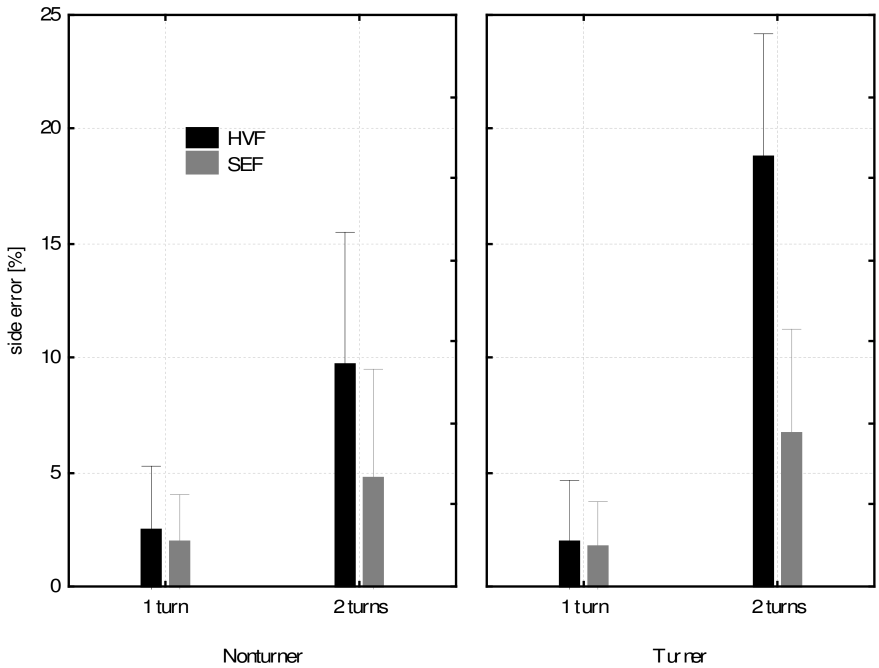

Figure 3.2. Percentage of side-errors (± 1 standard error) for Nonturners (left panel) and Turners (right panel) as a function of reaction format (black bars for the HVF and grey bars for the SEF) and number of turns (1 or 2 turns, on the x-axis).

For tunnels with one turn, subjects committed very view side errors (less than 3%) irrespective of the required reaction format. Using the HVF, both strategy groups revealed less side errors for tunnels with one turn compared to tunnels with two turns (HSD: $p<.001$ and $p<.040$ for Turners and Nonturners, respectively). In contrast, the differences between tunnels with one and tunnels with two turns did not reach significance in the SEF. Finally, Turners revealed a higher percentage of side errors for tunnels with two turns when a homing vector had to be adjusted compared to the adjustment of the SEF (HSD: $p<.001$). For Nonturners, no differences in the percentage of side errors dependent on the reaction format were revealed (HSD: all $p>.27$).

Format errors

Format errors (less than 0.6%) were too few and thus no further statistical analyses were computed. Small numbers of format errors were observed under all experimental conditions for both strategy groups.

Angular fit

The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions revealed a significant positive relationship for both Nonturners [r(1363)=.985; p<.010] and Turners [r(1475)=.989; p<.010]. Both strategy groups revealed high positive correlations in the HVF ([r(675)=.992; p<.010] and [r(715)=.997; p<.010] for Nonturners and Turners, respectively) as well as in the SEF ([r(688)=.916; p<.010] and [r(760)=.874; p<.010] for Nonturners and Turners, respectively). Both strategy groups solved tunnels with one turn with high accuracy (Nonturners [r(701)=991; p<.010] and Turners [r(781)=993; p<.010]) and this was the same for tunnels with two turns (Nonturners [r(662)=980; p<.010] and Turners [r(694)=985; p<.010]).

Absolute error

A mixed design ANOVA was performed with ‘preferred strategy’ (Turner, Nonturner) as between-subject factor and ‘side of end-position’ (left, right), ‘reaction format’ (HVF, SEF), ‘number of turns’ (1 or 2 turns), and ‘eccentricity of end-position’ (15°, 30°, 45°, 60°) as repeated measures. Greenhouse-Geisser correction was applied if necessary.

Overall, higher absolute errors for Turners as compared to Nonturners resulted in a strong tendency for significance [F(1,17)=4.333, p<.053; eta^2=.203] with Turners and Nonturners revealing 13.15° and 14.98° deviation from the expected angular adjustments. Increasing complexity of the traversed passage resulted in increased absolute errors (main effect 'number of turns' [$F(1,17)=33.868$, $p<.001$; $eta^2=.666$]). The additional main effect of 'eccentricity of end-position' [$F(3,51)=4.651$, $p<.014$; $eta^2=.215$] replicated previous results demonstrating increasing absolute errors with increasing eccentricity of end position. Finally, the main effect of 'reaction format' [$F(1,17)=31.699$; $p<.001$; $eta^2=.651$] revealed higher absolute errors for the SEF (15.46°) as compared to the HVF (12.68°). Due to the high number of significant interactions, the following results focus on the factors directly associated with the questions regarding the number of spatial representations being active during spatial orienting (as reflected by the factor reaction format) and the model (configural or history-free) for the respective representation (as reflected by the number of turns) dependent on the strategy used during the task.

The interaction 'reaction format' x 'preferred strategy' [$F(1,17)=50.03$, $p<.001$; $eta^2=.746$] as well as 'reaction format' in interaction with 'number of turns' revealed a tendency to have an influence on the absolute error [$F(1,17)=4.04$, $p<.061$; $eta^2=.192$]. These effects were qualified by the interaction of all three factors [$F(1,17)=6.78$, $p<.019$; $eta^2=.285$].

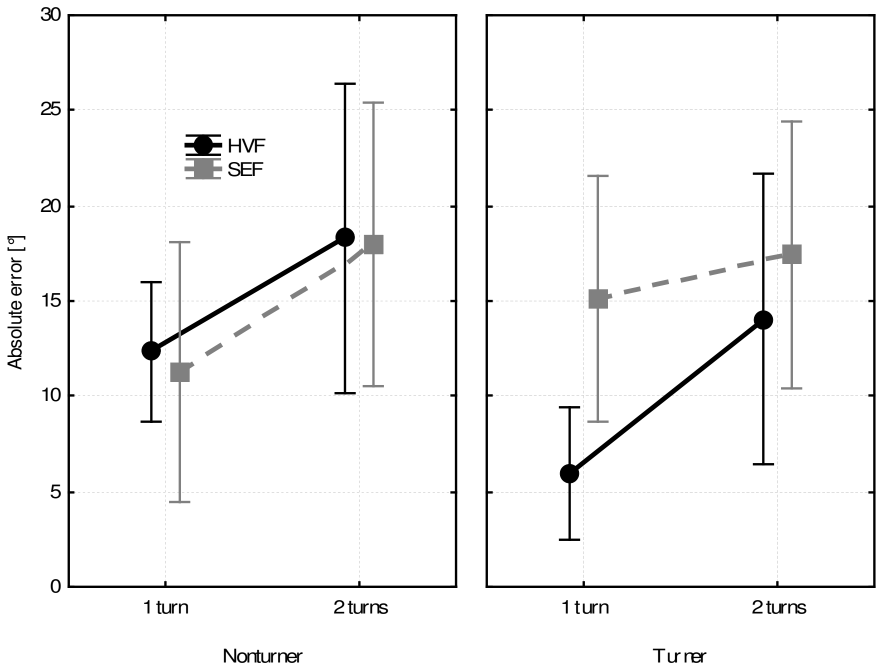

Figure 3.3. Mean absolute error (± 1 standard error) for Nonturners (left panel) and Turners (right panel) as a function of reaction format (continuous line for the HVF and dashed line for the SEF) and number of turns (1 or 2 turns).

As can be seen from Figure 3.3, Nonturners demonstrated comparable absolute errors for both reaction formats with increasing errors for more complex tunnel passages. In contrast, Turners revealed comparable absolute errors for both reaction formats only in the case of tunnels with two turns. For less complex tunnel passages, this strategy group was significantly more accurate when the HVF had to be adjusted ($p<.001$). Thus, Turners demonstrated significantly more accurate angular adjustments for tunnels with one turn when the HVF was used as compared to all other conditions with no difference for the latter ($p>.18$).

Reaction times

Prior to RT data analysis, trials with reaction times outside the range of two standard deviations from the mean were removed from the data set for each individual subject. On the remaining correct trials, a mixed-design ANOVA was conducted with ‘preferred strategy’ as between-subject factor and ‘reaction format’ and ‘number of turns’ as repeated measures. Neither the preferred strategy [$F(1,17)=.004$, $p<.951$; $eta^2=.001$] nor the reaction format [$F(1,17)=1.028$, $p<.325$; $eta^2=.057$] revealed any influence on RTs. Both strategy groups reacted relatively fast and showed no RT differences in reacting to the HVF (935.78 ms and 1093.72 ms for Turners and Nonturners, respectively) as compared to the SEV format (887.92 ms and 763.30 ms for Turners and Nonturners, respectively). However, there was a strong tendency for longer RTs for tunnels with two turns (X=967.42, SD=625.44 ms) as compared to tunnels with only one turn (X=872.07, SD=524.48 ms) [$F(1,17)=3.7137$, $p<.071$; $eta^2=.179$]. There were no further effects.

Discussion

In accordance with earlier investigations using the tunnel paradigm (Gramann et al., 2005; Gramann et al., 2006), the results of the first experiment confirmed that pure visual flow information is sufficient for spatial updating. This was demonstrated by the relatively small number of side errors and the high angular fit obtained for both strategy groups, irrespective of the complexity of the tunnel passage and the frame of reference used for adjusting distinct reaction formats. Both strategy groups demonstrated a stable use of their preferred reference frame during the first block of the experiment, as indicated by the high positive interrelation of expected and actual angular adjustments. During the second block of the experiment both strategy groups revealed comparable pointing accuracy, based on an allocentric reference frame.

The aim of the first experiment was to determine whether subjects are able to use distinct reference frames during path integration dependent on the reaction format given at the end of a trial. The results revealed comparable RTs for both strategy groups, independent of the reference frame underlying the reactions.

Comparable RTs for reactions based on distinct reference frames across and within strategy groups strongly support the assumption that subjects are able to use either an egocentric reference frame or an allocentric reference frame during path integration. Thus, the results failed to confirm Wang's and Spelke's hypothesis (2000), that path integration is supported only by an egocentric reference frame. Nonetheless, it might be possible that only an egocentric representation was built up during path integration and that an allocentric representation was derived at a later stage in the tunnel passage but before the response prompt (e.g., during the last straight segment). Such a re-computation of allocentric parameters from primitive parameters of an egocentric representation should be reflected in higher errors or at least more variance in the angular adjustments.

However, the analysis of adjustment errors further supported the assumption that distinct reference frames can be used during path integration. The percentage of side errors did not completely follow the prediction that Nonturners used the same allocentric reference frame as the basis for their angular adjustments, irrespective of the reaction format. In fact, this strategy group showed slightly increased losses of orientation with increasing path complexity in the HVF but not in the SEF. Nevertheless, no format dependent differences achieved significance and Nonturners' percentage of side-errors was reduced compared to Turners' side errors percentage. Importantly, Turners, preferentially using an egocentric reference frame, showed no decline in accuracy for reactions based on an allocentric reference frame. Instead, this strategy group demonstrated improved performance as indicated by a significant decrease in the percentage of side errors. One draw-back of the present investigation was the presentation order of the two reaction formats with the SEF being always presented in a second block after the HVF. Thus, any effect of the reaction format on the percentage of side errors might be rather a consequence of a practice effect. In order to see whether training effects took place, each experimental block (HVF and SEF) was divided into successive time intervals. For each interval, the percentage of side errors was computed. The presence of a practice effect should be evident not only in the comparison between the first and second experimental block but also within each experimental block. The percentage of side errors did not decrease over the course of the experiment in neither reaction format, disproving thus the presence of a practice effect.

The pattern of absolute errors lends further support to the assumption that subjects are able to compute distinct frames of reference during path integration. As expected, Nonturners showed comparable adjustment errors for both reaction formats with decreasing accuracy for increasing complexity of the tunnel passage. This error pattern supports the assumption that Nonturners use an allocentric reference frame to adjust homing vectors as well as start-to-end vectors. Increasing errors with increasing number of turns thus reflect a general loss of spatial accuracy with increasing complexity of the passage during path integration based on an allocentric reference frame. In contrast, Turners revealed the highest accuracy in angular adjustments for tunnels with one turn as compared to more complex tunnels or the use of an allocentric reference frame. Differences between the reaction formats for less complex tunnels but comparable accuracy for tunnels with two turns make it unlikely that the start-to-end vector was re-computed from some egocentric representation. The additional transformation should have led to a significant increase in absolute error in both conditions. However, when Turners used an allocentric reference frame for their reaction no influence of task complexity was observed. This supports the assumption that Turners used two distinct reference frames in the two experimental blocks.

The last question of the first experiment concerned the nature of the representation that could be based on a configural or, alternatively, on a history-free model (May & Klatzky, 2000). In this experiment, RTs were affected by the number of turns and were independent of other variables, i.e. reaction format and preferred strategy. This provides a first evidence that both strategy groups used a configural model to answer the HVF as well as the SEF. This is further supported by angular adjustments of the strategy groups with tunnel complexity influencing subjects' angular accuracy. Turners' and Nonturners' accuracy in the HVF was affected by the number of turns as reflected in the percentage of side errors and the degree of absolute errors. Path complexity also influenced Turners' and Nonturners' performance in the SEF. Both strategy groups were more accurate for less complex passages even though Turners revealed no significant differences between tunnels with one or tunnels with two turns when they used an allocentric reference frame for their reaction.

In the first experiment, the blocked presentation of reaction formats allowed subjects to construct and employ one spatial representation at one time. The question whether or not more representations can co-exist in parallel was addressed in the second experiment, with reaction formats presented in a random sequence and unpredictable on a trial.

EXPERIMENT 2

Method

Subjects

18 healthy volunteers aged between 20 and 35 years (X=25.2, SD=3.8 years) were selected to take part in the experiment. All subjects with normal or corrected-to-normal vision were financially compensated for their participation. All but one

participant were right-handed. From all participants categorized, nine Nonturners and nine Turners were selected to take part in the main experiment. Different subject pools were employed in the two experiments.

Task, Material, and Procedure

The experimental design stayed unaltered with the exception of the presentation order regarding the reaction format: whereas in the first experiment the presentation order of the reaction formats was blocked, here the sequence of reaction formats was randomized. At the end of each tunnel, one of the two reaction formats appeared unpredictable on a trial. An additional albeit minor change with respect to the previous experiment was the number of tunnels with two turns. The first experiment was equally divided into tunnels with one or two turns. In the present experiment, two-third of the tunnels had two turns. However, only the proportion changed and not the kind of tunnels included in the task.

Therefore, the current experimental design included the following factors: 'side of end-position' (left or right with respect to the starting point), 'reaction format' (HVF, SEF), 'number of turns' (1 or 2 turns), and 'eccentricity of end-position' (15°, 30°, 45°, and 60°). There were 10 trials for each combination of 'side of end-position' x 'reaction format' x 'eccentricity of end-position' for tunnels with two turns resulting in a total of 160 trials as well as 5 trials for each combination of the same 2 x 2 x 4 factorial design regarding tunnels with one turn adding up to a total of 80 tunnels. 20 filler trials with straight and curved segments were added. The filler trails should increase material variability.

Results

Side Errors

Overall, the percentage of side errors was 5.48% with Turners demonstrating a higher percentage of side errors (6.97% and 3.99% for Turners and Nonturners, respectively). To further analyze the influence of reaction format and number of turns on the percentage of side errors, a mixed-design ANOVA was conducted with 'preferred strategy' as between-subject factor and 'reaction format' and 'number of turns' as repeated measures. The results revealed the main effects of 'preferred strategy' [$F(1,16)=5.36$; $p<.014$; $eta^2=.252$] and 'number of turns' [$F(1,16)=24.22$; $p<.001$; $eta^2=.602$] to be significant. These were qualified by the tendentially significant interaction of both factors ('preferred strategy' x 'number of turns': $F(1,16)=3.8361$, $p<.068$; $eta^2=.193$) (Figure 3.5).

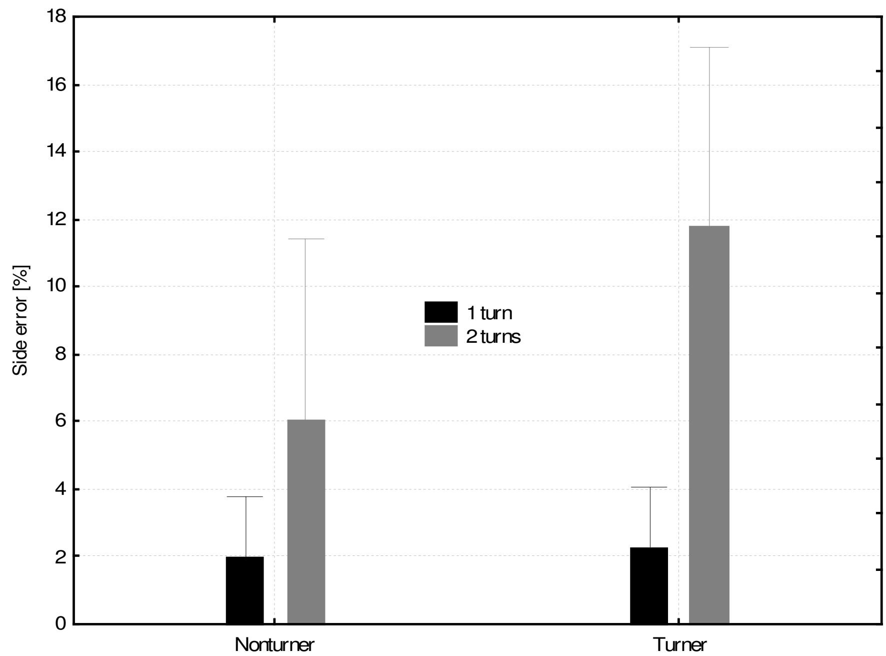

Figure 3.5. Percentage of side-errors (± 1 standard error) for Nonturners (left) and Turners (right) as a function of the number of turns (black and grey bars for tunnels with 1 and 2 turns, respectively).

Turners showed a higher percentage of side errors for tunnels with two turns as compared to tunnels with one turn (HSD: $p<.001$). In addition, the percentage of side errors was higher for Turners compared to Nonturners for tunnels with two turns (HSD: $p<.030$) but there were no differences between the strategy groups for tunnels with only one turn (HSD: $p<.999$). For Nonturners, the percentage of side errors was comparable for tunnels with one and tunnels with two turns (HSD: $p<.197$).

Format Errors

Format errors (less than 1.7%) were too few and thus no further statistical analysis was conducted. Small numbers of format errors were observed over all experimental conditions and for both strategy groups.

Angular Fit

The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions revealed a significant positive relationship for both Nonturners [$r(2013)=.985$; $p<.010$] and Turners [$r(1947)=.988$; $p<.010$]. Both strategy groups revealed high positive correlations in the HVF ([$r(994)=.992$; $p<.010$] and [$r(960)=.995$; $p<.010$] for Nonturners and Turners, respectively) as well as in the SEF ([$r(1019)=.898$; $p<.010$] and [$r(987)=.870$; $p<.010$] for Nonturners and Turners, respectively). Both strategy groups solved tunnels with one turn with high accuracy (Nonturners [$r(690)=989$; $p<.010$] and Turners [$r(697)=.993$; $p<.010$]), which was the same for tunnels with two turns (Nonturners [$r(1323)=.983$; $p<.010$] and Turners [$r(1250)=.986$; $p<.010$]).

Absolute Error

A mixed design ANOVA with ‘preferred strategy’ as between-subject factor and ‘side of end-position’, ‘reaction format’, ‘number of turns’, and ‘eccentricity of end position' as repeated measures was conducted for the absolute error. Greenhouse-Geisser correction was applied, if necessary.

Overall, the main effect of 'reaction format' [$F(1,16)=6.408$, $p<.022$; $eta^2=.286$] revealed higher absolute errors for the SEF (15.43°) as compared to the HVF (13.83°). Increasing complexity of the traversed passage resulted in increased absolute errors (main effect 'number of turns' [$F(1,16)=20.925$, $p<.001$; $eta^2=.567$]) with 12.86° deviation from the expected angular adjustment for tunnels with one turn and 16.41° for tunnels with two turns. Finally, the main effect of 'eccentricity of end-position' [$F(3,48)=8.825$, $p<.002$; $eta^2=.355$] replicated previous results demonstrating increasing absolute errors with increasing eccentricity of end position. Like Experiment 1, only results focusing on the factors directly associated with the number of spatial representations being active during spatial orienting (as reflected by the factor reaction format) as well as with the model for the respective representation (as reflected by the number of turns) dependent on the strategy used during the task will be shown.

Figure 3.6 displays the interaction 'reaction format' x 'preferred strategy' [$F(1,16)= 22.056$, $p<.001$; $eta^2=.580$]. Nonturners demonstrated comparable absolute errors for both reaction formats. Turners revealed significantly more accurate adjustment in the HVF compared to the SEF ($p<.001$) as well as compared to Nonturners in the HVF ($p<.027$).

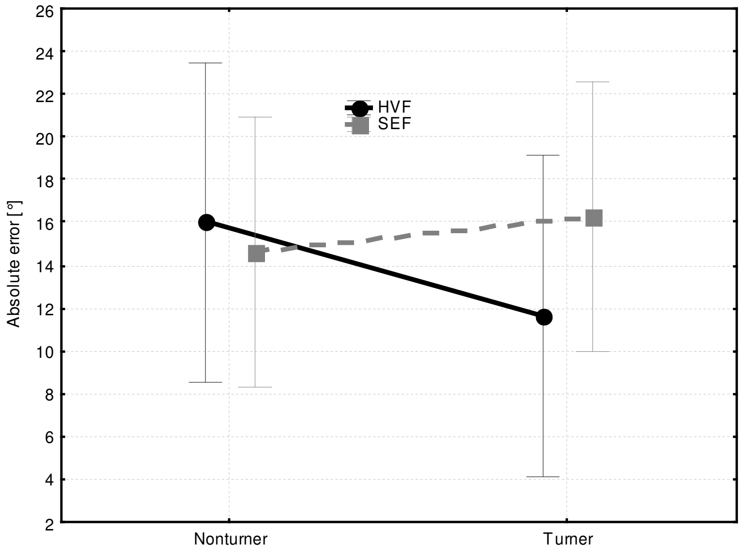

Figure 3.6. Mean absolute error (± 1 standard error) for Nonturners (left) and Turners (right) as a function of reaction format (continuous line for the HVF and dashed line for the SEF).

Reaction times

Prior to RT data analysis, trials with reaction times outside the range of two standard deviations from the mean were removed from the data set for each individual subject. Overall, RTs were higher as compared to Experiment 1 with 1681.8 ms and 1716.16 ms for Turners and Nonturners, respectively. A mixed-design ANOVA for RTs with 'preferred strategy' as between-subject factor and 'reaction format' and 'number of turns' as repeated measures revealed two main effects. The 'number of turns' [$F(1, 16)=14.894$, $p<.001$; $eta^2=.482$] revealed a strong tendency for longer RTs for tunnels with two turns (X = 1736.05, SD = 647.7 ms) as compared to tunnels with only one turn (X = 1627.55, SD = 622.28 ms). The main effect of 'reaction format' [$F(1, 16)=4.7747$, $p<.044$; $eta^2=.230$] was qualified by the interaction 'reaction format' x 'preferred strategy'' [$F(1, 16)=5.5467$, $p<.032$; $eta^2=.257$]: Turners reacted faster in the SEF (X=1472.76, SD=559.45 ms) compared to the HVF (X=1890.85, SD=788.63 ms) [HSD: $p<.025$]. In contrast, Nonturners revealed comparable RTs in both reaction formats (Figure 3.4). No differences between strategy groups reached significance (HSD: $p<.974$ and $p<.937$ for reactions in the HVF and SEF, respectively).

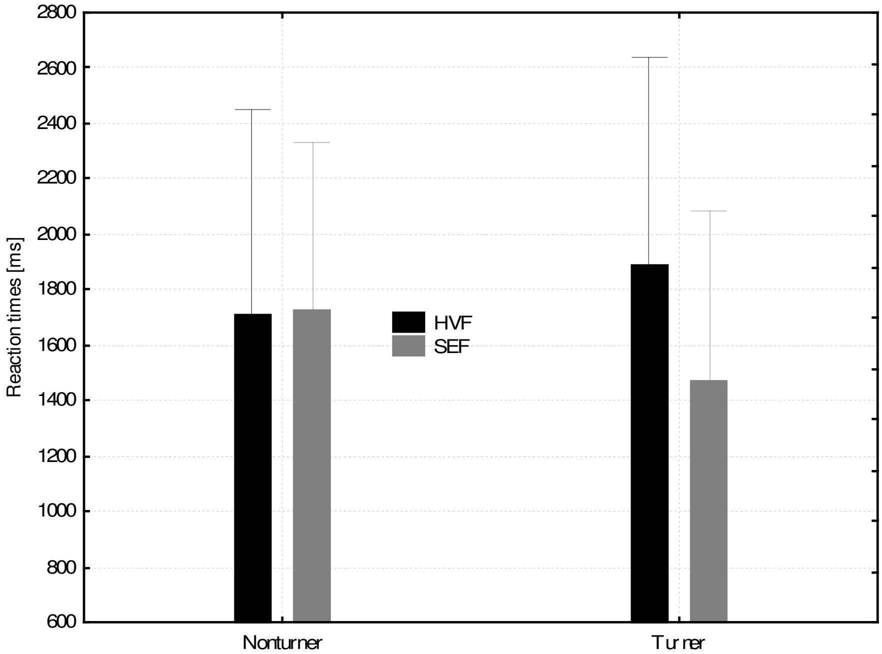

Figure 3.4. Mean reaction times (± 1 standard error) for Nonturners (left) and Turners (rights) as a function of reaction format (black bars for the HVF and grey bars for the SEF).

Discussion

In Experiment 2, the presentation order of the reaction formats was randomized and subjects were not informed about the expected reaction until the end of the passage. This modification allowed to test whether subjects were able to build up two spatial representations in parallel from sparse visual flow. The behavioral data supplied evidence that both strategy groups were able to solve both reaction formats with high accuracy as indicated in the high angular fit and small absolute errors. The question remained open whether or not the representations employed in the two formats were updated in parallel. Alternatively, only one representation might be constructed online while a further representation would be elaborated offline at the end of each passage when required by the reaction format. In the latter case, slower

RTs and less accurate adjustments for the derived representation would be expected.

The experimental evidences supported the first hypothesis. The analysis of error measures supplied evidence that Turners could process and use two distinct representations in parallel. Turners' accuracy in the HVF was higher than in the SEF. In this case either the representations used in the two formats were distinct and the accuracy differences were due to distinct characteristics inherent to the representations or, alternatively, the representation applied in the SEF was derived from the egocentric representation used in the HVF. In the latter case we should expect shorter RTs for reactions based on an egocentric representation. This was clearly not the case. In fact, Turners' reactions were faster in the SEF than in the HVF. Nonturners presented in the two reaction formats similar error patterns with respect to the side-errors as well as to the absolute error, thus confirming the employment of the same spatial representation in both tasks.

Finally, the fact that tunnel complexity influenced RTs of both strategy groups, irrespective of the reaction format that was used, supports the idea that the spatial representation computed during path integration represents some kind of configural model. Moreover, the configural model predicts that tunnel complexity influences not only RTs but also reaction accuracy, as actually revealed in this experiment by decreasing pointing accuracy for increasing tunnel complexity (number of turns) independent of reaction format and subject's preferred strategy.

General Discussion

Gramann and colleagues (2005) showed that accurate spatial representations can be built up during path integration based on an allocentric or an egocentric reference frame with sparse optic flow as exclusive source of information. Their experiments also supplied evidences that distinct representations co-exist in parallel. The present study provided additional evidence for the existence of more than one spatial representation. However, as compared to previous investigations using the tunnel paradigm the present investigation employed i) two distinct reaction formats requiring both angular judgments but relying on different reference frames, ii) different levels of complexity in both reaction formats, and iii) appropriate instructions for measuring RTs. This way, the first experiment investigated whether distinct reference frames can be used for path integration, whereas the second experiment tested whether more than one reference frame can be adopted in parallel during path integration, and what kind of information is implemented in the resultant spatial representation based on distinct reference frames.

Reference Frames subserving Path Integration

In the first experiment, the analysis of angular adjustments and RTs supported the assumption that two distinct reference frames can be used during path integration. Turners, using an egocentric reference frame, adjusted the homing vector based on a spatial representation that included the egocentric bearing from the starting point. However, the same strategy group demonstrated the ability to react based on an allocentric reference frame when the endpoint of the passage had to be indicated. Distinct angular adjustment patterns for Turners in the two reaction formats (HVF and SEF) together with comparable RTs corroborated the hypothesis that the reference frames used to react in the two formats were both updated during the passage and relied on different coordinate systems.

Nonturners demonstrated comparable angular adjustment patterns as well as RTs in both reaction formats confirming the hypothesis according to which this strategy group employs the same allocentric reference frame to react in both reaction formats. Results of the side errors analysis alone do not agree with this assumption, with the percentage of side errors being differently affected by tunnel complexity in the two formats. However, the differences between reaction formats in the two tasks did not achieve significance.

A last point regards Turners' and Nonturners' performances in the SEF. Both strategy groups were supposed to employ a locational allocentric representation in this format. Therefore, no performance differences between the two strategy groups were expected. This is exactly what was found. Thus, it can be assumed that both strategy groups used the same allocentric reference frame when they reacted based on the start-to-end vector.

Path integration and parallel updating

The second experiment confirmed the results of the prior experiment showing Nonturners to employ the same allocentric frame of reference in both HVF and SEF and Turners to process spatial information with respect to different reference frames. In fact, Nonturners showed comparable pointing accuracy in both formats with respect to the absolute error as well as to the percentage of side-errors whereas Turners presented different patterns in the two reaction formats. Moreover, the analysis of pointing accuracy and RT indicated that multiple spatial representations could be updated in parallel by Turners.

A comparison of the two experiments gives further insights into the parallel updating of different spatial representations. If Turners process more than one spatial representation independent of the reference frame required for the reaction, then no differences between a blocked or a randomized order of reaction formats should be observed. However, the number of side errors for Turners was influenced by the presentation order of the reaction format. In the blocked condition of Experiment 1, less side errors were observed for Turners when the start-to-end vector had to be adjusted (second block) as compared to the homing vector (first block). In contrast, the random presentation order of reaction formats in Experiment 2 resulted in comparable side errors for both formats. The possibility that the results of the first experiment have to be attributed to a practice effect rather than to an influence of the reaction format has already been refused in the discussion to the first experiment.

In summary, the present research confirms and extends findings from previous studies (Gramann et al., 2005) regarding the co-existence of distinct spatial reference frames during path integration. Importantly, evidence is supplied that the parallel computation of more than one reference frame takes place only when required by the task. Otherwise, a single spatial representation that is employed preferentially is computed and used for a reaction. Although subjects are able to update multiple representations, the RTs analysis of the second experiment showed that Turners' spatial representations (in the HVF and SEF) were not available at the same time. This finding supports Bryant's claim (Bryant, 1992) asserting that, even if more spatial representations exist, only a single representation can be active on a moment because of working memory limits (see also Mani & Johnson-Laird, 1982). Why reactions based on the preferred egocentric representation (in the HVF) took longer compared to reactions based on an allocentric representation (in the SEF), remains an open question. It might be speculated that the differences observed have to be led back to characteristics of the different spatial systems involved in egocentric and allocentric updating (Gramann et al., 2006). Alternative explanations of this effect can be ruled out. Already in the discussion to the second experiment, the hypothesis was disproved that the longer reactions in the HVF reflected the re-computation of egocentric parameters derived from an allocentric representation. Moreover, the lack of any correlation (analyses not reported here) between angular displacements of the response vector and RTs refutes the possibility that the differences between the RTs were attributable to mental rotation effects (Cooper & Shepard, 1973) of different extent in the two reaction formats as a consequence of the different angular adjustments required. Nonturners, on the contrary, did not show any difference in the RTs with respect to the reaction formats providing further evidence that this strategy group uses preferentially an allocentric reference frame during path integration in the tunnel task.

Finally, we wanted to specify whether the representations used by the subjects in both task (HVF and SEF) include geometric properties of the outbound path or, alternatively, only direction and distance required to reach the origin.

Configural or history-free model

May & Klatzky (2000) investigated path-integration in navigation tasks focusing on two possible types of spatial representation, namely the history-free and the configural representation. The authors provided evidence supporting the configural hypothesis both for real navigation and virtual navigation in blindfolded subjects. Evidence of path complexity effects on RTs was already demonstrated by Loomis and colleagues (1993). The present investigation provided further support to the configural model on the basis of several performance measures (RTs, side errors, and absolute error).

The strongest evidence supporting the configural hypothesis was delivered by the RTs analysis. All subjects reacted faster after passages through tunnels with one turn compared to tunnels with two turns. The fact that the complexity of the tunnel passage did not interact with any other factor implies that the resultant spatial representation computed during the tunnel passage is based on a configural model, irrespective of the reference frame used. Furthermore, error measures analyses in both experiments revealed tunnel complexity to affect Turners’ as well as Nonturners’ performance independent of the reaction format.

In summary, the results showed that spatial representations include information about the whole route traversed during the tunnel passage. The configural nature of the spatial representations implies that the characteristics of the path traversed strongly influences the accuracy of the representation itself. The behavioral results presented in this chapter are supported by electrocortical data presented in the subsequent chapters: a frequency data analysis will reveal important features of spatial updating during the travel through the tunnel, whereas ERP-data will supply further insights into the time-course of the retrieval of spatial information with onset of the reaction format.

CHAPTER IV

Influence of task requirements on the encoding of spatial information in a virtual navigation task: an electro-physiological investigation

Abstract

The aim of the present study was to analyse information processing underlying spatial navigation by means of electrocortical parameters. Subjects had to keep up orientation during a desktop simulated passage through tunnels with one or two turns. When the spatial orienting task consisted in the adjustment of a dimensional arrow from the tunnel end position to the starting point two group of subjects reacted differently: the 'Turner' group adjusted the homing vector based on an egocentric spatial representation, whereas the 'Nonturner' group was supposed to rely on an allocentric representation. The second reaction format required all subjects to react based on an allocentric representation. In two subsequent experiments the reaction formats were presented in a blocked (Experiment 1) and random order with reaction format unpredictable on a trial (Experiment 2). Nonturners were assumed to construct the same allocentric representation in both tasks and thus not to be affected by the reaction format order. Turners, by contrast, were expected to update one representation at one time in the blocked experiment and two representations in parallel in the second experiment. Against the predictions, the analysis of lower oscillatory EEG-bands indicated that both strategy groups update more than one representation at one time when reaction formats were given unpredictable on a trial (Experiment 2). The data implies that also Nonturners compute and use different reference frames in the two spatial tasks.

Introduction

Navigation through our natural environment is a complex task solvable by means of different strategies. Analyzing subjects' spatial behavior in indoor and outdoor environments, Lawton (1996) identified two different groups of subjects: those preferring a route-based strategy, relying on an egocentric frame of reference, and those favoring an orientation strategy, based on an allocentric reference frame. Denis (Denis, Pazzaglia, Cornoldi, & Bertolo, 1999) as well as Pazzaglia & De Beni (2001) supplied further evidences for different spatial strategies: to solve a navigational task, one group of subjects used a survey strategy (comparable to the orientation strategy mentioned above) whereas another group applied a strategy based on visual memory for salient landmarks. Beyond the existence of different strategies, experimental research on spatial navigation is confronted with the complex interplay of information from several sensory modalities, for example, visual (Loomis, Klatzky, Golledge, & Philbeck, 1999), vestibular (Peruch, Borel, Gaunet, Thinus-Blanc, Magnan, & Lacour, 1999), and proprioceptive information (Chance, Gaunet, Beall, & Loomis, 1998). The integration of the acquired polymodal sensory information into one coherent spatial representation is assumed to take place in higher order brain areas (Andersen, Snyder, Bradley, & Xing, 1997; Bremmer, Schlack, Duhamel, Graf, & Fink, 2001). Thus, under ecological circumstances navigation is a highly complex process, which results in very accurate spatial representations (Fujita, Klatzky, Loomis, & Golledge, 1993; Klatzky, Beall, Loomis, Golledge, & Philbeck, 1999; Tversky, 1993).

Recently, virtual reality environments and desktop-based simulations proved to be an efficient tool for reducing the environmental complexity, i.e., the type of information sources available at one time, and for selectively investigating the influence of distinct information sources on the accuracy of the resulting spatial representation. Witmer and colleagues (Witmer, Bailey, Knerr, & Parsons, 1996) and Richardson and colleagues (Richardson, Montello, & Hegarty, 1999) showed that visual input is sufficient for constructing a mental representation of the environment. That holds true even if no landmarks were present and the visual input consisted of sparse visual information (Gramann, Muller, Eick, & Schonebeck, 2005; Riecke, van Veen, & Bulthoff, 2002). During navigation in space without landmarks, a path integration process is assumed to take place updating the navigator's position and orientation through the integration of translational and rotational information with respect to a reference frame (Klatzky, 1998). Several studies showed that path integration might rely on an egocentric (Shelton & McNamara, 1997; Wang & Simons, 1999; Wang & Spelke, 2000), an allocentric (Burgess, Spiers, & Paleologou, 2004), or on both types of reference frames (Burgess, 2006). The use of an ego-, or alternatively, allocentric frame of reference as a means of representing entities in space leads to differences in the primitive parameters of the resultant spatial representations (Klatzky, 1998). A locational allocentric representation is defined by an origin and a reference direction external to the navigator. Within this kind of representation the navigator is represented without axis of orientation. In contrast, within the egocentric representation the navigator represents the origin of the reference system and his axis of orientation defines the reference axis.

Numerous brain imaging studies supplied evidence for different neural substrates underlying the use of an allocentric or an egocentric frame of reference (Galati, Lobel, Vallar, Berthoz, Pizzamiglio, & Le Bihan, 2000; Mellet, Bricogne, Tzourio-Mazoyer, Ghaem, Petit, Zago, Etard, Berthoz, Mazoyer, & Denis, 2000; Shelton & Gabrieli, 2002, 2004). These studies induced the use of one or the other frame of reference by presenting different spatial materials. This way, distinct cognitive processes might be attributed to differences inherent to the material employed and not to the reference frame applied. To overcome this restriction, Gramann investigated the influence of the preferred use of distinct reference frames on subjects' performance (Gramann et al., 2005) as well as on the neural networks underlying the encoding of spatial information (Gramann, Muller, Schönebeck, & Debus, 2006) adopting identical material and instruction for all subjects.

Strategy differences in spatial navigation. In a series of three experiments (Gramann et al., 2005), after passages through tunnels with curved and straight segments, subjects had to adjust a homing vector from the end point of a virtual tunnel to indicate the origin of the passage. The task was solvable only if subjects updated their position during the passage with respect to a frame of reference. The visual flow supplied spatial information about translations and rotations in a first person perspective. Therefore, an egocentric reference frame had to be active continuously. However, not necessarily the same egocentric reference frame was employed for the updating of a spatial representation. During navigation, the egocentric information might be transferred into an allocentric frame of reference for the updating of an allocentric representation. The instruction did not induce the use of a particular frame of reference and subjects were free to adopt either an egocentric or an allocentric reference frame for the construction of a spatial representation. Two groups of subjects were identified, revealing a stable preference to use one or the other reference frame. One group of subjects, referred to as 'Turner', updated the cognitive heading according to the perceived heading changes during a turn and built up an egocentric representation. The second group, referred to as 'Nonturner', computed an additional allocentric frame of reference where heading was not updated and thus remained identical to the perceived heading before the stimulus turns. Gramann and colleagues (2005) found different error patterns for Turners and

Nonturners, corroborating the hypothesis of distinct reference frames supporting Turners' and respectively Nonturners' spatial updating.

Moreover, in the third experiment Gramann (et al., 2005) showed that Turners were also able to compute and use an allocentric representation: in addition to the homing vector format, a second format was introduced, the map format, requiring the subjects to process allocentric information. As the two tasks (homing vector and map) were presented in a random sequence and unpredictable on a trial, Turners were forced to compute egocentric and allocentric information in parallel during the whole path. Nonturners, in contrast, were supposed to react based on the same allocentric frame of reference independent of the task. Reconstructing sources of brain electrical activity, Gramann and colleagues (2006) supplied first electrophysiological evidences that the encoding of spatial information for Turners and Nonturners relies on distinct neural networks. However, the description of the origins of the surface potentials does not give further information regarding the nature of the cognitive processes (e.g. attentional or working memory processes) involved. One method to investigate the nature of cognitive processes is the analysis of EEG-oscillation patterns.

Electrophysiological correlates of spatial cognitive processes. Several studies showed a relation of EEG-oscillations to different forms of cognitive processing, allowing for a functional communication among large amounts of neuronal populations (e.g., Basar, Basar-Eroglu, Karakas, & Schurmann, 2001). In particular, alpha and theta frequency bands seem to play an important role in top-down processing (see also von Stein & Sarnthein, 2000). For the present investigation, the function of theta and alpha bands with respect to the encoding of information is of particular interest.

Activity within the theta band has often been associated with several working memory processes (Klimesch, 1996; O'Keefe & Burgess, 1999) including the encoding of new information (Klimesch, 1999). More recent studies (Caplan, Kahana, Sekuler, Kirschen, & Madsen, 2000; Caplan, Madsen, Raghavachari, & Kahana, 2001) revealed the presence of pronounced theta activity also related to the encoding of spatial information in virtual navigation tasks. Furthermore, Bischof & Boulanger (2003) supplied evidences that theta relates to task difficulty during navigation through virtual mazes. Several studies (Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005; Schack, Klimesch, & Sauseng, 2005) showed theta to be selectively distributed over the whole scalp and in particular over prefrontal, central and parietal regions.

A second frequency band important for the present research is the alpha band. Başar (Basar & Schurmann, 1997) assumed the alpha band to be associated with sensory, motor, and memory functions. Pfurtscheller and Aranibar (1977) supplied evidence that a reduction in band power or desynchronization (Klimesch, 1996) during a task compared to a rest interval reflects a state of mental activity. Within the alpha band (7-13 Hz), it is possible to identify two different and functionally independent alpha sub-bands, the lower (7-10 Hz) and the upper (11-13 Hz) alpha bands (Klimesch, 1996; Pfurtscheller & Lopes da Silva, 1999). Klimesch (1997) suggested that lower alpha desynchronization might be related to different memory processes with exception of the encoding. Nevertheless, de Araujo (and colleagues, 2002) showed alpha desynchronization to be also present during the encoding of spatial information in a navigation task.

In the present study, the analyses of distinct frequency bands was applied to gain further insights into the time course of information processing during spatial navigation. To this end, the tunnel paradigm was adopted and two different reaction formats were used based on the identical 3-dimensional arrow: in the homing vector format (HVF) subjects had to indicate the starting position of the passage relative to the end point and were free to adopt either an allocentric or an egocentric frame of reference; in contrast, in the start-to-end format (SEF) subjects had to indicate the end point of the passage relative to the origin and thus the response required the use of an allocentric frame of reference. In two subsequent experiments, the reaction formats were presented in a blocked and, respectively, random order with format unpredictable on a trial in the latter condition.

According to the differences in brain networks subserving the computation of an egocentric and an allocentric reference frame, differences in encoding visual flow information dependent on the strategy were expected. In addition, due to the fact that Turners preferentially use an egocentric reference frame for adjusting the HVF but have to use an allocentric reference frame to adjust the SEF, differences between the two tasks were expected for this strategy group. Furthermore, Nonturners were supposed to compute and use the same allocentric representation in both tasks and thus not to be affected by the reaction format order. Turners, by contrast, were expected to update one representation at one time according to the task in the blocked experiment and two representations in parallel in the second experiment.

The hypotheses were proofed by means of behavioral data, presented in the previous chapter. The analyses of electrocortical data presented here focus on theta power fluctuations as an indicator of mental effort (Bischof & Boulanger, 2003; Caplan et al., 2001). In addition, according to de Araujo's findings (de Araujo, Baffa, & Wakai, 2002), revealing alpha desynchronization during a navigation task compared to a rest period, alpha was expected to be associated with encoding of spatial information and to reflect the allocation of attentional resources (Klimesch, 1997).

EXPERIMENT 1

Method

Subjects

19 healthy volunteers aged between 21 and 33 years (X=23.8, SD=3.6 years) were selected to take part in the experiment. All subjects with normal or corrected-to-normal vision were paid for their participation. Three participants were left-handed. Due to prior findings (Postma, Jager, Kessels, Koppeschaar, & Honka, 2004), handedness was not considered a decisive factor. Due to gender-specific differences in performing way-finding tasks (Lawton & Morrin, 1999; Sandstrom, Kaufman, & Huettel, 1998; Shelton & Gabrieli, 2004), only male subjects were selected. Nine participants were categorized as Nonturner and ten as Turner, respectively.

Task, material, and procedure

Subjects were seated in a darkened room in order to eliminate additional reference information. The task was presented with a beamer (Sanyo PLCXU-47) on a screen positioned at a 1,5 meter distance from the subject. Prior to the main experiment, subjects were categorized with respect to their preferential use of an allo- or egocentric reference frame, respectively (Gramann et al., 2005). A subsequent training ensured that participants became familiar with the task: the tunnels used in the training session were the same as in the main task but subjects always received strategy-specific feedback concerning their pointing accuracy.

Subjects had to maintain orientation during passages through virtual tunnels. The first and the last segment of each passage were always straight, all tunnels were of constant length (5 segments), and included one or two turns of varying angles (ranging from 10° to 90°). Each tunnel had a turn in the second segment. Half of the tunnels had one additional turn prior to the last segment. Tunnels ended at eccentricities of 15°, 30°, 45°, and 60° on either side of the starting point. Overall, a total number of 200 trials were tested, including 40 additional tunnels with 3 straight segments serving as baseline.

Trials started with a fixation cross for 500 ms followed by a picture of the tunnel entrance shown for 500 ms. Then, the virtual journey began. At the end of each tunnel, the view out of the last segment was shown for 500 ms followed by the reaction format. Subjects' performance was tested in two reaction formats that were blocked in the first experiment: i) a homing vector format (HVF) and ii) a start-to-end format (SEF), respectively. In the HVF, subjects were asked to adjust an arrow from the tunnel end-position back to the origin of the passage. In the SEF, subjects were required to adjust a response arrow pointing from the origin of the tunnel passage to the end point of the passage. In the first experimental block, only the HVF was used whereas in the second experimental block the SEF was used. For both formats, the same tunnel material was used.

Performance measures

Error measures. In the study of cognitive processes, it is important to separate correct and incorrect responses. Two criteria were used as indicators of correct reactions, side-errors and format-errors. Reactions indicating the wrong side i) of the tunnel's starting point (left or right) relative to the tunnel's end-point in HVF or, alternatively, ii) of the side of the tunnel's end point relative to the starting point in the SEF were considered side-errors. The format error was introduced due to the necessity of distinguishing errors that resulted from a confusion of the two reaction formats from side errors. These two types of error were eliminated from further analyses.

Angular fit. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions provided a measure of the subject's ability to discriminate among varying eccentricities.

EEG-recording

The electroencephalogram (EEG) was recorded continuously at a sampling rate of 500 Hz using 128 Ag/AgCl electrodes, mounted in an elastic cap (FMS, Herrsching, Germany), according to the extended 10-10 system (American Electroencephalographic Society, 1994). Electrophysiological signals were amplified using a 0.1–100 Hz bandpass filter via BrainAmps (Brain Products, Munich, Germany). Input impedance was kept below 10 kOhm (Ferree, Luu, Russell, & Tucker, 2001). All electrodes were recorded using Cz as reference and were re-referenced off-line to linked mastoids. Vertical and horizontal eye-movements were recorded by means of electrodes placed at the outer canthi of the eyes and the superior and inferior orbits to monitor eye blinks and eye movements.

FFT-data analyses

Only trials with correct responses were included in the further analyses. Ocular correction was computed by means of Gratton and Cole's algorithm (Gratton, Coles, & Donchin, 1983). The continuous EEG-data were filtered with a 0.0159 Hz high pass and a 30 Hz low pass filter and segmented into epochs of 3800 ms including each single tunnel segment ±500 ms. Each episode was further segmented by means of overlapping moving windows (window of 1000 ms with 90% overlap). Epochs exceeding ± 70 µV, violating a voltage step criterion of 80 µV, or with a difference of two values greater than 120 µV were excluded in the individual channel mode from further analyses. Three subjects (one Nonturner and two Turners) were excluded from EEG-analyses due to excessive artefacts. For the remaining subjects, the mean band power was computed by means of a Fast Fourier Transform (Hanning window 10%, full spectrum, normalized) for each epoch and then averaged for each segment. Finally, the power values obtained for single trials were averaged, on single subject level and for each tunnel segment, for tunnels with the same number of turns (one or two turns) according to the reaction format (HVF vs. SEF). The resulting power spectra were baseline-corrected by subtracting baseline activity in the defined frequency bands during control trials consisting of tunnels with only straight segments that required only a key press, without any arrow adjustment.

The investigation focused on the frequency bands theta (4-6 Hz) and lower alpha (8-10 Hz). For each frequency band, a topographic analysis of variance was calculated for left, midline, and right electrodes at occipital, parieto-occipital, parietal, central, fronto-central, and frontal regions. On the bases of post-hoc contrasts, only electrode locations are reported that demonstrated sensitivity for material ('number of turns' and 'segment') and reaction format (HVF vs. SEF) and their eventual interaction with subject's preferred strategy.

Results

Behavioral data

<u>Error measures</u>. Overall, the percentage of side errors was 6.09% with Turners showing a higher percentage of side errors overall (7.31% and 4.72% for Turners and Nonturners, respectively). Format errors (less than 0.63%) were observed under all experimental conditions for both strategy groups.

<u>Angular fit</u>. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions revealed a significant positive relationship for both Nonturners [$r(1363)=.985$; $p<.001$] and

Turners [r(1475)=.989; p<.001]. Both strategy groups revealed high positive correlations adjusting the HVF ([r(675)=.992; p<.001] and [r(715)=.997; p<.001] for Nonturners and Turners, respectively). The same was observed for reactions based on the SEF ([r(688)=.916; p<.001] and [r(760)=.874; p<.001]) for Nonturners and Turners, respectively. Both strategy groups solved tunnels with one turn with high accuracy (Nonturners [r(701)=991; p<.001] and Turners [r(781)=993; p<.001]), which was the same for tunnels with two turns (Nonturners [r(662)=980; p<.001] and Turners [r(694)=985; p<.001]).

FFT-analyses

Theta band

A topographical analysis of variance was performed with 'preferred strategy' (Turner, Nonturner) as between-subject factor and 'electrode site' (left, midline, right), 'lobe' (occipital, parieto-occipital, parietal, central, fronto-central, and frontal), 'reaction format' (HVF, SEF), and 'number of turns' (1 or 2 turns) as repeated measures. Greenhouse-Geisser correction was applied, if necessary. The results focus on electrodes revealing sensitivity to material ('number of turns' and 'segment') and task (HVF and SEF) changes.

Interactions of the factors 'number of turns' x 'electrode site' x 'lobe' [F(10,140)=2.2387, p<.019; eta^2=.138] as well as 'format' x 'electrode site' x 'lobe' [F(10,140)=2.6988, p<.040; eta^2=.162] revealed task- and reaction format dependent differences in theta power at posterior as well as at anterior electrodes with the most prominent differences over anterior midline electrodes. A follow-up analysis of variance therefore included FCz and Fz.

Theta activity at FCz and Fz. The main effect of 'number of turns' [F(1,14)=6.2136, p<.026; eta^2=.307] was qualified by the higher order interaction 'number of turns' x 'segment' [$F(4,56)=5.5259$, $p<.001$; $eta^2=.283$] (Figure 4.1). Post hoc contrasts revealed increasing theta activity during the passage for tunnels with two turns with a maximum in the third and forth segment. Theta activity decreased in the last segment. A comparison of tunnels with different number of turns revealed significantly higher theta power during the third (HSD: $p<.003$) and forth (HSD: $p<.036$) segment for tunnels with two as compared to tunnels with one turn.

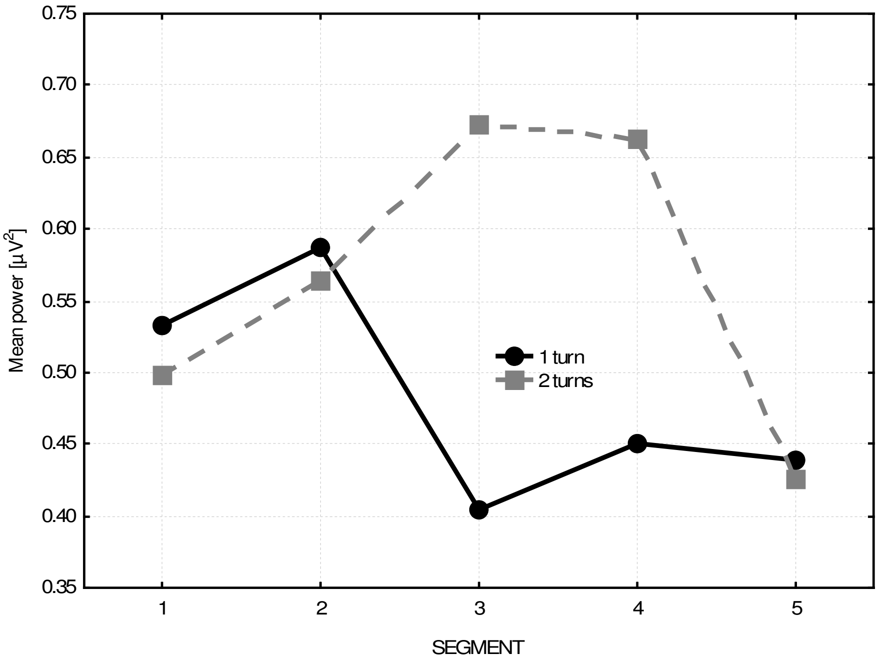

Figure 4.1. Mean theta power over FCz and Fz as a function of number of turns (continuous line for tunnels with 1 turn and dashed line for tunnels with 2 turns) and segment (segment 1 to 5).

The main effect of 'reaction format' [$F(1,14)=10.115$, $p<.007$; $eta^2=.419$] was qualified by the higher order interaction 'reaction format' x 'electrode site' [$F(1,14)=5.0018$, $p<.042$; $eta^2=.263$] (Figure 4.2). The highest theta synchronization was present in the HVF as compared to the SEF at both leads (HSD: at both locations $p<.001$). Differences between electrode sites achieved significance only in the HVF (HSD: $p<.003$) with higher activity at FCz compared to Fz.

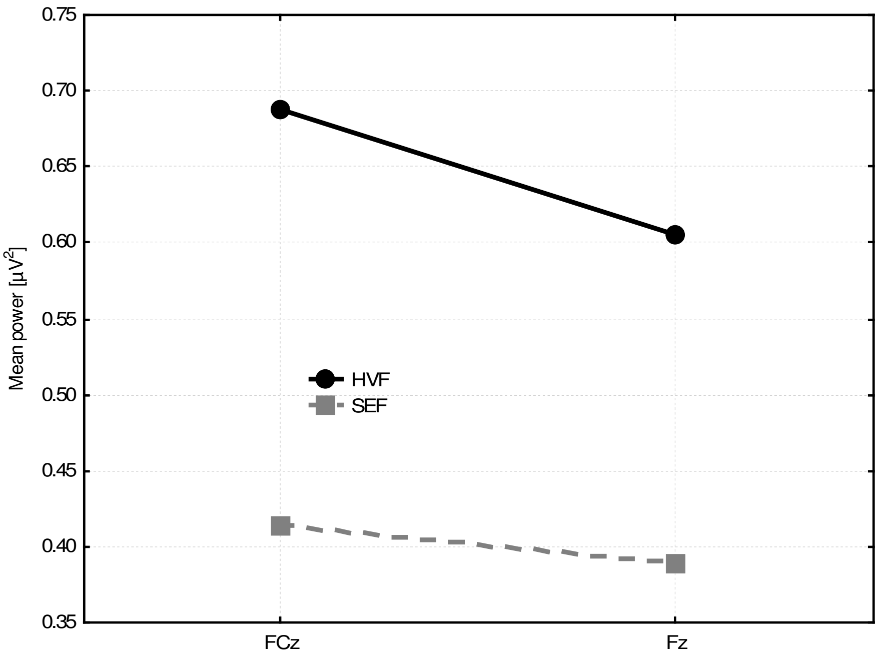

Figure 4.2. Mean theta power over FCz and Fz as a function of reaction format (continuous line for the HVF and dashed line for the SEF).

<u>Lower alpha band</u>

A topographical analysis of variance was performed with ‘preferred strategy’ (Turner, Nonturner) as between-subject factor and ‘electrode site’ (left, midline, right), ‘lobe’ (occipital, parieto-occipital, parietal, central, fronto-central, and frontal), ‘reaction format’ (HVF, SEF), and ‘number of turns’ (1 or 2 turns) as repeated measures. Greenhouse-Geisser correction was applied, if necessary. The following results focus on the factors directly associated with electrodes demonstrating an effect of material and task.

Interaction of the factors ‘number of turn’ x ‘segment’ x ‘lobe’ [$F(20,280)=2.7155$, $p<.001$; $eta^2=.162$] revealed material-dependent differences in lower alpha power over the whole scalp and in particular over posterior regions. Follow-up analyses of variance therefore included lateral as well as vertex electrodes covering occipital and parietal areas.

Occipital lower alpha effects. The main effects of 'number of turns' [F(1,14)=7.3832, p<.017; eta^2=.345] and 'segment' [F(4,56)=4.0019, p<.022; eta^2=.222] were qualified by the interaction 'number of turns' x 'segment' [F(4,56)=10.178, p<.001; eta^2=.421] (Figure 4.3). For tunnels with one turn, alpha synchronization increased after the first turn, reached a maximum during the forth segment, and desynchronized during the last segment. For tunnels with two turns, by contrast, alpha desynchronization remained constant over the whole passage.

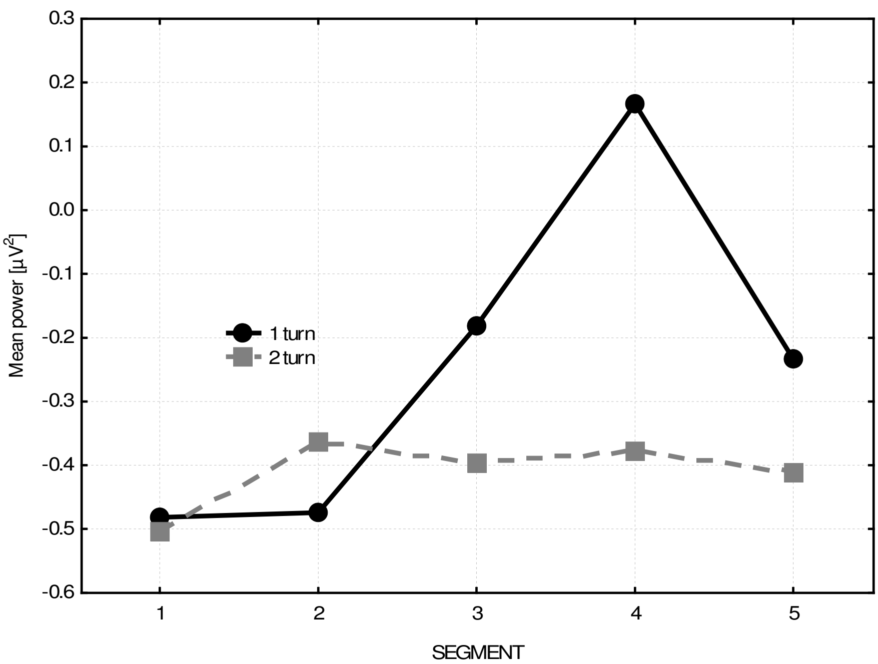

Figure 4.3. Mean lower alpha power over occipital electrodes as a function of number of turns (continuous line for tunnels with 1 turn and dashed line for tunnels with 2 turns) and segment (segment 1 to 5).

The interaction 'reaction format' x 'segment' [F(4,56)=4.7911, p<.018; eta^2=.255] was qualified by the higher order interaction 'reaction format' x 'electrode site' x 'segment' [F(8,112)=2.8834, p<.029; eta^2=.171] (Figure 4.4). Alpha power synchronized after the second segment and reached a maximum during the forth segment. During the last segment before the response prompt, alpha desynchronized again. This pattern was similar for both reaction formats but more pronounced in the SEF as compared to the HVF. In the SEF, the same activation pattern was present at each electrode position (left, middle, or right). In the HVF, on the contrary, alpha desynchronization was more pronounced at O2 as compared to Oz and O1 during the most segments.

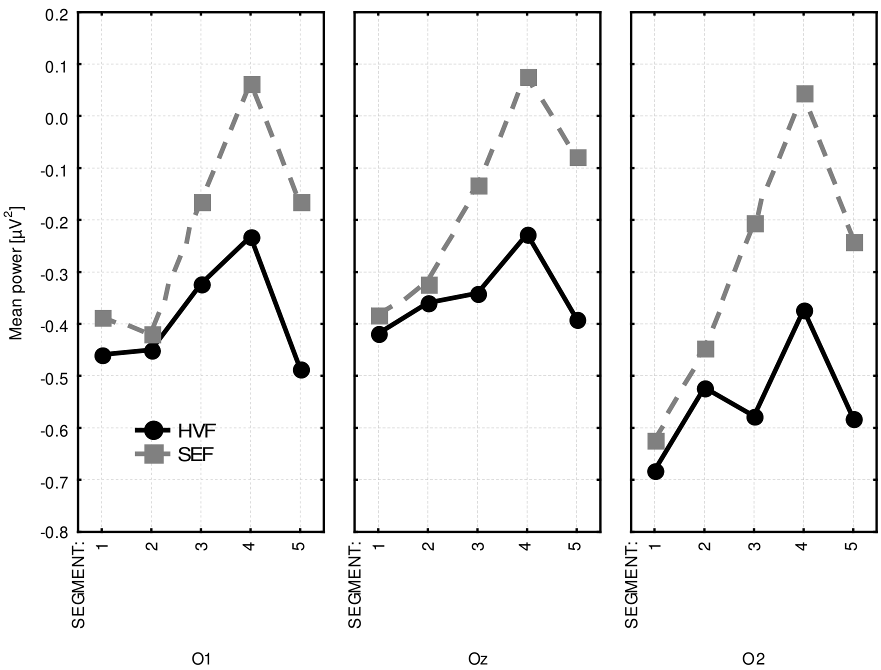

Figure 4.4. Mean lower alpha power over O1 (left panel), Oz (middle panel), as well as O2 (right panel) as a function of reaction format (continuous line for the HVF and dashed line for the SEF) and segment (segment 1 to 5).

Parietal lower alpha effects. The main effects of 'number of turns' [$F(1,14)=10.211$, $p<.006$; $eta^2=.422$] and 'segment' [$F(4,56)=4.0722$, $p<.035$; $eta^2=.225$] were qualified by the higher order interaction 'number of turns' x 'segment' [$F(4,56)=8.9993$, $p<.003$; $eta^2=.391$]. Post hoc contrasts (HSD) revealed an activation pattern comparable to that over occipital regions. The main effect of 'reaction format' [$F(1,14)=6.6801$, $p<.022$; $eta^2=.323$] revealed stronger desynchronization in the HVF compared to the SEF.

Discussion

The behavioral data supplied evidence that all subjects were able to solve both reaction formats with high accuracy (high angular fit) and the analysis of the distinct frequency bands supplied several insights into spatial information processing.

Theta power was distributed over the whole scalp according to several studies (Mizuhara, Wang, Kobayashi, & Yamaguchi, 2004; Sarnthein et al., 1998; Sauseng et al., 2005; Schack et al., 2005; von Stein & Sarnthein, 2000). The strongest effects of material and task were evident over midline, anterior electrodes (Onton, Delorme, & Makeig, 2005).

The influence of experimental manipulations on theta power revealed this band to be an adequate indicator of cognitive effort during spatial encoding processes. In fact, theta synchronization increased according to task difficulty, as revealed by the comparison of tunnels with one and two turns. Confirming Bischof's and Boulanger's (2003) and Caplan's (et al., 2001) findings, theta reflects higher cognitive demands related to critical stages during the tunnel passage rather than to the elaboration of rotations *per se*. In fact, theta power increment during the passage achieved significance only for tunnels with two turns from the third segment. Moreover, theta synchronized not only during stimulus turns but also during the third segment for tunnels with two turns when subjects did not rotate but had to integrate information about the previous turn with the rotational information of the upcoming turn. Finally, when the tunnel's end became visible theta decreased in tunnels with two turns.

If theta reflects the cognitive demands to encode spatial information dependent on the reference frame that has to be used for a reaction, the absence of any strategy-specific effects implies a comparable cognitive effort for Nonturners and Turners dependent on distinct reaction formats. This would reflect a higher cognitive effort for both strategy groups when subjects encode spatial information in order to adjust a homing vector as compared to a start-to-end vector. However, it is to remark that the SEF was always presented in a second block after the HVF. Therefore, reduced theta power in the SEF might also reflect decreased cognitive effort with increasing practice of the tunnel task. In the latter case, there would not be any evidence for a distinction between the reference frames supporting path integration in the two tasks. In order to see whether training effects took place, each experimental block (HVF and SEF) was divided into five successive time intervals. For each interval the mean power was computed. The presence of a practice effect should be evident not only in the comparison between the first and second experimental block but also within each experimental block. Mean theta power decreased over the course of the experiment with respect to each reaction format and thus suggested the presence of a practice effect. However, theta decrement was not linear and during a sequence of tunnels in the middle of each block theta power was even higher in the SEF compared to the HVF. This effect might be a consequence of the subdivision of the whole experiment into several intervals that respected a temporal criterion but did not take the distribution of different kinds of tunnel (number of turns, end positions, etc.) into account. Consequently, the present data should be handled with caution.

In accordance with Pfurtscheller and Lopez Da Silva (1999), desynchronization in the lower alpha band revealed a widespread scalp distribution. Nevertheless, the effect of material and task on alpha desynchronization was most pronounced over posterior regions. Resembling de Araujo's and colleagues' (2002) findings, alpha power decreased during the navigation task as compared to baseline activity. Moreover, alpha power was shown to be sensitive to material changes during encoding of spatial information.

Over both, occipital and parietal electrodes, all subjects showed a continuous desynchronization during the whole passage for tunnels with two turns. For tunnels with one turn alpha activity synchronized after the stimulus turn. According to Klimesch (1997) and Gevins (et al., 1997), alpha desynchronization reflects the demand of attentional resources. In case of the tunnel paradigm, the elaboration of more complex stimuli supplying rotational and translational information would be more demanding as compared to stimuli providing translational information alone.

In the two tasks (HVF and SEF), the same visual information was supplied but the reaction at the end of the passage differed. Higher activity was present in the HVF compared to the SEF. Such power differences between formats might be interpreted as a different attentional involvement in the two tasks, thus corroborating Petsche's findings (Petsche, Kaplan, von Stein, & Filz, 1997) that the modulation of the lower alpha band can behave task dependent. Alternatively, different desynchronization levels might reflect a practice effect (e.g., Gevins et al., 1997). Similarly to the theta band, the time course of alpha desynchronization changes during the experiment was analyzed. The HVF revealed higher alpha desynchronization compared to the SEF but within each block (HVF and SEF) alpha did not significantly decrease over time confuting the presence of a practice effect. Nevertheless, the same lacks as for the theta band hold true and no conclusive data can be supplied.

In the first experiment, the blocked presentation of reaction formats was supposed to allow subjects to construct and use one spatial representation at a time. In the second experiment, a random presentation order of reaction formats unpredictable on a trial allowed for testing the influence of parallel processing of ego- and allocentric information on Turners' and Nonturners' spatial encoding.

EXPERIMENT 2

Method

Subjects

18 healthy volunteers aged between 20 and 35 years (X=25.2, SD=3.8 years) were selected to take part in the experiment. All subjects with normal or corrected-to-normal vision were financially compensated for their participation. All but one participant were right-handed. Nine participants were categorized as Nonturner and nine as Turner.

Task, material, and procedure

The experimental design remained unaltered with the exception of the presentation order regarding the reaction format: whereas in the first experiment the presentation order of the reaction formats was blocked, in this experiment the sequence of reaction formats was randomized and unpredictable on a trial. At the end of each passage, a response arrow appeared: when the arrowhead pointed towards the subjects, they had to indicate the end-position with respect to the origin of the path (SEF). When the arrowhead pointed into the depth of the screen, subjects had to adjust a homing vector back to the origin of the tunnel (HVF). In addition, the number of tunnels with two turns was increased with two-thirds of the tunnels including two turns. However, the material was identical to that used in Experiment 1.

Therefore, the current experimental design included the following factors: 'side of end-position' (left or right with respect to the starting point), 'reaction format' (format HV, format SE), 'number of turns' (1 or 2 turns), and 'eccentricity of end-position' (15°, 30°, 45°, and 60°). There were 10 trials for each combination of 'side of end-position' x 'reaction format' x 'eccentricity of end-position' for tunnels with two turns resulting in a total of 160 trials as well as 5 trials for each combination of the same 2 x 2 x 4 factorial design regarding tunnels with one turn adding up to a total of 80 tunnels. 20 filler trials were added. The filler trials consisted of tunnels with straight and curved segments and thus differed from the control trials employed in the first experiment.

EEG-recording and FFT-data analyses

In the second experiment, the same EEG-recording and data-analyses criteria were employed as in the first experiment with the exception of the number of electrodes in the second experiment included only 64 channels, and a different baseline. Since filler trials consisted of straight and curved segments and not only straight segments as in Experiment 1, a different baseline had to be used. A segment prior to the beginning of tunnel's movement served as baseline.

Results

Behavioral data

Error measures. Overall, the percentage of side errors was 5.49% with Turners showing a higher percentage of side errors (6.98% and 3.99% for Turners and Nonturners, respectively). Format errors (less than 1.71%) were observed under all experimental conditions for both strategy groups.

Angular fit. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions revealed a significant positive relationship for both Nonturners [$r(2013)=.985$; $p<.001$] and Turners [$r(1947)=.988$; $p<.001$]. Both strategy groups revealed high positive correlations in the HVF ([$r(994)=.992$; $p<.001$] and [$r(960)=.995$; $p<.001$] for Nonturners and Turners, respectively). The same was observed for the SEF ([$r(1019)=.898$; $p<.001$] and [$r(987)=.870$; $p<.001$] for Nonturners and Turners, respectively). Both strategy groups solved tunnels with one turn with high accuracy (Nonturners [r(690)=989; p<.001] and Turners [r(697)=.993; p<.001]), which was the same for tunnels with two turns (Nonturners [r(1323)=.983; p<.001] and Turners [r(1250)=.986; p<.001]).

FFT-analyses

Theta band

In order to compare the present results to those of the first experiment, we adopted the same analysis described previously.

Theta activity at FCz and Fz. The main effect of 'electrode site' [F(1,15)=8.338, p<.011; eta^2=.357] revealed stronger theta synchronization at FCz compared to Cz. The main effects 'number of turns' [F(1,15)=12.095, p<.003; eta^2=.446] and 'segment' [F(4,60)=10.881, p<.001; eta^2=.420] were qualified by the higher order interaction 'number of turns' x 'segment' [F(4,60)=3.096, p<.041; eta^2=.171] (Figure 4.5). For tunnels with one turn, theta activity increased during the first turn and then remained constant during the rest of the passage until the forth segment (all p<.001). In the last segment theta decreased. For tunnels with two turns, by contrast, theta activity increased constantly during the passage and reached a maximum during the second turn and then slightly decreased again. Comparing tunnels with different numbers of turns, post-hoc contrasts indicated higher activation for tunnels with two turns during the forth segment (HSD: p<.030).

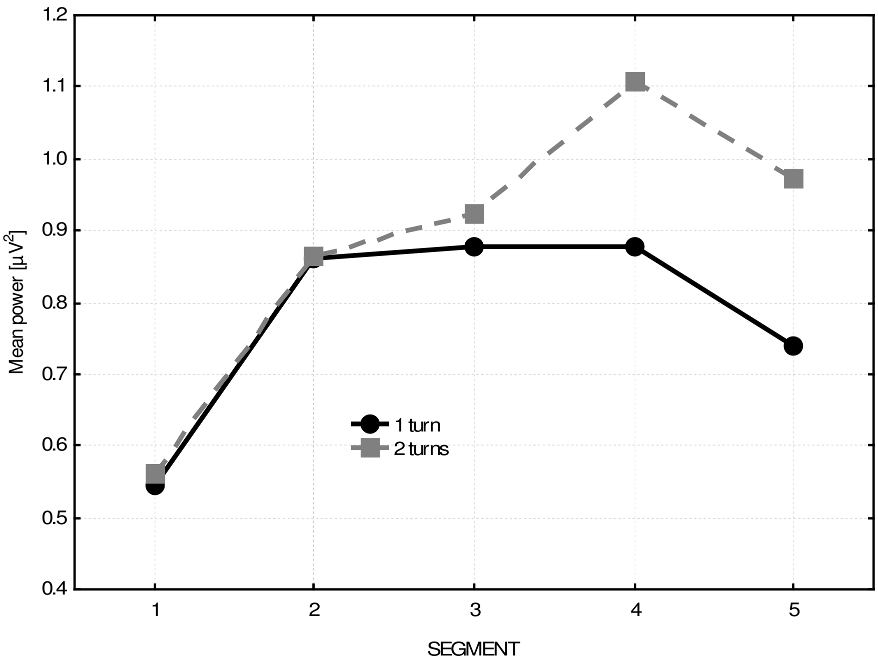

Figure 4.5. Mean theta power at FCz and Fz as a function of number of turns (continuous line for tunnels with 1 turn and dashed line for tunnels with 2 turns) and segment (segment 1 to 5).

Lower alpha band

In order to compare the present results to those of the first experiment, we adopted the same analysis described in Experiment 1.

Occipital lower alpha effects. The main effect 'number of turns' [$F(1,15)=9.5105$, $p<.008$; $eta^2=.388$] and the interaction 'number of turns' x 'segment' [$F(4,60)=6.3398$, $p<.001$; $eta^2=.297$] were qualified by the higher order interaction 'number of turns' x 'segment' x 'preferred strategy' [$F(4,60)=2.8741$, $p<.030$; $eta^2=.161$] (Figure 4.6). Despite some strong differences between strategy groups, no significant post-hoc contrasts (HSD) were found (all $p>.736$). Turners and Nonturners revealed different patterns of alpha power modulation with Nonturners demonstrating comparable alpha power for all segments and number of turns. In contrast, Turners revealed a strong synchronization for tunnels with one turn during the third and forth segment compared to all other segments. For tunnels with two turns, Turners demonstrated a comparable level of alpha desynchronization over the whole passage. Finally, Turners showed activation differences between tunnels with one and two turns in the third and forth segment.

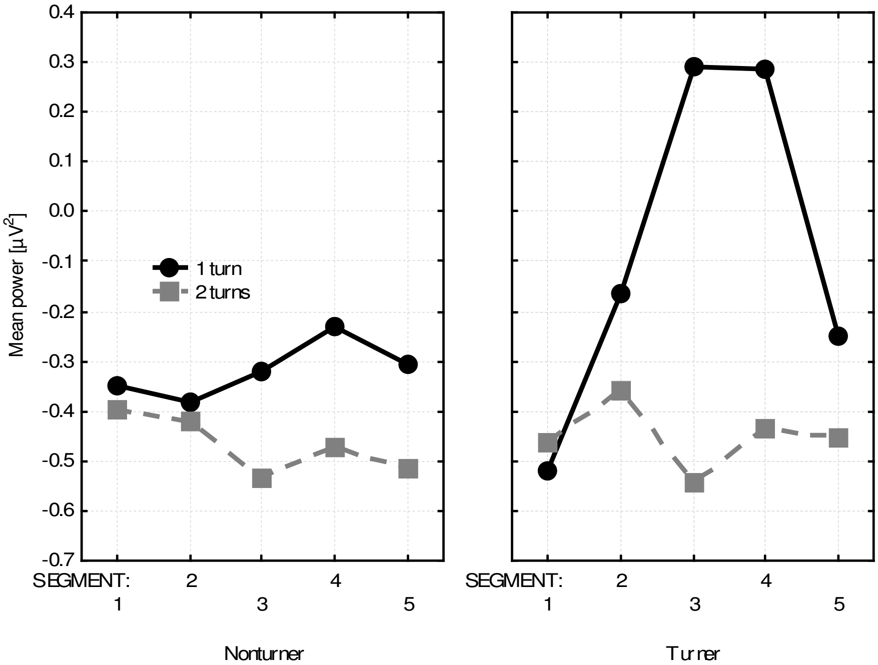

Figure 4.6. Mean lower alpha power over occipital electrodes for Nonturners (left panel) and Turners (right panel) as a function of number of turns (continuous line for tunnels with one turn and dashed line for tunnels with two turns) and segment (segment 1 to 5).

Parietal lower alpha effects. The main effect 'number of turns' [$F(1,15)=9.4924$, $p<.008$; $eta^2=.388$] was qualified by the higher order interaction 'number of turns' x 'segment' [$F(4,60)=5.7627$, $p<.001$; $eta^2=.278$] (Figure 4.7). Tunnels with two turns revealed a constant desynchronization during the whole path, whereas for tunnels with one turn alpha desynchronization was reduced during the third and forth segment compared to the other segments for the same tunnels and to the corresponding segments for tunnels with two turns.

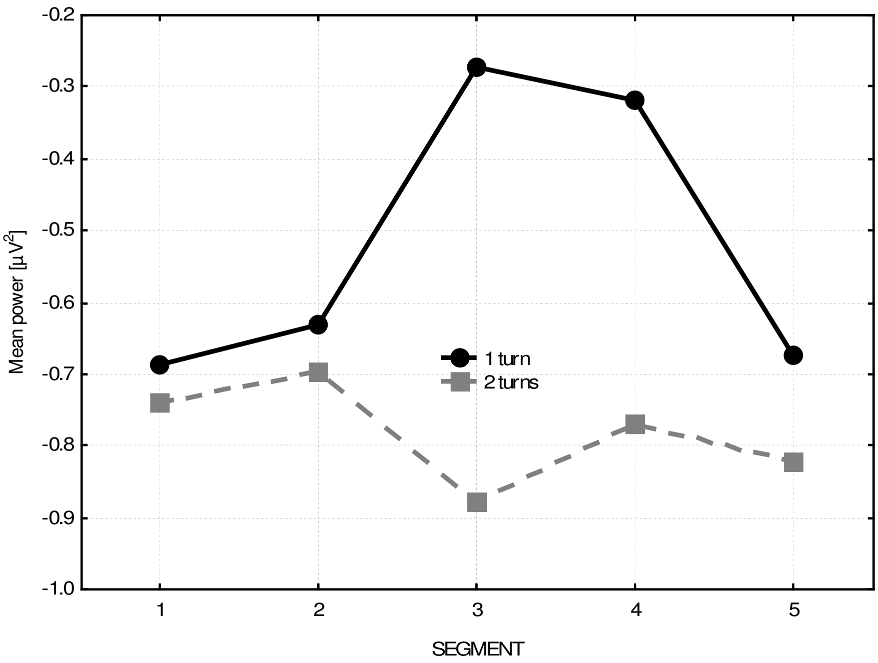

Figure 4.7. Mean lower alpha power over parietal electrodes as a function of number of turns (continuous line for tunnels with 1 turn and dashed line for tunnels with 2 turns) and segment (segment 1 to 5).

Discussion

The behavioral data demonstrated that all subjects were able to solve both reaction formats with high accuracy. This was reflected in the high correlation between subject's reactions and expected angular adjustments.

In this experiment, the reaction formats were presented in a random order and unpredictable on a trial. Strategy dependent differences were expected with respect to the cognitive effort during the task. While Turners were expected to update two distinct representations based on an egocentric and an allocentric reference frame (in the HVF and SEF, respectively), Nonturners were expected to update only one allocentric representation during the tunnel passage, that could be employed in both reaction formats. However, no differences between strategy groups were found.

For tunnels with one turn, theta power increased during the turn and remained constant for the following segments, indicating a continuous mental effort, even when no rotational information was given. For tunnels with two turns, theta activity increased up to the forth segment, indicating even higher effort during the processing of more complex tunnels. This synchronization pattern was comparable for both strategy groups.

Over parietal regions, alpha desynchronized during segments containing rotational information as well as in the last segment, whereas synchronization was observed only when translational information was perceived (in tunnels with one turn after the second segment). Similar patterns were present also at occipital leads but differences between tunnels with one and two turns, even if present for both strategy groups, achieved significance only for Turners. The lack of any difference between strategy groups indicates that independent of the reference frame used posterior regions support spatial orientation in a comparable way and require the same amount of attentional resources.

Further insights regarding the influence of different reference frames on the encoding of spatial information can be gained from a comparison between experiments.

General discussion

The aim of the present study focussed on the influence of distinct reference frames on the encoding of spatial information in a virtual navigation task. Gramann and colleagues (2006) already showed that the strategy subjects adopted during path integration affected the way spatial information was encoded. However, distinct contributions of allocentric and egocentric reference frames to the encoding process could not be distinguished since the experimental design required subjects to process allo- and egocentric information in parallel.

The first experiment reported here overcame this problem by presenting two tasks solvable on the basis of different reference frames (HVF and SEF) in a blocked fashion. This way it was possible to delineate the main features of allo- and egocentric encoding as reflected in the modulation of the theta- and the alpha band with respect to subject's strategy and reaction format. However, no strategy dependent differences were present and the different oscillation power in the HVF compared to the SEF with respect to the alpha and theta band could not be unequivocally attributed to different encoding processes since the pattern might be also due to a practice effect. Therefore, results from the first experiment did not allow to distinguish between the two possibilities. Different encoding processes were observed dependent on the reference frame used and the task to solve. However, assuming that the cognitive effort and the stimulus relevance was the same under all conditions possible differences in spatial updating observed from homing adjustments were not mirrored by alpha and theta band power analyses. Alternatively, only one egocentric representation (e.g., Wang & Spelke, 2000) was constructed and allocentric parameters, when necessary, were derived at a later stage in the tunnel passage but before the response arrow onset (e.g., during the last straight segment).

In a second experiment the two spatial tasks (HVF and SEF) were presented in a random sequence. If subjects were able to update only one egocentric representation, the modulation of different frequencies reflecting the encoding process should be similar in both experiments and no strategy dependent differences should be present. In contrast, differences between the two experiments would suggest that the spatial representations employed by Turners and Nonturners for their reactions in the two formats relied on distinct reference frames in the first experiment. During the second experiment, in contrast, different reference frames were active in parallel with each frame of reference supporting the updating of a distinct spatial representation. Moreover, in the latter case the order in which the reaction formats were presented (blocked vs. random) might have influenced the strategy groups differently. Turners were supposed to update spatial representations based on distinct reference frames for different reaction formats. Thus, the presentation order of the two reaction formats should determine the number of spatial representations updated at one time and thus influence the mental effort. Nonturners, by contrast, were supposed to adopt the same reference frame in both formats and in this case the presentation order should not have any effect on the mental effort.

Theta and mental effort

The analysis of the theta modulations during path integration corroborated previous findings (Bischof & Boulanger, 2003; Caplan et al., 2001) revealing theta synchronization as an indicator of cognitive effort during spatial encoding. Thus, an increase in cognitive effort in the second as compared to the first experiment should be reflected by increased theta activity, which was exactly the case. However, a direct comparison of the two experiments is not possible since different baselines were used for the computation of individual power spectra. Possible differences could not unequivocally be attributed to differences in mental effort but might be a result of the different baselines. Nevertheless, it is possible to compare the experiments on the basis of the time course of theta power during the tunnel passage.

The two experiments revealed some similarities but also an important difference. In both experiments theta significantly synchronized during tunnels with two turns. The difference between experiments regarded the processing of tunnels with one turn. In the first experiment, theta power was higher as compared to a baseline but did not significantly increase during the tunnel passage, indicating low mental effort also when rotational information was supplied. In contrast, in the second experiment, theta synchronization increased during the turn and remained sustained during the whole passage.

The presence of different oscillation patterns in the two experiments does not support the assumption of a unique reference system underlying path integration independently of the task to solve. Thus, it is more likely that in the first experiment distinct reference systems supported path integration in the two tasks whereas in the second experiment two reference systems supported the updating of distinct spatial representations in parallel. This evidence agrees with the expectation of Turners' increased mental effort in the second experiment. During the first segment the reference axes of the allocentric and egocentric reference frame still coincide. Even if the rotational information of the upcoming turn becomes visible early during the first segment, at this point in time the encoding of spatial information is not demanding: theta has a minimum power value, although higher compared to a baseline. During the turn in the second segment the reference axes of the two frames begin to diverge and remain misaligned during the whole passage. From the beginning of the turn, spatial information is processed in parallel with respect to distinct reference frames with diverging axes of reference. Thus, the sustained theta activity during the last three straight segments in tunnels with one turn could reflect the difficulty of updating distinct spatial representations with respect to diverging reference frames.

The presence of comparable theta effects for Nonturners was unexpected. The Nonturner group was supposed to adopt the same allocentric reference frame for the updating of the spatial representation to use for the reactions independent from the task and consequently independent from the presentation order of the tasks.

However, this group, similarly to the Turner group, revealed increased cognitive effort in the second compared to the first experiment suggesting that Nonturners might use a further reference frame in one of the two formats. It might be argued that Turners' and Nonturners' representations in the HVF are based on similar reference frames with the difference that 1) Turners include their cognitive heading in the representation, whereas 2) Nonturners refer to the physical body's axis of orientation that, in our task, remained unchanged during the travel. The features of this kind of spatial processing resemble those of the "external reference frame" described by Bryant (1992; Bryant & Tversky, 1992) that combines features of an allo- and an egocentric frame of reference. Similarly to the allocentric reference frame the origin of the reference system is external to the perceiver whereas the axes of orientation are the same as the perceiver's, comparable to an egocentric reference frame. In the SEF, on the contrary, Nonturners would employ an allocentric reference system. Although other investigations (Coluccia, Mammarella, De Beni, Ittyerah, & Cornoldi, 2007; Grush, 2000) assumed the existence of other reference frames beyond the allocentric and egocentric ones, the explanation of Nonturners' behavior remains speculative and further research is required.

Alpha and attentional demands

The analysis of electrocortical oscillation in the lower alpha band revealed a widespread topography with the most pronounced effects of task and material over posterior regions. Alpha desynchronization patterns proved to reflect attentional processes during the encoding of spatial information, confirming Araújo findings (Araújo et al., 2002) and disagreeing with Klimesch' assumption (1997) that lower alpha does not reflect encoding processes. More precisely, alpha activity showed to be a sign of attentional demand with respect to the amount of information supplied by a stimulus: alpha desynchronization was associated with the processing of stimuli delivering rotational and translational information whereas alpha synchronized when only translational information was present. Furthermore, alpha activity seemed to be independent from task difficulty. Firstly, alpha desynchronization did not linearly increase for increasing number of turns, as theta did, but remained on the same level during the passage when rotational information was supplied. Secondly, similar alpha desynchronization patterns were present in both experiments (blocked and random) although the mental effort and experimental requirements changed.

Finally, in the first experiment alpha activity seemed to vary according to the task to solve although the same information was supplied. The presence of this task dependent effect might reflect a differential weighting of the information gained from the visual input due to the implementation of heading changes into a spatial representation in the HVF and not in the SEF. Although several studies showed posterior areas to be implemented in the processing of heading changes (e.g., Maguire, Burgess, Donnett, Frackowiak, Frith, & O'Keefe, 1998; Morrone, Tosetti, Montanaro, Fiorentini, Cioni, & Burr, 2000), in the present research alpha sensitivity to practice (Gevins et al., 1997) could not be disproved with certainty and further investigations are needed.

In summary, induced oscillatory activity was revealed to be a very useful tool for investigating the encoding of spatial information. Nevertheless, not all hypotheses could be verified. Whereas first evidences could be supplied that both strategy groups employ different spatial representations in the two spatial tasks, the oscillatory bands analyzed did not allow for a distinction of egocentric and allocentric encoding. There are two possible explanations: either some strategy dependent influences were present but did not achieve significance or, alternatively, frontal theta and posterior alpha might reflect features of information encoding processes that are present independent of the strategy or reference frame employed.

CHAPTER V

Early temporal dynamics of retrieval of spatial information in a spatial orienting task: an electrophysiological investigation.

Abstract

The present study investigated the retrieval of spatial information in a virtual navigation tasks by means of behavioral and electrocortical data. After passages through virtual tunnels, two different pointing tasks were employed. The first task allowed subjects to react based on an egocentric or an allocentric reference frame, whereas the second pointing task forced all subjects to react based on an allocentric reference frame. The use of a particular reference frame determines the primitive parameters stored in the resultant spatial representation and reactions based on primitive parameters of a representation are faster compared to reactions based on parameters that need to be derived. Based on reaction times and event-related potentials associated with the onset of the response arrow that had to be adjusted, it was investigated whether subjects used primitive or derived parameters of the spatial representation computed during the task. Analysis of reaction times corroborated the hypothesis that i) Nonturners employed the identical spatial representation in both tasks, whereas ii) Turners adopted distinct reference frames in the two tasks. The analysis of electrocortical parameters revealed the temporal dynamics of several processes preceding the retrieval of spatial information but failed to further support the behavioral results.

Introduction

Neisser referred to the term “cognition” as the sum “of all processes by which the sensory input is transformed, reduced, elaborated, stored, recovered, and used” (Neisser, 1967, p. 4). Spatial cognition as a specific area within the field of Cognitive Psychology focuses on processes regarding the encoding, storage, and retrieval of spatial information. It is almost impossible to investigate each single information-processing step on the bases of inferences from subjects’ reactions at the end of an experimental trial. However, additional recordings and analyses of psychophysiological activity increase the explanatory power of behavioral data and supply further insights about the neural processes accompanying encoding and recalling of spatial information (e.g., Maguire, Frackowiak, & Frith, 1997; Shelton & Gabrieli, 2002). Further, it provides information about processes whose influence on subjects’ reactions is not evident in performance data (see for example Vogel, Luck, & Shapiro, 1998).

The present study focused on the temporal dynamics of retrieval of spatial information using a virtual navigation task that supplies only sparse visual flow information (Gramann, Muller, Eick, & Schönebeck, 2005). Since no landmarks are provided during passages through virtual tunnels, the only process suitable for updating and integrating position and orientation within a spatial representation of the virtual environment is path integration (Loomis, Klatzky, Golledge, & Philbeck, 1999). Burgess (2006) suggested that path integration relies on either an allocentric or an egocentric reference frame. Earlier work using the virtual tunnel task (Gramann et al., 2005; Gramann, Muller, Schönebeck, & Debus, 2006) corroborated this assumption showing that, when subjects had to adjust a homing vector from the tunnel end position to the starting point, the employment of either reference frame was determined by subject’s individual preference. One group of subjects, referred to as

'Turner', adjusted the homing vector based on an egocentric reference frame in which the egocentric bearing from the starting-point was updated during turns and subsequent translations. A second group of subjects, referred to as 'Nonturner', reacted based on an allocentric reference frame not taking heading changes during the passage into account. As a result, this strategy group systematically overturned the homing vector by the amount of the turning angles during the passage (Gramann et al., 2005; Gramann et al., 2006). In the latter study, Turners used the preferred egocentric reference frame for homing vector adjustments but were forced to use an allocentric reference frame to successfully react in a map-like reaction format. Nonturners, in contrast, were supposed to use the same allocentric reference frame in both reaction formats. The reaction formats were randomized and unpredictable on a trial.

A current density reconstruction based on the electrocortical data recorded during the encoding of spatial information revealed different sources of activity for Turners and Nonturners. The presence of distinct neural substrates supporting spatial encoding reflected the use of an egocentric reference frames by Turners and the use of an allocentric reference frame by Nonturners. With respect to the Nonturner group, a single allocentric reference frame was supposed to subserve spatial encoding in both tasks. Turners, in contrast, did not only adopt an egocentric frame of reference. This strategy group also performed well using the allocentric map-like format and therefore allocentric information had to be processed to some extent. There are two possibilities to explain the observed pattern of results: either Turners adopted an egocentric reference frame only and reactions in the map-like format were based on the further processing of egocentric information or, alternatively, ego- and allocentric reference frames were active in parallel. The results from spatio-temporal coupled source reconstruction clearly supported the latter explanation.

In order to gain further insight into the retrieval process, the present investigation adopted two different tasks, the homing vector format (HVF), also employed before (Gramann et al., 2005), and an additional allocentric reaction format, the start-to-end format (SEF). This format required subjects to process the tunnel end-position with respect to the origin of the path. This is possible only on the basis of an external, allocentric reference frame. In a first experiment (blocked condition) the reaction formats were presented in a blocked sequence beginning with the HVF and ending with the SEF. In a second experiment (random condition) the reaction formats were presented in a randomized order with format unpredictable on a trial.

The use of a particular reference frame determines the primitive parameters stored in the spatial representation (Klatzky, 1998). Reactions based on primitive parameters are faster compared to reactions that need to be derived. Based on reaction times, it is thus possible to distinguish whether subjects use primitive or derived parameters for their reactions. If Turners updated distinct spatial representations based on different reference frames according to the task, then their reaction times should be comparable in the HVF and SEF. On the contrary, if only one reference frame is computed during the task, then reaction times would be longer for reactions based on derived parameter as compared to reactions based on primitive parameters. Nonturners were supposed to adopt the same allocentric reference frame in both reaction formats. Thus, their reactions should be equally fast in the HVF and SEF.

Moreover, reactions of both strategy groups should be faster in the first compared to the second experiment. In fact, in the first experiment subjects already know in which format they have to react and thus, with onset of the response arrow, they can directly retrieve information from the mentally computed spatial representation. In the random condition, by contrast, subjects have to discriminate the reaction format to adjust before they can retrieve spatial information.

Besides reaction times, further information about the dynamics of spatial information retrieval can be gained from the analysis of event-related potentials (ERP) associated with the onset of the response arrow. Up to now, only very few studies have applied ERP-methodology to spatial navigation research (Mollison, 2005). Moreover, no one has taken into account the preferred use of distinct spatial strategies hitherto. Consequently, hypotheses about the time-course and waveform of ERP-components elicited during the retrieval of spatial information can only be tentative. The present study was designed to identify components that distinguish between processes supporting reactions based on distinct reference frames. ERPs might reveal processes associated with the discrimination of different spatial representations or the computation of derived parameters needed for a reaction based on a distinct reference frame than the one used during path integration.

Vogel and Luck (2000) identified a posterior N1 effect reflecting a generalized discrimination process. In this study, the authors showed that the N1 elicited during discrimination tasks was larger compared with the N1 elicited by identical stimuli during simple-RT tasks. Similarly, in the present investigation we expected a larger visual evoked N1 with onset of the reaction format for the second as compared to the first experiment. This component should reflect the presence of a discrimination process between different stimuli (response arrows) associated with distinct tasks (HVF vs. SEF) in the second experiment. However, it cannot be concluded that this component also reflects a discrimination of distinct spatial representations. In fact, a distinction between the two reaction formats has to take place before subsequent processes, irrespective of whether this would be a discrimination between spatial representations or a further computation of derived parameters.Any process that may lead to the retrieval of spatial information begins after the response arrows have been identified, and thus this process should be reflected by a component following the N1. One possible component is the P300. This component is supposed (Duncan-Johnson, 1981; Polich, 1987) to be associated with cognitive processes beginning after the signal analysis is completed. Moreover, the P300 is often related to higher attentional demands (e.g., Rösler, 1992). Mollison (2005) identified a posterior P300 component associated with the recognition of target stimuli during drives through complex virtual environments. Referring to Donchin and Coles (1988), the author suggested that this component might be related to the updating of environmental relationships when relevant information is present and thus to reflect attentional processes during navigation. In Mollison's and colleagues' paper, the P3 component was investigated comparing task-relevant and irrelevant cues. This is not the case in the present study, since all response arrows were task-relevant. Nevertheless, some differences in the P3-amplitude might reflect different attentional demands with respect to the task, experiment and preferred strategy.

Method

Subjects

Experiment 1. Due to gender specific differences in navigation tasks (Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000; Lawton & Morrin, 1999; Sandstrom, Kaufman, & Huettel, 1998; Shelton & Gabrieli, 2004) 19 male, healthy volunteers aged between 21 and 33 years (X=23.8, SD=3.6 years) were selected to take part in the experiment. All subjects with normal or corrected-to-normal vision were paid for their participation. Three participants were left-handed. Due to prior findings in the literature (Postma, Jager, Kessels, Koppeschaar, & Honka, 2004), handedness was not considered a decisive factor. Nine participants were categorized as Nonturner and ten as Turner, respectively.

Experiment 2. 18 healthy volunteers aged between 20 and 35 years (X=25.2, SD=3.8 years) were selected to take part in the experiment. All subjects with normal or corrected-to-normal vision were financially compensated for their participation. All but one participant were right-handed. Nine participants were categorized as Nonturner and nine as Turner.

Task, material, and procedure

Experiment 1. Subjects were seated in a darkened room in order to eliminate additional reference information. The task was presented with a beamer (Sanyo PLCXU-47) on a screen positioned at a 1,5 meter distance from the subject. Prior to the main experiment, subjects were categorized with respect to their preferential use of an allo- or egocentric reference frame (Gramann et al., 2005). In a subsequent training session, participants became familiar with the task: the tunnels used in the training session were the same as in the main task but subjects always received strategy-specific feedback about their pointing accuracy.

In the main experiment, subjects had to maintain orientation during passages through virtual tunnels. The first and the last segment of each passage were always straight and all tunnels were of constant length. Tunnels included one turn or two turns (each 50%) of varying angles and ended at eccentricities of 15°, 30°, 45°, and 60° on either side of the starting point. Overall, a total number of 160 trials were tested with 40 additional tunnels with 3 straight segments serving as baseline for the FFT-analyses presented in the previous chapter.

Trials started with a fixation cross for 500 ms followed by a picture of the tunnel entrance shown for 500 ms. Then the virtual journey began. At the end of each tunnel the view out of the last segment was shown for 500 ms followed by the reaction format. Subjects' performance was tested in two reaction formats that were blocked in the first experiment: the first block used the homing vector format (HVF) and the second block used the start-to-end format (SEF). In the HVF, a response arrow was presented on the screen pointing into the depth of the screen and subjects were asked to adjust the arrow from the tunnel end position back to the starting point of the passage. In the SEF, the same arrow was presented pointing towards the navigator and subjects were required to adjust the arrow so that it pointed from the origin of the tunnel passage to the end point of the passage (Figure 5.1).Identical tunnel material was used for both formats.

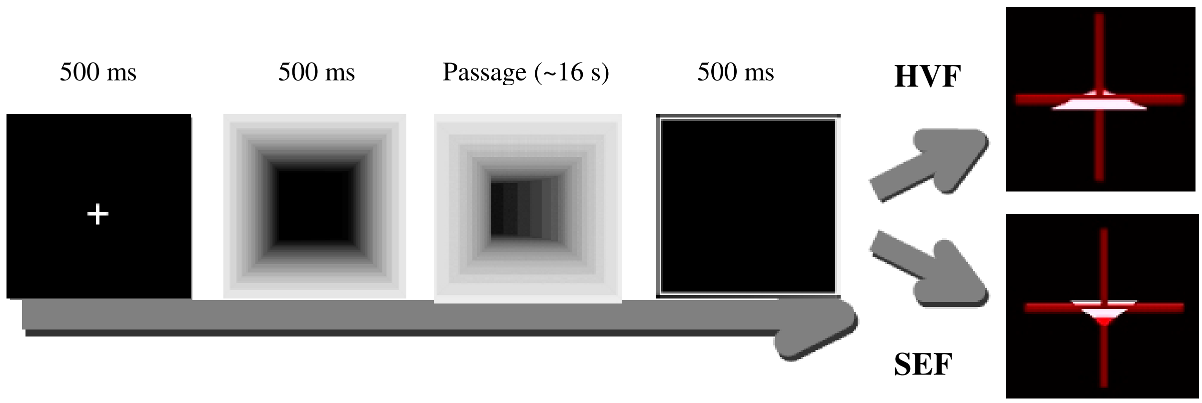

Figure 5.1. A passage through a tunnel is schematically represented. After the passage, reported on the left side, a fixation-cross appeared followed by the response arrow. When the upper arrow appeared subjects had to react in the HVF, whereas the lower arrow required subjects to react in the SEF.

<u>Experiment 2</u>. The experimental design stayed unaltered with the exception of the presentation order of the reaction format: whereas in the first experiment the presentation order of the reaction formats was blocked, here the sequence of

reaction formats was unpredictable on a trial. At the end of each passage, a response arrow appeared: when the arrowhead pointed in the subjects' direction, subjects had to indicate the end-position with respect to the origin of the path (SEF), whereas when the arrowhead pointed into the depth of the screen, subjects had to adjust a homing vector back to the origin of the tunnel (HVF). The same arrows were used in both experiments. An additional change with respect to the previous experiment was the number of tunnels with two turns. The first experiment was equally divided into tunnels with one or two turns. In the present experiment, two-third of the tunnels had two turns. However, only the proportion changed and not the material included in the task. Overall, a total number of 240 experimental trials were used with 20 catch trials that ended up on end positions between the experimental trials to avoid that subjects built up categories of end positions.

Performance measures

Error measures. For studying cognitive processes, it is important to separate correct and incorrect responses. Two criteria were used to indicate incorrect responses, side-errors and format-errors. Reactions indicating the wrong side i) of the tunnel's starting point (left or right) relative to the tunnel's end-point in the HVF or, ii) of the side of the tunnel's end point relative to the starting point in the SEF were considered side-errors. The format error was introduced to distinguish errors that resulted from a confusion of the two reaction formats. Given that the eccentricity of tunnel's end positions varied between 15° and 60° on each side relative to the origin, any reaction corresponding to end positions greater than 90° was considered to be a format error. These two types of error were eliminated from further behavioral as well as electrocortical analyses.

Angular fit. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions provided a measure of the subject's ability to discriminate among varying eccentricities.

Reaction times. To measure reaction times (RT), the delay between the onset of the response arrow and the subject's response was computed.

EEG-recordings

Experiment 1. The electroencephalogram (EEG) was recorded continuously at a sampling rate of 500 Hz using 128 Ag/AgCl electrodes, mounted in an elastic cap (FMS, Herrsching, Germany), according to the extended 10-10 system (American Electroencephalographic Society, 1994). Electrophysiological signals were amplified using a 0.1–100 Hz bandpass filter via BrainAmps (Brain Products, Munich, Germany). Input impedance was kept below 10 kOhm (Ferree, Luu, Russell, & Tucker, 2001). All electrodes were recorded using Cz as reference and were re-referenced off-line to linked mastoids. Vertical and horizontal eye-movements were recorded by means of electrodes placed at the outer canthi of the eyes and the superior and inferior orbits. Ocular correction was computed by means of Gratton and Cole's algorithm (Gratton, Coles, & Donchin, 1983). The continuous EEG-data were filtered with a 0.0159 Hz high pass and a 30 Hz low pass filter and segmented into epochs (-200 ms to 1000 ms) relative to the onset of the reaction format. Epochs exceeding ± 70 µV, violating a voltage step criterion of 80 µV, or with a difference of two values greater than 120 µV were excluded in the individual channel mode from further analyses. Two Turners were excluded from EEG-analyses due to excessive artefacts. Only trials with correct responses were included in further analyses. After a baseline correction using the 200 ms interval preceding the onset of the reaction format, the segments were averaged separately for the HVF and SEF.

The P1, N1, and P3 components were identified by visual inspection of the grand average potentials and the mean amplitudes were calculated separately for the HVF and the SEF using the following time windows: 110-150 ms for the P1-component, 170-200 ms for the N1, and 250-350 ms for the P3.

Experiment 2. In the second experiment, the same EEG-recording and data-analyses criteria were employed as in the first experiment with the exception of the number of electrodes reduced to 64 channels. One Turner was excluded from EEG-analyses due to excessive artefacts.

Results

Behavioral data

Error measures

Experiment 1. Overall, the percentage of side errors was 6.09% with Turners showing a higher percentage of side errors overall (7.31% and 4.72% for Turners and Nonturners, respectively). Format errors (less than 0.63%) were observed under all experimental conditions for both strategy groups.

Experiment 2. Overall, the percentage of side errors was 5.49% with Turners showing a higher percentage of side errors (6.98% and 3.99% for Turners and Nonturners, respectively). Format errors (less than 1.71%) were observed under all experimental conditions for both strategy groups.

Angular fit

Experiment 1. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions revealed a significant positive relationship for both Nonturners [$r(1363)=.985$; $p<.010$] and Turners [$r(1475)=.989$; $p<.010$]. Both strategy groups revealed high positive correlations in the HVF ([r(675)=.992; p<.010] and [r(715)=.997; p<.010] for Nonturners and Turners, respectively) as well as in the SEF ([r(688)=.916; p<.010] and [r(760)=.874; p<.010] for Nonturners and Turners, respectively). Both strategy groups demonstrated high accuracy in angular adjustments for tunnels with one turn (Nonturners [r(701)=991; p<.010]; Turners [r(781)=993; p<.010]) and two turns (Nonturners [r(662)=980; p<.010]; Turners [r(694)=985; p<.010]).

Experiment 2. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions revealed a significant positive relationship for both Nonturners [r(2013)=.985; p<.010] and Turners [r(1947)=.988; p<.010]. Both strategy groups revealed high positive correlations in the HVF ([r(994)=.992; p<.010] and [r(960)=.995; p<.010] for Nonturners and Turners, respectively) as well as in the SEF ([r(1019)=.898; p<.010] and [r(987)=.870; p<.010] for Nonturners and Turners, respectively). Both strategy groups demonstrated high accuracy in angular adjustments for tunnels with one turn (Nonturners [r(690)=989; p<.010]; Turners [r(697)=.993; p<.010]) and two turns (Nonturners [r(1323)=.983; p<.010]; Turners [r(1250)=.986; p<.010]).

Reaction times

A mixed-design ANOVA for reaction times with ‘preferred strategy’ (Turner and Nonturner) and ‘experiment’ (random and blocked experiment) as between-subject factors, and ‘reaction format’ (HVF and SEF) as repeated measure revealed the main effect of ‘experiment’ to be significant [F(1,29)=11.898, p<.002; eta^2=.291], showing longer reaction times for the random (X=981.8 ms, SD=599.2 ms) as compared to the blocked experiment (X=1741.6 ms, SD=625.6 ms). The analysis revealed no further effects.

Electrophysiology

Figure 5.2 displays the grand-average event-related potential (ERP) waveforms (collapsed over reaction format and subject's preferred strategy) elicited with onset of the response arrow for both experiments.

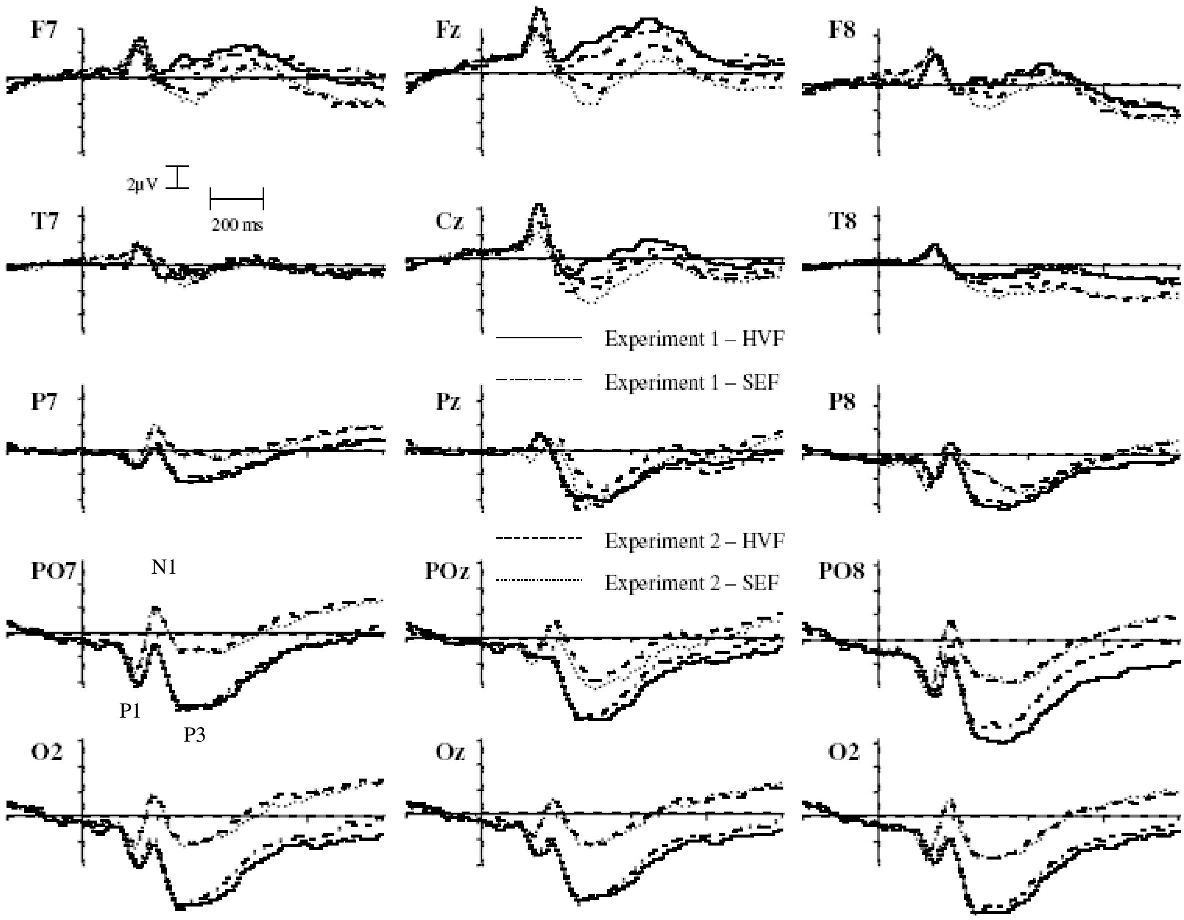

Figure 5.2. Topographical representation of ERP-waveforms (collapsed over strategy) elicited with onset of the response arrow in the HVF and, respectively, SEF for the blocked and random condition.

The waveforms consisted of an early positive deflection with a peak around 130 ms (P1), followed by a negative deflection peaking around 185 ms (N1) and a later positive component around 300 ms (P3). Mean amplitudes of the P1 and N1 components were analyzed by a mixed-design ANOVA with 'preferred strategy' and 'experiment' as between-subject factors and 'reaction format', 'electrode site' (lateral left and lateral right), and 'lobe' (occipital, parieto-occipital, and parietal) as repeated measures. Mean amplitudes of the P3 were analyzed by a similar mixed designed ANOVA except for the 'electrode site' (midline electrodes were added to the lateral left and lateral right ones). Greenhouse-Geisser correction was applied, if necessary.

P1. ANOVA of the mean amplitudes of the P1 component revealed the main effect of 'lobe' [$F(2,60)=37.083$, $p<.001$; $eta^2=.553$] to achieve significance. The effect was qualified by the interaction with the factor 'experiment' [$F(2,60)=3.6802$, $p<.048$; $eta^2=.109$] (Figure 5.3).

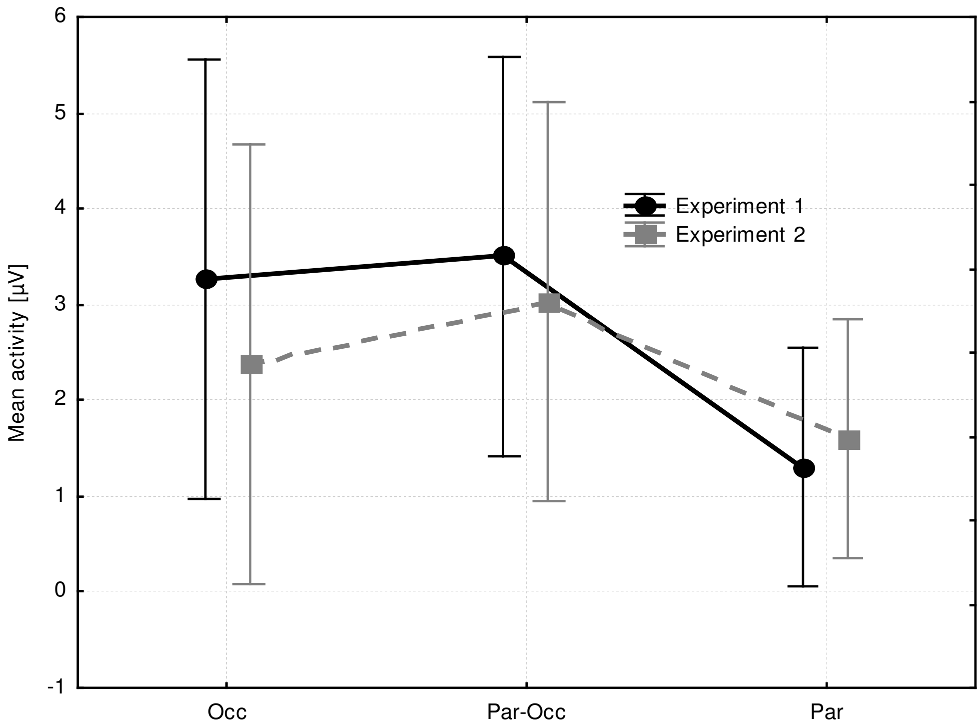

Figure 5.3. Mean activity (± 1 standard error) for the first (continuous line) and second experiment (dashed line) over occipital, parieto-occipital and parietal electrodes (on the x-axis).

The analysis of post-hoc contrasts (LSD) did not reveal any difference between experiments to reach significance. However, slightly different activity patterns were present in the two experiments. In the blocked experiment, higher activity was present over more posterior (occipital and parieto-occipital) electrodes compared to parietal electrodes. In the random experiment, the highest activity was present over parieto-occipital electrodes followed by occipital and then parietal leads.

N1. ANOVA of the mean amplitudes of the N1 component revealed the main effect of 'lobe' [$F(2,60)= 11.166$, $p<.001$; $eta^2=.271$] and 'experiment' [$F(1,30)=8.642$, $p<.006$; $eta^2=.224$] to achieve significance. The effects were qualified by their interaction [$F(2,60)=10.719$, $p<.001$; $eta^2=.263$] (Figure 5.4).

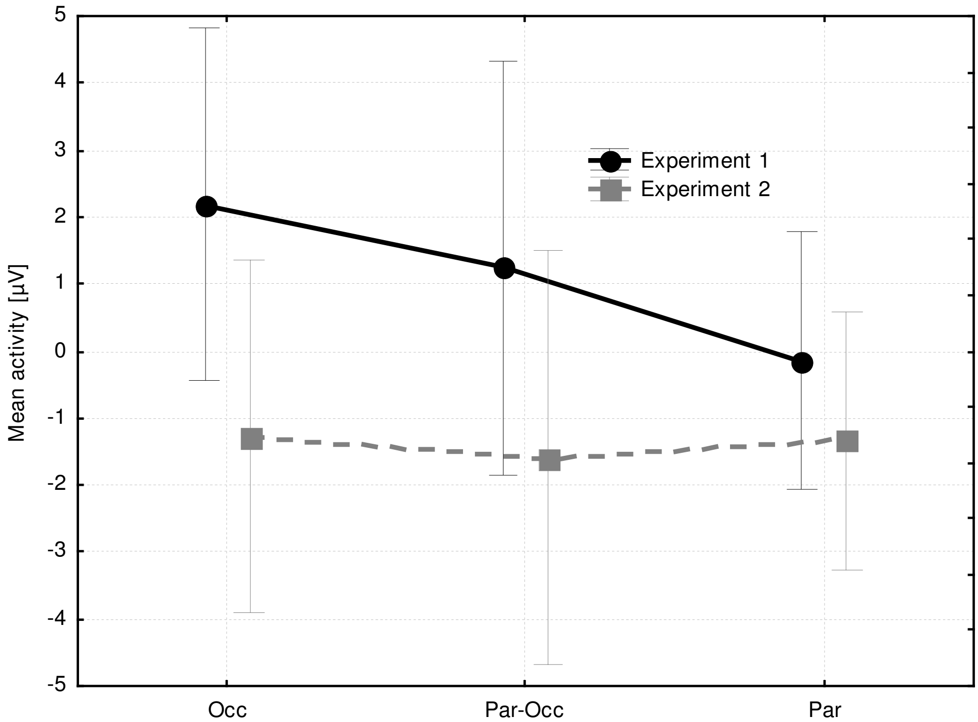

Figure 5.4. Mean activity (± 1 standard error) for the first (continuous line) and second experiment (dashed line) over occipital, parieto-occipital and parietal electrodes (on the x-axis).

The analysis of the post-hoc contrasts (LSD) revealed significant differences between experiments over occipital ($p<.029$) and parieto-occipital ($p<.069$) but not parietal electrodes ($p<.444$) with the N1 deflection being more negative going in the second compared to the first experiment. Furthermore, whereas in the second experiment similar activity was present over all electrodes, in the first experiment the mean activity decreased from parietal to occipital electrodes.

P3. ANOVA of the mean amplitudes of the P3 component revealed the main effects of ‘experiment’ [$F(1,30)=15.297$, $p<.001$; $eta^2=.338$] and ‘lobe’ [$F(2,60)=29.499$, $p<.001$; $eta^2=.496$] to achieve significance. The effects were qualified by the interaction of both factors [$F(2,60)=13.500$, $p<.001$; $eta^2=.310$] (Figure 5.5).

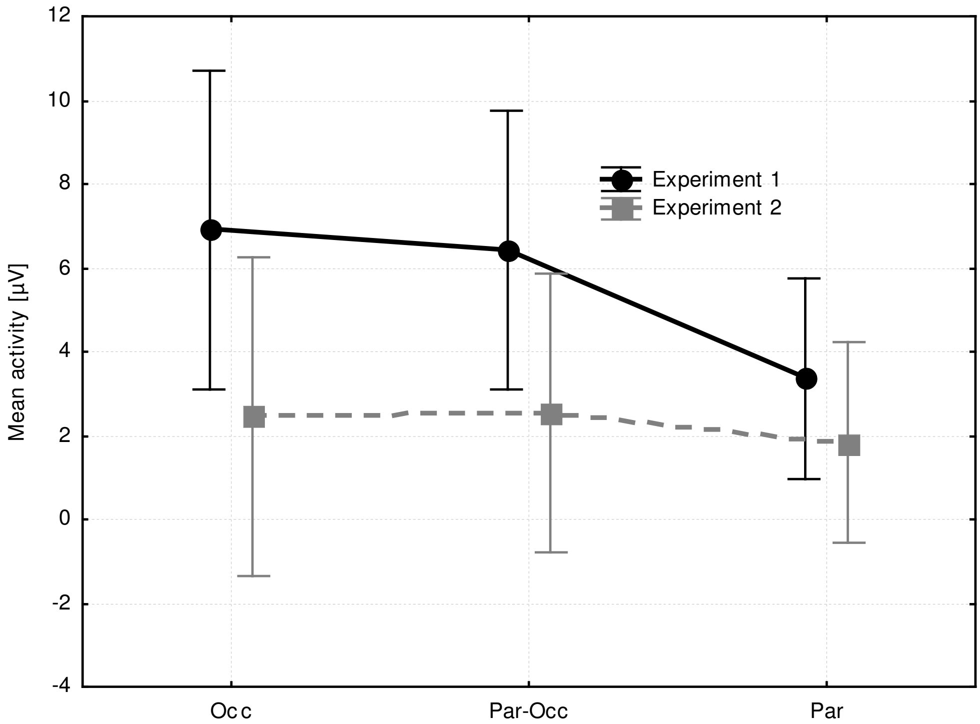

Figure 5.5. Mean activity (± 1 standard error) for the first (continuous line) and second experiment (dashed line) over occipital, parieto-occipital and parietal electrodes (on the x-axis).

The analysis of the post-hoc contrasts (LSD) revealed significant differences between experiments over occipital ($p<.005$) and parieto-occipital ($p<.013$) but not parietal electrodes ($p<.314$) with the P3 deflection being more positive going in the first compared to the second experiment. Furthermore, whereas in the second experiment similar activity was present over all electrodes, in the first experiment the mean activity decreased from occipital and parieto-occipital to parietal electrodes.

The main effects of ‘lobe’ and ‘electrode site’ [$F(2,60)=10.939$, $p<.001$; $eta^2=.267$] as well as the interactions ‘reaction format x electrode site’ [$F(2,60)=6.0757$, $p<.004$; $eta^2=.168$], ‘reaction format x lobe’ [$F(2,60)=3.1742$, $p<.049$; $eta^2=.096$], and ‘electrode site x lobe’ [$F(4,120)=7.9533$, $p<.001$; $eta^2=.210$] were qualified by the higher order interaction ‘reaction format x electrode site x lobe’ [$F(4,120)=4.3109$, $p<.003$; $eta^2=.126$] (see Figure 5.6).

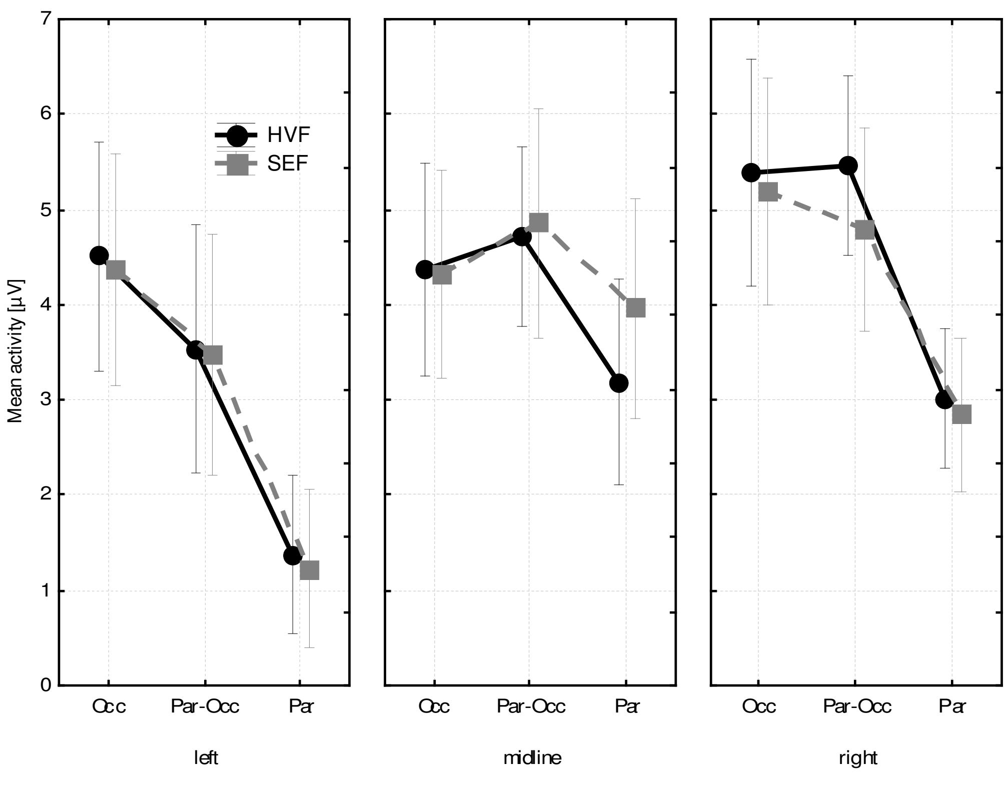

Figure 5.6. Mean activity (± 1 standard error) for the HVF (continuous line) and SEF (dashed line) over occipital, parieto-occipital and parietal regions (on the x-axis) along the lateral left, midline, and lateral right saggittal axis in the left, middle, and respectively right panel.

The analysis of the post-hoc contrasts (LSD) revealed decreasing activity from occipital to parietal electrodes over left, midline, and right regions. The same activity level was present over all leads with exception of PO8 and Pz. At the right parieto-occipital electrode, the P3 was more positive going in the HVF compared to the SEF ($p<.001$). On the contrary, at the midline parietal electrode the P3 component reached higher values in the SEF compared to the HVF ($p<.001$). Finally, different lateralisation effects were present over distinct regions. At occipital electrodes, the highest activity was present at O2 compared to O1 (in both formats: $p<.001$) and Oz (in both formats: $p<.001$). At parieto-occipital and parietal regions, the highest activity was present at midline and right electrodes compared to left electrodes (all $p<.001$) independent of the reaction format.

Discussion

The aim of the present study focused on the nature of the spatial representation adopted for the reaction in two different reaction formats. To this end, two different pointing tasks were employed after passages through virtual tunnels. The HVF allowed two groups of subjects, the Turner and the Nonturner group, to react based on an egocentric or an allocentric reference frame respectively. The SEF, on the contrary, forced all subjects to react based on allocentric coordinates. The analysis of the angular fit revealed both strategy groups to accurately react independent of the task. It remained an open question whether the reactions were based on primitive parameters of the spatial representation employed or, alternatively, whether a further processing of non-primitive spatial information was necessary. For this purpose, the reaction times as well as event-related potentials associated with the onset of the response arrow were analyzed.

The analysis of the RTs confirmed the hypothesis of slower reactions in the second compared to the first experiment. In the first experiment with blocked reaction formats, subjects already knew the task to solve and thus, as soon as the response arrow appeared, they directly retrieved the necessary spatial information. In the second random condition, before subjects retrieved spatial information they had to discriminate between two response arrows related to distinct tasks. This discrimination process required time and led to prolonged reaction times. None of the other factors (reaction format and subject’s preferred strategy) achieved significance. With respect to the Nonturner group, the lack of any reaction format effect supports the hypothesis that this group employed the same spatial representation in both formats. Turners reacted based on spatial parameters relying on different reference systems in the two reaction formats. Nevertheless, no differences in the RTs were present. The comparable reaction speed in the HVF and the SEF supplied evidence that reactions were based on primitive parameters of the spatial representations in both tasks and that no further information processing was required. Further insights into the early dynamics of spatial information retrieval might be gained from the analysis of ERPs.

The first deflection with onset of the response arrow was positive going and reached a peak at about 130 ms. This deflection over posterior lateral electrodes resembled the features of a P1 component (Luck, 2005). In general, the P1 component is associated with early top-down attentional control of ongoing visual information (Taylor, 2002) and is evoked by the visual presentation of stimuli relevant for the task to solve. The P1 can be influenced by the spatial location of stimulus presentation (Hillyard & Anllo-Vento, 1998), the display size (Taylor, Chevalier, & Lobaugh, 2001) or the features of the stimuli used (Wolfe, Cave, & Franzel, 1989). However, all these factors were not manipulated in the present study. The experimental manipulations in the experiments presented here were not expected to affect this component. This was exactly what occurred. In fact, although the presentation order of the reaction formats interacted with the electrode position, P1 amplitudes did not significantly differ at different locations. Thus, in the present investigation the P1 wave reflects the detection of a stimulus that requires a reaction irrespective of the kind of reaction.

The second deflection observed with onset of the response arrow was negative going and reached a maximum at about 185 ms. This component was particularly pronounced over lateral posterior electrodes with a maximum over parietal electrodes and could be categorized as N1 (Vogel & Luck, 2000). Vogel and Luck (2000) have shown in a series of three experiments that under conditions that either required or did not require the subject to perform a discrimination, the N1 elicited during choice-RT tasks was larger compared with the N1 elicited by identical stimuli during simple-RT tasks. The larger N1-component was associated with longer reaction times. The authors excluded an influence on the N1-amplitude modulation of different factors (e.g., arousal or motor-related activity) and suggested this component to reflect the operation of a visual discrimination mechanism. According to Vogel and Luck (2000), the longer reaction times and the enhanced N1-amplitudes found in the present investigation in the random compared to the blocked experimental condition should reflect the presence of a discrimination process. In the blocked condition subjects knew about the task to solve and thus, with onset of the response arrow, they could directly retrieve the spatial information needed to react. In the random condition, by contrast, subjects ignored the task to solve until the response arrow appeared. In this case, it was not sufficient to detect the presence of a response arrow rather it was necessary two discriminate between two different arrows (see Figure 5.1) related to distinct tasks (HVF and SEF). However, it is not possible to conclude that this component also reflects a discrimination of distinct spatial representations: a distinction between the two arrows and the related tasks has to take place before subsequent processes can be initiated, independent of the nature of such processes.

A late positive deflection was observed over posterior electrodes with a maximum at occipital and parieto-occipital electrodes at about 300 ms. This component, classified as a posterior P3, is present in a broad range of experimental paradigms (Rösler, 1992) and, in general, can be associated with cognitive processing beginning after the signal analysis is concluded (Duncan-Johnson, 1981; Polich, 1987). Once the response arrow and thus the orienting task have been identified, different processes might take place. If the spatial representations employed for the reaction are based on distinct reference frames, the spatial information necessary for the reaction can be directly retrieved from the respective representation selected according to the task. In this case, the retrieval of spatial information is supposed to require the same processing resources in both tasks. On the contrary, if only one spatial representation is computed, any reaction requiring a distinct reference frame necessitates a further computation of the spatial information available. This further processing step should require additional resources as compared to the retrieval of information already present in the representation. According to Neumann and colleagues (Neumann, Ullsperger, Gille, Pietschmann, & Erdmann, 1986) and Ullsperger and colleagues (Ullsperger, Gille, Pietschmann, & Neumann, 1986), the P3 might be an adequate indicator of processing difficulty showing increasing amplitudes for increasing task difficulty. In line with this assumption, the P3 was the first ERP component to show an influence of the reaction formats but it was not possible to unequivocally associate one of the two reaction formats to increased processing difficulty. In fact, different amplitude patterns were present over distinct areas: at Pz the onset of the SEF was accompanied by increased amplitudes as compared to the onset of the HVF, whereas the inverse pattern was observed over PO8. However, differential effects dependent on reaction format over distinct regions might also reflect the contributions of different cortical systems to the retrieval of spatial information. This explanation is speculative and further research is necessary.

A further P3-effect was present over occipital and parieto-occipital leads independent of the reaction format and showed the P3-amplitude to be reduced in the second compared to the first experiment. Since there are no reasons to suppose the first experiment to be more demanding than the second experiment, Neumann's (et al., 1986) and Ullsperger's (et al., 1986) assumption of the P3-component as indicator of processing difficulty does not seem to be applicable in the present context. It might be speculated that the P3-amplitude reduction is in fact a sign of a fatigue effect (Polich, 2004; Uetake & Murata, 2000). The parallel computation of several representations in the second experiment could have caused more fatigue than the calculation of individual representations in the first experiment (see also Chapter III and IV). The increased fatigue would thus have resulted in decreased activity of the central nervous system (temporal prolongation of cognitive information processing and a decreased level of attention), which in turn would have been reflected in the lower P3-amplitude (Uetake & Murata, 2000).

In conclusion, the goal of the present research was not completely fulfilled. On the one side, reaction times supplied evidence that Nonturners adopted the same reference frame independent of the task whereas Turners employed different reference frames in the HVF and in the SEF. On the other side, the analysis of electrocortical data did not provide corroborating results. Nevertheless, based on early ERP components some insights into the temporal dynamics of processes preceding the proper retrieval of spatial information could be given. That is, the onset of the response arrow was detected within the first 130 ms as reflected by the P1-component. If the experimental paradigm required subjects to discriminate between two stimuli instead of simply detect their presence, a discrimination process was initiated after about 180 ms from stimulus presentation as reflected by the N1-component. Finally, the P3-component showed to be associated with processes following the stimulus identification. Nevertheless, the nature of the processes related to this latter component could not be determined.

CHAPTER VI

Influence of subject's body position on performance in a virtual path integration task

Abstract

The present study investigated the influence of subject's body position on the processing of spatial information. After the passage through virtual tunnels subjects were asked to adjust a dimensional arrow from the tunnel end position back to the origin of the path. Two groups of subjects performed this task based on different reference frames: 'Turners' were supposed to base their spatial representation on an internal (egocentric) reference frame that remains constant, independently from subject's position. By contrast, 'Nonturners' were assumed to refer to an external (allocentric) reference system that might be more sensitive to changes of their body position with respect to a larger external reference frame. The analysis of several behavioral measures did not reveal any influence of body position for neither subject group.

Introduction

The acquisition of spatial representations during navigation through an environment is a complex task that requires the encoding and integration of multimodal sensory information. However, efficient accurate spatial representations can also be acquired by means of information from one single source, i.e. the visual modality. Several studies (Gramann, Muller, Eick, & Schonebeck, 2005; Richardson, Montello, & Hegarty, 1999; Riecke, van Veen, & Bulthoff, 2002; Witmer, Bailey, Knerr, & Parsons, 1996) supplied evidences that visual input alone is sufficient to compute a spatial representation of the environment experienced. When the available visual information includes only translational and rotational changes and no landmarks are present, the only process that allows for building up a spatial representation is path integration (Loomis, Klatzky, Golledge, & Philbeck, 1999). In this case, the integration of spatial information into a coherent representation can rely on two different reference frames (Klatzky, 1998): the egocentric and the allocentric reference frame. Gramann and colleagues (2005), using a homing vector task after virtual path integration, were able to show that the use of either one of the reference frames was determined by the subject's individual preference for an egocentric or an allocentric reference frame. This preference proved to be stable over the time course of an experiment and even multiple experimental sessions. Subjects preferring an egocentric reference frame were referred to as 'Turner', whereas subjects preferring an allocentric frame of reference were referred to as 'Nonturner'.

In a further EEG-study, Gramann (Gramann, Muller, Schonebeck, & Debus, 2006) localized the sources of electrocortical activity and thus supplied evidences for the existence of distinct neural networks underlying ego- and allocentric encoding during path integration. A subsequent study was designed to validate and further improve the spatial resolution of the source localization by combining EEG and fMRI methods. Both measures were conducted on consecutive days on the same subjects using the identical material. A major problem of this combined study might be the body orientation of subjects during the experiment: while in the EEG-experiment subjects are sitting, in the fMRI-experiment subjects are lying. The present study was designed in order to determine the influence of subject's position (sitting vs. lying) on path integration performance.

Everyday navigation through the environment is always supported by sensory inputs from the vestibular system, which delivers information about movements and orientation. The vestibular system consists of two components: the semicircular canals supply information about rotational acceleration and the otoliths deal with linear acceleration and head orientation with respect to the gravity. Therefore, whereas the semicircular canals are only active during movements, the otoliths are constantly active, even when people are sitting or lying (Mittelstaedt, 1999). That holds true also in case of navigation through virtual environments when only visual information is supplied: the otoliths are always active and, consequently, could influence the navigation performance to some extent under particular conditions. Vidal and colleagues (Vidal, Amorim, & Berthoz, 2004) showed in two experiments requiring subjects to perform 3D-navigation tasks through virtual tunnels that the alignment of the body vertical axis with both, the gravitational axis as well as the axis of references induced by the visual information supplied, improved performance accuracy. Vidal concluded that the gravitational axis might work as key reference axis in human navigation. With a further experiment testing navigation performances in absence of gravity, Vidal and colleagues (Vidal, Lipshits, McIntyre, & Berthoz, 2003) specified that not the gravity played a decisive role in granting more stability to complex spatial representations, but rather a mental representation of an upright position of the body.

According to Vidal's findings, it is possible to expect a deterioration of subject's performance in the lying (fMRI) compared to the sitting (EEG) condition due to a misalignment between subject's upright reference axis and the gravitational axis (see Experiment 2 in Vidal et al., 2004). Furthermore, Turners are supposed to base their spatial representation on an internal reference frame, possibly relying on the midsagittal axis, and this reference frame remains constant, independently from subject's position. By contrast, Nonturners are assumed to refer to an external reference system and, thus, might be more sensitive to changes of their body position (sitting vs. lying) with respect to a larger external reference frame, e.g. the room, where the experiment is taking place.

Method

Subjects

4 female and 5 male, healthy volunteers (aged between 23 and 37 years; X=30.6 years, SD=3.9) participated in the experiment. All subjects had normal or corrected-to-normal vision and were paid for their participation. All participants were right-handed. Five participants were categorized as Nonturner and 4 as Turner.

Task, material, and procedure

Subjects were seated in a darkened room in order to eliminate additional reference information. The task was presented with a beamer (Sanyo PLCXU-47) on a screen positioned at a distance of 2 meter from the subject. Prior to the main experiment, subjects were categorized with respect to their preferred use of an allocentric or an egocentric reference frame (Gramann et al., 2005). In a subsequent training, participants became familiar with the task. In a training session, identical tunnels as in the experiment were used but subjects always received strategy-specific feedback concerning their pointing accuracy.

In the main experiment, subjects had to maintain orientation during passages through virtual tunnels. The first, the third, and the last segment of each passage were always straight, whereas the second and forth segment included turns of varying angles. Tunnels ended at eccentricities of 15°, 30°, 45°, and 60° on either side of the starting point. Subjects' performances in two conditions, the sitting and the lying condition, were compared. The experimental conditions were presented in a balanced design and employed the same material. Overall, a total number of 128 trials were tested with 12 additional filler trials ending up between the end positions of interest to avoid subjects' forming of expected eccentricities.

Trials started with a fixation cross for 500 ms followed by a picture of the tunnel entrance shown for 500 ms. Then, the virtual journey began. At the end of each tunnel, the view out of the last segment was shown for 500 ms followed by the reaction format. When the response arrow appeared, subjects were asked to adjust the arrow from the tunnel end-position back to the origin of the passage.

Performance measures

<u>Side errors</u>. Similar to previous work (Gramann et al., 2005), an important criterion regarding correct reactions was valid indications of the side of the tunnel's start position (left or right) relative to the tunnel's end-point. Side errors might reflect random errors due to a lack of attention or a total loss of orientation. However, previous experiments showed that the amount of side-errors systematically varied with specific tunnel features dependent on the strategy used. Side errors were analyzed separately and eliminated from further analysis.

Angular fit. The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions provided a measure of the subject's ability to discriminate among varying eccentricities.

Absolute error. The absolute error was defined as the absolute difference between the subject's adjustment and the expected reaction. It supplied a valid measure of reaction accuracy.

Relative Error. The signed difference between the subject's and the expected reaction provided a measure of the relative error. This way, possible differences in reactions between Turners and Nonturners with respect to the direction of error (under- or overestimation) were taken into consideration.

Results

Side errors

A mixed design ANOVA was performed with 'preferred strategy' (Turner vs. Nonturner) as between-subject factor and 'condition (sitting vs. lying) as repeated measure. The percentage of side errors was used as dependent variable.

The variable 'condition' did not influence the performances in any way. The results revealed only the main effect of 'strategy' to reach significance [$F(1,7)=28.437$; $p<.001$; $eta^2=.802$], with Turners committing a higher percentage of side errors than Nonturners.

Angular fit

The correlation between the adjusted response vector and the expected angular vector for the various eccentricities of end positions revealed a significant positive relationship for both Nonturners [$r(487)=.990$; $p<.010$] and Turners [$r(336)=.999$; $p<.010$]. Both strategy groups revealed high positive correlations in the 'lying condition' ([r(245)=.991; p<.010] and [r(168)=.999; p<.010] for Nonturners and Turners, respectively) as well as in the 'sitting condition' ([r(242)=.990; p<.010] and [r(168)=.999; p<.010] for Nonturners and Turners, respectively).

Absolute error

A mixed design ANOVA was performed with 'preferred strategy' (Turner, Nonturner) as between-subject factor and 'side of end-position' (left, right), 'condition' (sitting vs. lying), and 'eccentricity of end-position' (15°, 30°, 45°, 60°) as repeated measures. Following main effects 'preferred strategy' [F(1,7)=22.296, p<.002; eta^2=.761], 'side of end position' [F(1,7)=6.796; p<.035; eta^2=.493], and the interaction 'side of end position' x 'preferred strategy' [F(1,7)=7.678, p<.028; eta^2=.523], were qualified by the higher order interaction 'side of end position' x 'condition' x 'preferred strategy' [F(1,7)=7.8159, p<.027; eta^2=.528], displayed in the Figure 6.1. The only post-hoc contrast (HSD) achieving significance regarded the difference between the sides of end position in the lying condition for Nonturners (error < 4°), with the performances being more accurate after tunnels ending at the left compared to the right side of the starting point.

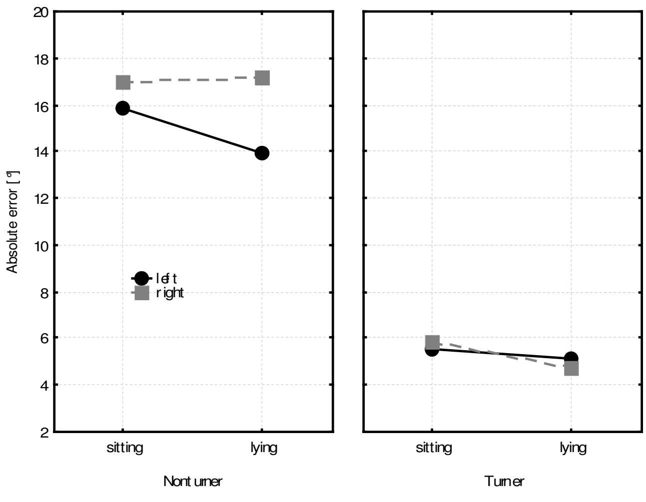

Figure 6.1. Mean absolute error for Nonturners (left panel) and Turners (right panel) as a function of side of end position (continuous line for left end positions and dashed line for right end position) and condition (sitting or lying, on the x-axis).

Relative error

A mixed design ANOVA was performed with 'preferred strategy' (Turner, Nonturner) as between-subject factor and 'side of end-position' (left, right), 'condition' (sitting vs. lying), and 'eccentricity of end-position' (15°, 30°, 45°, 60°) as repeated measures. Greenhouse-Geisser correction was applied, if necessary.

The variable 'condition' did not influence the performances in any way. The main effect of 'eccentricity of end position' [$F(3,21)=12.687$, $p<.007$; $eta^2=.644$], on the other hand, reached significance and was qualified by the interaction with 'preferred strategy' [$F(3,21)=18.620$, $p<.002$; $eta^2=.727$]. Turners did not present any tendency to under- nor over-estimate the eccentricity of end positions. Nonturners, by contrast, increasingly underestimated the eccentricity of the more eccentric end positions (HSD post hoc contrasts). Differences between strategy groups did not reach any significant level.

Discussion

Analyzing the sources of electrocortical activity during path integration, Gramann and colleagues (2006) supplied evidences for the existence of distinct neural networks underlying ego- and allocentric encoding. A further study combining EEG and fMRI methods was conducted for further validate the previous EEG results. Since subject's body position changed in the EEG and fMRI experiments, the present study was designed in order to determine whether subject's position (sitting vs. lying) affects path integration performance. Basing on previous findings (Vidal et al., 2004), changes in the body position were expected to influence Nonturners alone.

The high angular fit supplied evidence that all subjects were able to employ visual input in order to build up high accurate spatial representations (see Gramann et al., 2005, 2006), whereas the analysis of further performance measures corroborated the hypothesis that subject's position (sitting vs. lying) did not influence subject's performance.

The side error-analysis did not reveal any influence of the factor 'condition' and resembled previous findings showing Turners to commit more side errors than Nonturners (see also Gramann et al., 2005). Neither the analysis of the relative error nor the analysis of the absolute error revealed any effect of the factor condition. Nevertheless, this factor appeared in a higher order interaction with respect to the absolute error: the side of end position influenced Nonturners' accuracy in the lying condition alone whereas the effect was not present in the sitting condition. This interaction between 'condition' and 'side of end position' might suggest an influence of Nonturners' position on the performance. However, it is to note that, even if the difference between sitting and lying condition was not significant, the performances in the lying condition were slightly better as compared to the sitting condition and not the other way around. Therefore the results did not agree with Vidal's findings (Experiment 2 in Vidal et al., 2004), according to which the performance would deteriorate in the lying compared to the sitting condition due to a misalignment of subject's upright reference direction and the gravity axis (or its internal representation, see also Vidal et al., 2003). One important difference between Vidal's paradigm and the paradigm employed in this experiment might explain the disagreement: in Vidal's experiments subjects moved through three-dimensional environments, whereas in the present experiment subjects moved within the same level, on a plane.

In summary, subject's position did not affect performances and eventual differences between EEG- and fMRI-measurements cannot be attributed to the position of subjects. The results of this study justify the use of the tunnel paradigm for fMRI measurements.

DEUTSCHE ZUSAMMENFASSUNG

(German summary)

Hintergrund

Zu den zentralen Fragen der Wegfindungs-Forschung gehört die Thematik der Wegintegration (*path integration*). Loomis und Kollegen (Loomis, Klatzky, Golledge, and Philbeck, 1999) definieren Wegintegration als den Integrationsprozess translatorischer und rotationaler Veränderungen während Eigenbewegung einer Person im Raum. Das Resultat dieses Prozesses ist die Aktualisierung der aktuellen Lokation und Orientierung des Navigators innerhalb eines spezifischen Referenzsystems. Die sensorische Information, die für die Aktualisierung einer kohärenten Repräsentation des Raumes notwendig ist, wird aus unterschiedlichen sensorischen Systemen erworben (z.B., Chance, Gaunet, Beall, & Loomis, 1998; Klatzky, Loomis, Beall, Chance, & Golledge, 1998; Mittelstaedt & Mittelstaedt, 1982). Während realer Navigation in natürlichen Umgebungen ist sensorische Information aus allen relevanten Sinnessystemen vorhanden und trägt zur Wegintegration bei. Jedoch genügt auch Information aus einzelnen sensorischen Modalitäten. Zum Beispiel zeigen einige Studien, dass allein visuelle Information den Prozess der Wegintegration unterstützen kann (Gramann, Muller, Eick, & Schonebeck, 2005; Riecke, van Veen, & Bulthoff, 2002).

Die erfolgreiche Aktualisierung einer räumlichen Repräsentation erfordert die Integration sensorischer Inputs innerhalb eines Referenzsystems (Loomis et al., 1999; Kerkhoff, 2000). Klatzky (1998) definierte ein Referenzsystem als ein Mittel für die Repräsentation von Objekten und deren Lokation. Innerhalb der Kognitionsforschung wird angenommen, dass zwei unterschiedliche Arten von Referenzsystemen, ein allozentrisches oder ein egozentrisches System, der Navigation zugrunde liegen kann. Allerdings besteht Uneinigkeit innerhalb der Literatur auf welchem der beiden Referenzsysteme Wegintegration beruht: einige Untersuchungen sprechen dafür, dass Wegintegration auf einem egozentrischen (z.B., Wang & Spelke, 2000), auf einem allozentrischen (z.B., Burgess et al., 2004) oder aber auf einer Kombination beider Systeme beruhen kann (Burgess, 2006).

In einer desktop-basierten Orientierungsaufgabe, die nach einer virtuellen Tunnelfahrt die Einstellung eines Pfeils vom Tunnelausgang zum Startpunkt erforderte (‚Homing-Vektor'), identifizierten Gramann und Kollegen (Gramann et al., 2005) eine individuelle Präferenz für die Verwendung entweder eines egozentrischen oder aber eines allozentrischen Referenzsystems. Eine Gruppe von Versuchspersonen, sogenannte *Turner*, benutzte vorzugsweise ein egozentrisches Referenzsystem, innerhalb dessen das egozentrische *Bearing* des Startpunkts während der Kurven und der darauffolgenden geraden Segmente aktualisiert wurde. Eine zweite Gruppe, als *Nonturner* bezeichnet, integrierte hingegen keine *Heading*-Änderungen innerhalb die räumliche Repräsentation, die für die Reaktion verwendet wurde. Infolgedessen überschätzte diese Strategiegruppe die Ausrichtung des Homing-Vektors um einen der Winkel der Kurvensegmente entsprechenden Wert (Gramann et al., 2005; Gramann, Muller, Schonebeck, & Debus, 2006). Die Autoren interpretierten diese Befundlage dahingehend, dass Nonturners auf Basis allozentrischer Raumkoordinaten antworteten.

Unabhängig von der Strategie der Versuchspersonen musste während der Navigation durch virtuelle Tunnel jedoch ein egozentrisches Referenzsystem aktiv sein, um die aus der Ersten-Person-Perspektive dargebotene Information verarbeiten zu können. Es wurde angenommen, dass Turners nur ein egozentrisches Referenzsystem verwendeten, um eine räumliche Repräsentation während der Fahrt aufzubauen. Welches Koordinatensystem Nonturners verwendeten war unklar: Diese Strategiegruppe konnte egozentrische Information bereits während der Tunnelfahrt in ein allozentrisches Referenzsystem übertragen. Anderenfalls könnten Nonturners nur eine egozentrische Repräsentation aktualisieren. In diesem Fall wäre eine

Weiterverarbeitung der egozentrischen Information am Ende der Fahrt notwendig, um die allozentrischen Parameter zu erwerben, die für die Reaktion verwendet wurden. Für ein besseres Verständnis der der Wegintegration zugrundeliegenden kognitiven Prozesse analysierte Gramann (Gramann et al., 2005) die Homing-Leistungen von Turners und Nonturners in drei Experimenten und konnte zeigen, dass Wegintegration auf unterschiedlichen Koordinatensystemen basieren kann.

Zusammenfassung der durchgeführten Untersuchungen

Die Experimente der vorliegenden Untersuchung wurden mit dem Ziel durchgeführt, den Einfluss unterschiedlicher Referenzsysteme auf die Verarbeitung räumlicher Informationen zu erforschen. Während einer desktop-basierten virtuellen Navigations-Aufgabe wurden sowohl Verhaltens- als auch elektrophysiologische Analysen verwendet. In Kapitel III werden zunächst Verhaltensdaten aus zwei aufeinander folgenden Experimenten analysiert, um zu überprüfen, ob menschliche Wegintegration auf unterschiedlichen Referenzsystemen basieren kann und ob abgrenzbare Referenzsysteme parallel verwendet werden konnten. Die Ergebnisse der in Kapitel III analysierten Leistungsdaten werden durch die Analyse elektrokortikaler Daten in den folgenden Abschnitten ergänzt. In Kapitel IV wird die Enkodierung räumlicher Information anhand langsamer Frequenzbänder (Alpha und Theta) untersucht. In Kapitel V werden Reaktionszeiten und ereigniskorrelierte Potentiale (EKPs) analysiert, um Erkenntnisse über den zeitlichen Verarbeitungsverlauf sowie den Abruf räumlicher Information zum Zeitpunkt der Reaktionsausführung zu gewinnen. Kapitel VI stellt abschließend eine Voruntersuchung für die kombinierte Messung von EEG und fMRT-Daten vor. Diese Untersuchung ist notwendig, um den Einfluss der Körperposition der Versuchspersonen auf die Navigationsleistung zu bestimmen.

Kapitel III. Frühere Untersuchungen (Gramann et al., 2005) zeigten, dass spärlicher visueller Fluss ausreicht, um eine auf verschiedenen Koordinatensystemen basierende räumliche Repräsentation aufzubauen. Mit dem Ziel weiterführende Befunde für diese Daten zu liefern, wurden in der vorliegenden Untersuchung zwei unterschiedliche Reaktionsformat verwendet. Das erste Reaktionsformat (Homing Vektor) konnte von Turners und Nonturners anhand eines egozentrischen oder eines allozentrischen Referenzsystems beantworten werden. Ein zweites Reaktionsformat (Start-to-End-Vektor) hingegen zwang alle Versuchspersonen ein allozentrisches Referenzsystem für die Reaktion zu verwenden. Die Reaktionsformate wurden in einer geblockten (Experiment 1) beziehungsweise zufälligen Reihenfolge (Experiment 2) dargeboten. Die geblockte Abfolge der Formate ermöglichte den Versuchspersonen, jeweils nur eine Repräsentation zu aktualisieren. Die zufällige Reihenfolge sollte hingegen zum gleichzeitigen Aufbau mehrerer Repräsentationen führen. Das Ziel der Untersuchung bestand darin, zu bestimmen, ob beide oder aber nur ein egozentrisches Referenzsystem (z.B., Wang und Spelke, 2000) die Aktualisierung einer räumlichen Repräsentation während menschlicher Wegintegration unterstützt. Falls verschiedene Repräsentationen der Aufgabe entsprechend aktualisiert werden können, sollte die für eine Reaktion notwendige Information am Ende der Fahrt unmittelbar zur Verfügung sein. Sollte hingegen nur ein egozentrisches Referenzsystem verwendet werden, so muss eine auf allozentrischen Parametern basierte Reaktion nach der Fahrt aus einer egozentrischen Repräsentation abgeleitet werden. Weiterhin ist ein unterschiedlicher Einfluss der Darbietungsabfolge der Reaktionsformate (geblockt vs. randomisiert) in Abhängigkeit von der Anzahl der parallel existierenden Referenzsysteme zu erwarten. Die Experimente bestätigen frühere Befunde (Gramann et al., 2005) und zeigen, dass unterschiedliche

Referenzsysteme der Wegintegration zugrunde liegen können. Insbesondere zeigt die Leistungsdatenanalyse, dass Turners in den zwei Aufgaben unterschiedliche Koordinatensysteme für die Aktualisierung verschiedener räumlicher Repräsentationen verwendeten. Schließlich zeigt ein Vergleich der beiden Experimente, dass Turners in der Lage sind, mehrere Repräsentationen parallel aufzubauen, wenn die Aufgabe dies erfordert. Nonturners hingegen scheinen die identische allozentrische Repräsentation in beiden Aufgaben zu aktualisieren.

Kapitel IV. In diesem Kapitel werden die für die Enkodierung räumlicher Information verantwortlichen Prozesse anhand spontaner EEG-Aktivität untersucht. Die Analyse der elektrokortikalen Aktivität beschränkt sich hierbei auf das Theta- und untere Alpha-Band. Die Analyse dieser Frequenzbänder ermöglicht die Analyse von Änderungen der mentalen Beanspruchung der Probanden in Bezug auf das verwendete Material (Bischof and Boulanger, 2003; Caplan et al., 2001) sowie die Allokation von Aufmerksamkeitsressourcen in Bezug auf verschiedene Reizcharakteristika (Klimesch, 1997). Die Ergebnisse weisen keinen Einfluss der Strategiegruppe oder des Reaktionsformates während der Enkodierung visuell-räumlicher Information auf. Jedoch zeigen sich deutliche Unterschiede zwischen der geblockten und der randomisierten Darbietung bezüglich der mentalen Beanspruchung. Eine Beanspruchungszunahme in Experiment 2 im Vergleich zu Experiment 1 weist darauf hin, dass die Wahl des Referenzsystems während der Wegintegration abhängig vom Reaktionsformat, bzw. der Anzahl möglicher Reaktionen ist. Die Daten weisen darauf hin, dass zwei verschiedene Referenzsysteme in Experiment 2 berechnet und verwendet wurden. Die Ergebnisse stimmen mit der Hypothese überein, dass Turners in der geblockten Bedingung (Experiment 1) eine einzige Repräsentation aufbauen, während dieselbe Strategiegruppe in Experiment 2 zwei separate Repräsentationen für die zwei

Aufgaben aktualisiert. Hingegen sollten Nonturners unabhängig von der Darbietungsabfolge der Reaktionsformate keine Zunahme der mentalen Beanspruchung aufweisen. Diese Strategiegruppe sollte in beiden Experimenten anhand eines vergleichbaren allozentrischen Referenzsystems antworten und daher vergleichbare mentale Beanspruchung zeigen. Ausbleibende Strategieeffekte weisen jedoch darauf hin, dass auch Nonturners in beiden Experimenten unterschiedliche Repräsentationen berechnen und nutzen. Am Ende des Kapitels wird die Möglichkeit eines weiteren Referenzsystems kritisch diskutiert.

Kapitel V. Kapitel V fokussiert auf die Analyse von Prozessen des Abrufs räumlicher Information mit Darbietung des Reaktionsformates am Ende der Tunnelfahrt. Anhand von Reaktionszeiten und ereigniskorrelierten Potentialen wird untersucht, ob die Reaktionen der Probanden auf Information beruht, die bereits während der Fahrt berechnet wurde oder, ob eine Berechnung zusätzlicher allozentrischer Information am Ende der Aufgabe notwendig ist. Die Verhaltensdaten zeigen, dass die für eine Reaktion notwendige Information vorhanden und sofort abrufbar ist. Dies spricht für die Annahme, dass die Probanden bereits während der Tunnelfahrt zwei Referenzsysteme nutzen. Die Analyse ereigniskorrelierter Potentiale identifiziert eine Komponente um 300 ms, die mit kortikaler Aktivität während des Abrufs räumlicher Information assoziiert ist. Frühere Komponenten zeigen Aufgabenspezifische Variationen, können jedoch keinen Effekt des Reaktionsformates innerhalb eines Experimentes, noch Unterschiede zwischen den Strategiegruppen nachweisen.

Kapitel VI. In diesem Abschnitt wird eine notwendige Überprüfung des Einflusses der Körperposition auf die Orientierungsleistung vorgenommen. Das Tunnelparadigma soll in Zukunft sowohl in EEG-Studien als auch in Studien mit funktioneller Magnetresonanztomographie (fMRT) eingesetzt werden. Beide

Methoden unterscheiden sich jedoch hinsichtlich der Position des Probanden während des Experimentes. Während die Probanden bei EEG-Untersuchungen zumeist sitzen, liegen sie während fMRT-Messungen in einem Scanner. Obwohl Vidal und Kollegen (2003, 2004) von einem Einfluss der Körperposition auf die Wegintegrationsleistung berichteten, wird in der vorliegenden Untersuchung kein Einfluss unterschiedlicher Körperlagen auf die Orientierungsleistung im Tunnel festgestellt. Somit ist die Verwendung des Tunnelparadigmas für fMRT-Studie gerechtfertigt.

Schlussfolgerungen

Die in der vorliegenden Arbeit dargestellten Experimente zeigen, dass während der menschlichen Wegintegration sowohl ein egozentrisches als auch ein allozentrisches Referenzsystem für den Aufbau räumlicher Repräsentationen verwendet werden kann. Welches spezifische Referenzsystem verwendet wird hängt von den Aufgabenanforderungen und einer individuellen Präferenz zusammen. Turners, die ein egozentrisches Referenzsystem bevorzugen, sind in der Lage abgrenzbare Referenzsysteme zu berechnen und für unterschiedliche Reaktionen zu nutzen. Mindestens zwei Repräsentationen werden während der Navigation aufgebaut und diese enthalten die für unterschiedliche Reaktionen notwendige Information (Kapitel III und V). Wenn Turners die zu lösende Aufgabe kannten, aktualisierten sie eine einzelne Repräsentation (Kapitel III: Experiment 1). Anderenfalls wurden mehrere Repräsentationen parallel aktualisiert, wie die Verhaltensdaten (Kapitel III: Experiment 2) und die gesteigerte mentale Beanspruchung in Experiment 2 (Kapitel IV) zeigten.

Die Verhaltensdaten (Kapiteln III und V) bestätigten die Annahme, dass Nonturners in beiden Aufgaben eine allozentrische Repräsentation verwendeten, die während der Fahrt aktualisiert wurde. Die für die Aufgabenlösung notwendige Information konnte unmittelbar aus der Repräsentation abgerufen werden, ohne dass weitere Verarbeitungsschritte stattfanden. Die Analyse oszillatorischer EEG-Aktivität während der Enkodierungsphase (Kapitel IV) konnte hingegen keine aufgaben-unabhängige Verwendung eines einzelnen Referenzsystems bestätigen. Ähnlich wie bei Turners zeigten Nonturners erhöhte Beanspruchung in Experiment 2 (im Vergleich zu Experiment 1). Eine Beanspruchungssteigerung könnte darauf zurückzuführen sein, dass Nonturners zwei verschiedene Referenzsysteme in den zwei Aufgaben berechneten und dass beide Referenzsysteme, wenn erforderlich, aufrechterhalten wurden. Der verminderte Arbeitsgedächtnisaufwand bei der Aktualisierung einer einzelnen Repräsentation könnte sich in geringerer Theta-Aktivität niederschlagen. Die Existenz einer dritten Form räumlicher Referenzsysteme kann anhand der vorliegenden Daten nur angenommen, nicht aber nachgewiesen werden.

In Vergleich zu vorherigen Untersuchungen (Gramann et al., 2005, 2006) führte die vorliegende Arbeit gewisse Neuerungen ein. Zuerst wurde ein neues Reaktionsformat verwendet, welches Winkeleinstellungen aufgrund von allozentrischen Raumkoordinaten erforderte. Diese Aufgabe zusammen mit der bereits von Gramann (et al., 2005) eingeführten Homing-Vektor-Aufgabe ermöglichte einen Vergleich zwischen egozentrischer und allozentrischer Informations-Verarbeitung nicht nur aufgrund von unterschiedlichen Strategiegruppen (Turner und Nonturner), sondern auch innerhalb einer Strategiegruppe. Eine weitere Neuerung betraf die Verwendung einer Instruktion, welche die Messung von Reaktionszeiten zuließ. Anhand der gemessenen Verhaltensparameter war möglich, zusätzliche Informationen über die Prozesse zu erwerben, die am Ende einer Tunnelfahrt stattfinden. Insbesondere trug die Reaktionszeitanalyse dazu bei nachzuweisen, ob die für eine Reaktion notwendigen Parameter bereits während der Fahrt berechnet wurden oder erst eine weitere Verarbeitung erforderlich war.

Neben den methodischen Neuerungen führte diese Arbeit zwei EEG-Parameter für die Beobachtung unterschiedlicher kognitiver Prozesses ein. Die induzierte oszillatorische Aktivität war mit verschiedenen Aspekten der Enkodierung von räumlichen Informationen assoziiert. Das Theta-Band war hierbei ein reliabler Indikator kognitiver Beanspruchung, während das untere Alpha-Band den Bedarf an Aufmerksamkeitsressourcen bezüglich des Informationsgehaltes eines Stimulus reflektierte. Entgegen den Erwartungen konnte die Analyse ereigniskorrelierter Aktivität jedoch keine entscheidende Erkenntnis in Hinsicht auf den Abruf räumlicher Information bringen. Eine weiterführende Analyse ereigniskorrelierter Aktivität war jedoch aufgrund der geringen Anzahl von Versuchsdurchgängen und der daraus resultierenden geringen Signalstärke eingeschränkt.

Abschließend zeigte die vorliegende Arbeit, dass die Körperposition keinen entscheidenden Einfluss auf die Orientierungsleistung hat (Kapitel VI). Dieser Befund rechtfertigte die Verwendung von Methoden, bei denen die Hirnaktivität der Probanden in einer liegenden Position gemessen wird (z.B. fMRT). Die Nutzung funktioneller Magnetresonanztomographie in Kombination mit EEG-Messungen verbindet die hohe zeitliche Auflösung der Elektroenzephalographie mit der hohen räumlichen Auflösung der bildgebenden Verfahren und ermöglicht somit in Zukunft die genaue Lokalisation von Hirnarealen, die bei der Berechnung und Nutzung unterschiedlicher räumlicher Referenzsystem aktiv sind.

REFERENCES

Aguirre, G. K., & D'Esposito, M. (1999). Topographical disorientation: A synthesis and taxonomy. *Brain: A Journal of Neurology*, **122**, 1613-1628.

Allison, T., Wood, C. C., & McCarthy, G. M. (1986). The central nervous system. In E. Donchin, M. G. H. Coles, and S. W. Porges (Eds.), *Psychophysiology: systems, processes, and applications* (pp. 5-25). New York: The Guilford Press.

Andersen, R. A., Snyder, L. H., Bradley, D. C., & Xing, J. (1997). Multimodal representation of space in the posterior parietal cortex and its use in planning movements. *Annual Review of Neuroscience*, **20**, 303-330.

Avraamides, M. N., Klatzky, R. L., Loomis, J. M., & Golledge, R. G. (2004). Use of Cognitive Versus Perceptual Heading During Imagined Locomotion Depends on the Response Mode. *Psychological Science*, **15**, 403-408.

Bakker, N. H., Werkhoven, P. J., & Passenier, P. O. (1999). The effects of proprioceptive and visual feedback on geographical orientation in virtual environments. *Presence-Teleoperators and Virtual Environments*, **8**, 36-53.

Basar, E., Basar Eroglu, C., Karakas, S., & Schurmann, M. (2001). Gamma, alpha, delta and theta oscillations govern cognitive processes. *International Journal of Psychophysiology*, **39**, 241-248.

Basar, E., & Schurmann, M. (1996). Alpha rhythms in the brain: functional correlates. *News in Pshysiological Science*, **11**, 90-96.

Basar, E., & Schurmann, M. (1997). Functional correlates of alphas panel discussion of the conference 'Alpha Processes in the Brain'. *International Journal of Psychophysiology*, **26**, 455-474.

Berger, H. (1929). Das Elektrenkephalogramm des Menschen. *Archiv fuer Psychiatrie und Nervenkrankheiten*, **87**, 527–570.

Bischof, W. R., & Boulanger, P. (2003). Spatial navigation in virtual reality environments: An EEG analysis. *Cyber-Psychology and Behavior*, **6**, 487-495.

Bremmer, F., Schlack, A., Duhamel, J. R., Graf, W., & Fink, G. R. (2001). Space coding in primate posterior parietal cortex. *Neuroimage*, **14**, 46-51.

Bryant, D. J. (1992). A spatial representation system in humans. *Psycoloquy*, **3**.

Bryant, D. J., & Tversky, B. (1992). Assessing spatial frameworks with object and direction probes. *Bulletin of the Psychonomic Society*, **30**, 29-32.

Bullock, T. H. (1992). Introduction to induced rhythms: A widespread, heterogeneous class of oscillations. In E. Basar & T. H. Bullock (Eds.), *Induced rhythms in the brain* (pp. 1-26). Boston: Birkhauser.

Burgess, N. (2006). Spatial memory: how egocentric and allocentric combine. *Trends in Cognitive Science*, **10**, 551-557.

Burgess, N., Spiers, H. J., & Paleologou, E. (2004). Orientational manoeuvres in the dark: Dissociating allocentric and egocentric influences on spatial memory. *Cognition*, **94**, 149-166.

Caplan, J. B., Kahana, M. J., Sekuler, R., Kirschen, M., & Madsen, J. R. (2000). Task dependence of human theta: The case for multiple cognitive functions. *Neurocomputing*, **32-33**, 659-665.

Caplan, J. B., Madsen, J. R., Raghavachari, S., & Kahana, M. J. (2001). Distinct Patterns of Brain Oscillations Underlie Two Basic Parameters of Human Maze Learning. *Journal of Neurophysiology*, **86**, 368-380.

Chance, S. S., Gaunet, F., Beall, A. C., & Loomis, J. M. (1998). Locomotion mode affects the updating of objects encountered during travel: The contribution of vestibular and proprioceptive inputs to path integration. *Presence-Teleoperators and Virtual Environments*, **7**, 168-178.

Coluccia, E., Mammarella, I. C., De Beni, R., Ittyerah, M., & Cornoldi, C. (2007). Remembering object position in the absence of vision: egocentric, allocentric, and egocentric decentred frames of reference. *Perception*, **36**, 850-864.

Cooper, L. A., & Shepard, R. N. (1973). Chronometric studies of the rotation of mental images. In G. Chase (Ed.), *Visual information processing* (pp. 75–176). New York: Academic Press.

de Araujo, D. B., Baffa, O., & Wakai, R. T. (2002). Theta oscillations and human navigation: A magnetoencephalography study. *Journal of Cognitive Neuroscience*, **14**, 70-78.

Denis, M., Pazzaglia, F., Cornoldi, C., & Bertolo, L. (1999). Spatial discourse and navigation: An analysis of route directions in the city of Venice. *Applied Cognitive Psychology*, **13**, 145-174.

Diwadkar, V. A., & McNamara, T. P. (1997). Viewpoint dependence in scene recognition. *Psychological Science*, **8**, 302-307.

Donchin, E., Callaway, E., Cooper, R., Desmedt, J. E., Goff, W. R., & Hillyard, S. A. (1977). Publication criteria for studies of evoked potentials (EP) in man. In J. E. Desmedt (Ed.), *Progress in clinical neurophysiology: Vol. 1. Attention, voluntary contraction and event-related cerebral potentials* (pp. 1-11). Basel: Karger.

Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, **11**, 357-427.

Donchin, E., Ritter, W., & McCallum, W. C. (1978). Cognitive psychophysiology: The endogenous components of the ERP. In E. Callaway, P. Tueting, & S. H. Koslow (Eds.), *Event-related brain potentials in man* (pp. 349-411). New York: Academic Press.

Duncan-Johnson, C. (1981). P300 latency: A new metric of information processing. *Psychophysiology*, **18**, 207-215.

Farrell, M. J., & Robertson, I. H. (1998). Mental rotation and automatic updating of body-centered spatial relationships. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **24**, 227-233.

Farrell, M. J., & Robertson, I. H. (2000). The automatic updating of egocentric spatial relationships and its impairment due to right posterior cortical lesions. *Neuropsychologia*, **38**, 585-595.

Ferree, T. C., Luu, P., Russell, G. S., & Tucker, D. M. (2001). Scalp electrode impedance, infection risk, and EEG data quality. *Clinical Neurophysiology*, **112**, 536-544.

Fujita, N., Klatzky, R. L., Loomis, J. M., & Golledge, R. G. (1993). The encoding-error model of pathway completion without vision. *Geographical analysis*, **25**, 295-314.

Galati, G., Lobel, E., Vallar, G., Berthoz, A., Pizzamiglio, L., & Le Bihan, D. (2000). The neural basis of egocentric and allocentric coding of space in humans: a functional magnetic resonance study. *Experimental Brain Research*, **133**, 156-164.

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, **7**, 374-385.

Golledge, R. G. (1999). Human wayfinding and cognitive maps. In R. G. Golledge (Ed.), *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes* (pp. 5-45). Baltimore, MD: John Hopkins University Press.

Gramann, K., Muller, H. J., Eick, E. M., & Schonebeck, B. (2005). Evidence of Separable Spatial Representations in a Virtual Navigation Task. *Journal of*

Experimental Psychology: Human Perception and Performance, **31**, 1199-1223.

Gramann, K., Muller, H. J., Schonebeck, B., & Debus, G. (2006). The neural basis of ego- and allocentric reference frames in spatial navigation: Evidence from spatio-temporal coupled current density reconstruction. *Brain Research*, **1118**, 116-129.

Gratton, G., Coles, M. G., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, **55**, 468-484.

Grön, G., Wunderlich, A. P., Spitzer, M., Tomczak, R., & Riepe, M. W. (2000). Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nature Neuroscience*, **3**, 404-408.

Grush, R. (2000). Self, world and space: The meaning and mechanisms of ego- and allocentric spatial representation. *Brain and Mind*, **1**, 59-92.

Hillyard, S. A., & Anllo-Vento, L. (1998). Event-related brain potentials in the study of visual selective attention. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 781-787.

Hillyard, S. A., Mangun, G. R., Woldorff, M. G., & Luck, S. J. (1995). Neural systems mediating selective attention. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (pp. 661-681). Cambridge: MIT Press.

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience*, **15**, 1395-1399.

Jordan, K., Schadow, J., Wuestenberg, T., Heinze, H. J., & Jaencke, L. (2004). Different cortical activations for subjects using allocentric or egocentric strategies in a virtual navigation task. *Neuroreport*, **15**, 135-140.

Kahana, M. J., Seelig, D., & Madsen, J. R. (2001). Theta returns. *Current Opinion in Neurobiology*, **11**, 739-744.

Kerkhoff, G. (2000). Räumlich-perzeptive, räumlich-konstruktive und räumlich-topographische Störungen. In W. Sturm, M. Herrmann, & C.-W. Wallesch (Eds.), *Lehrbuch der klinischenNeuropsychologie* (pp. 411-429). Lisse: Swets & Zeitlinger Publishers.

Kessels, R. P. C., de Haan, E. H. F., Kappelle, L. J., & Postma, A. (2001). Varieties of human spatial memory: A meta-analysis on the effects of hippocampal lesions. *Brain Research Reviews*, **35**, 295-303.

Kirschen, M. P., Kahana, M. J., Sekuler, R., & Burack, B. (2000). Optic flow helps humans learn to navigate through synthetic environments. *Perception*, **29**, 801-818.

Klatzky, R. L. (1998). Allocentric and Egocentric Spatial Representations: Definitions, Distinctions, and Interconnections. In C. Freksa, C. Habel, & K. F. Wender (Eds.), *Spatial cognition - An interdisciplinary approach to representation and processing of spatial knowledge* (pp. 1-17). Berlin: Springer-Verlag.

Klatzky, R. L., Beall, A. C., Loomis, J. M., Golledge, R. G., & Philbeck, J. W. (1999). Human navigation ability: Tests of the encoding-error model of path integration. *Spatial Cognition and Computation*, **1**, 31-65.

Klatzky, R. L., Loomis, J. M., Beall, A. C., Chance, S. S., & Golledge, R. G. (1998). Spatial Updating of Self-Position and Orientation During Real, Imagined, and Virtual Locomotion. *Psychological Science*, **9**, 293-298.

Klimesch, W. (1996). Memory processes, brain oscillations and EEG synchronization. *International Journal of Psychophysiology*, **24**, 61-100.

Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, **26**, 319-340.

Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: a review and analysis. *Brain Research Reviews*, **29**, 169-195.

Klimesch, W., Doppelmayr, M., Russegger, H., & Pachinger, T. (1996). Theta band power in the human scalp EEG and the encoding of new information. *Neuroreport*, **7**, 1235-1240.

Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., & Schwaiger, J. (1998). Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters*, **244**, 73-76.

Klimesch, W., Doppelmayr, M., Schimke, H., & Ripper, B. (1997). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology*, **34**, 169-176.

Klimesch, W., Russegger, H., Doppelmayr, M., & Pachinger, T. (1998). A method for the calculation of induced band power: implications for the significance of brain oscillations. *Electroencephalography and Clinical Neurophysiology*, **108**,123-130.

Klimesch, W., Schack, B., & Sauseng, P. (2005). The functional significance of theta and upper alpha oscillations. *Experimental Psychology*, **52**, 99-108.

Klimesch, W., Schimke, H., & Pfurtscheller, G. (1993). Alpha frequency, cognitive load and memory performance. *Brain Topography*, **5**, 241-251.

Koenderink, J. J. (1986). Optic Flow. *Vision Research*, **26**, 161-179.

Lawton, C. A. (1996). Strategies for indoor wayfinding: The role of orientation. *Journal of Environmental Psychology*, **16**, 137-145.

Lawton, C. A., & Morrin, K. A. (1999). Gender Differences in Pointing Accuracy in Computer-Simulated 3D Mazes. *Sex Roles*, **40**, 73-92.

Loomis, J. M., Klatzky, R. L., Golledge, R. G., Cicinelli, J. G., Pellegrino, J. W., & Fry, P. A. (1993). Nonvisual navigation by blind and sighted: Assessment of path integration ability. *Journal of Experimental Psychology: General*, **122**, 73-91.

Loomis, J. M., Klatzky, R. L., Golledge, R. G., & Philbeck, J. W. (1999). Human navigation by path integration. In R. G. Golledge (Ed.), *Wayfinding Behavior: Cognitive Mapping and Other Spatial Processes* (pp. 125-151). Baltimore (MD): John Hopkins University Press.

Luck, S. J. (2005). *An introduction to the event-related potential technique*. Cambridge (MA): MIT Press.

Maguire, E. A., Burgess, N., Donnett, J. G., Frackowiak, R. S. J., Frith, C. D., & O'Keefe, J. (1998). Knowing where and getting there: A human navigation network. *Science*, **280**, 921-924.

Maguire, E. A., Frackowiak, R. S., & Frith, C. D. (1997). Recalling routes around london: activation of the right hippocampus in taxi drivers. *Journal of Neuroscience*, **17**, 7103-7110.

May, M. (1996). Cognitive and embodied modes of spatial imagery. *Psychologische Beitraege*, **38**, 418-434.

May, M., & Klatzky, R. L. (2000). Path integration while ignoring irrelevant movement. *Journal of Experimental Psychology Learning, Memory, and Cognition*, **26**, 169-186.

Mecklinger, A., Kramer, A. F., & Strayer, D. L. (1992). Event related potentials and EEG components in a semantic memory search task. *Psychophysiology*, **29**, 104-119.

Mellet, E., Bricogne, S., Tzourio-Mazoyer, N., Ghaem, O., Petit, L., Zago, L., et al. (2000). Neural correlates of topographic mental exploration: The impact of route versus survey perspective learning. *Neuroimage*, **12**, 588-600.

Mittelstaedt, H. (1999). The role of the otoliths in perception of the vertical and in path integration. *Annals of the New York Academy of Sciences*, **871**, 334-344.

Mittelstaedt, H., & Mittelstaedt, M. L. (1982). Homing by path integration. In Papi F. & Walraff H.G. (Eds.), *Avian Navigation* (pp. 290-297). New York: Springer.

Mizuhara, H., Wang, L. Q., Kobayashi, K., & Yamaguchi, Y. (2004). A long-range cortical network emerging with theta oscillation in a mental task. *Neuroreport*, **15**, 1233-1238.

Mollison, M. V. (2005). *Event-related potentials in humans during spatial navigation.* Unpublished Undergraduate Senior Honors Thesis, Brandeis University, Waltham, MA, USA.

Morrone, M. C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., & Burr, D. C. (2000). A cortical area that responds specifically to optic flow, revealed by fMRI. *Nature Neuroscience*, **3**, 1322-1328.

Mou, W., McNamara, T. P., Valiquette, C. M., & Rump, B. (2004). Allocentric and Egocentric Updating of Spatial Memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **30**, 142-157.

Neisser, U. (1967). *Cognitive psychology*. New York: Appleton-Century-Crofts.

Neumann, U., Ullsperger, P., Gille, H. G., Pietschmann, M., & Erdmann, U. (1986). Effects of graduated processing difficulty on P300 component of the event-related brain potential. *Zeitschrift für Psychologie*, **194**, 25-37.

Niedermeyer. (1987). The normal EEG of the waking adult. In E. Niedermeyer & F. Lopez da Silva (Eds.), *Electroencephalography. Basic Principles, Clinical Applications and Related Fields.* (pp. 97-117). Baltimore/Munich: Urban and Schwarzenberg.

O'Keefe, J., & Burgess, N. (1999). Theta activity, virtual navigation and the human hippocampus. *Trends in Cognitive Sciences*, **3**, 403-406.

Onton, J., Delorme, A., & Makeig, S. (2005). Frontal midline EEG dynamics during working memory. *Neuroimage*, **27**, 341-356.

Pazzaglia, F., & Beni, R. D. (2001). Strategies of processing spatial information in survey and landmark-centred individuals. *European Journal of Cognitive Psychology*, **13**, 493-508.

Peruch, P., Borel, L., Gaunet, F., Thinus Blanc, G., Magnan, J., & Lacour, M. (1999). Spatial performance of unilateral vestibular defective patients in nonvisual versus visual navigation. *Journal of Vestibular Research: Equilibrium and Orientation*, **9**, 37-47.

Petsche, H., Kaplan, S., von Stein, A., & Filz, O. (1997). The possible meaning of the upper and lower alpha frequency ranges for cognitive and creative tasks. *International Journal of Psychophysiology*, **26**, 77-97.

Pfurtscheller, G. (2003). Induced Oscillations in the Alpha Band: Functional Meaning. *Epilepsia*, **44**, 2-8.

Pfurtscheller, G., & Aranibar, A. (1977). Event-related cortical desynchronization detected by power measurements of scalp EEG. *Electroencephalography and Clinical Neurophysiology*, **42**, 817-826.

Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: Basic principles. *Clinical Neurophysiology*, **110**, 1842-1857.

Polich, J. (1987). Task difficulty, probability, and interstimulus-interval as determinants of P300 from auditory stimuli. *Electroencephalography and Clinical Neurophysiology*, **68**, 311-320.

Polich, J. (2004). Neuropsychology of P3a and P3b: A theoretical overview. In N. C. Moore & K. Arikan (Eds.), *Brainwaves and mind: Recent developments* (pp. 15-29). Wheaton, IL: Kjellberg Inc.

Postma, A., Jager, G., Kessels, R. P. C., Koppeschaar, H. P. F., & Honka, J. v. (2004). Sex differences for selective forms of spatial memory. *Brain and Cognition*, **54**, 24-34.

Presson, C. C., & Montello, D. R. (1994). Updating after rotational and translational body movements: Coordinate structure of perspective space. *Perception*, **23**, 1447-1455.

Reber, A. S. (1985). *Dictionary of Psychology*. London: Penguin Books.

Richardson, A. E., Montello, D. R., & Hegarty, M. (1999). Spatial knowledge acquisition from maps and from navigation in real and virtual environments. *Memory & Cognition*, **27**, 741-750.

Riecke, B. E., van Veen, H. A. H. C., & Bulthoff, H. H. (2002). Visual homing is possible without landmarks: A path integration study in virtual reality. *Presence-Teleoperators and Virtual Environments*, **11**, 443-473.

Roskos-Ewoldsen, B., McNamara, T. P., Shelton, A. L., & Carr, W. (1998). Mental representations of large and small spatial layouts are orientation dependent. *Journal of Experimental Psychology: Learning Memory and Cognition*, **24**, 215-226.

Rösler, F. (1992). *Hirnelektrische Korrelate kognitiver Prozesse*. Berlin: Springer.

Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Cognitive Brain Research*, **6**, 351-360.

Sarnthein, J., Petsche, H., Rappelsberger, P., Shaw, G. L., & von Stein, A. (1998). Synchronization between prefrontal and posterior association cortex during human working memory. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 7092-7096.

Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology*, **57**, 97-103.

Schack, B., Klimesch, W., & Sauseng, P. (2005). Phase synchronization between theta and upper alpha oscillations in a working memory task. *International Journal of Psychophysiology*, **57**, 105-114.

Shelton, A. L., & Gabrieli, J. D. E. (2002). Neural correlates of encoding space from route and survey perspectives. *The Journal of Neuroscience*, **22**, 2711-2717.

Shelton, A. L., & Gabrieli, J. D. E. (2004). Neural Correlates of Individual Differences in Spatial Learning Strategies. *Neuropsychology*, **18**, 442-449.

Shelton, A. L., & McNamara, T. P. (1997). Multiple views of spatial memory. *Psychonomic Bulletin and Review*, **4**, 102-106.

Sholl, M. J. (2001). The role of a self-reference system in spatial navigation. In D. Montello (Ed.), *Spatial Information Theory: Foundations of Geographical Information Science* (pp. 217-232). Berlin: Springer-Verlag.

Squires, N. K., Squires, K. C., & Hillyard, S. A. (1975). Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*, **38**, 387-401.

Taylor, M. J., Chevalier, H., & Lobaugh, N. J. (2001). ERP measures of early processing in feature and conjunction search: increased speed with increased array size. *Psychophysiology*, **38 (Suppl 1)**, S94.

Tversky, B. (1993). Cognitive maps, cognitive collages, and spatial mental model. In A. U. Frank & I. Campari (Eds.), *Spatial information theory: Theoretical basis for GIS* (pp. 14-24). Berlin: Springer-Verlag.

Uetake, A., Murata, A., 2000. Assessment of mental fatigue during VDT task using event-related potential (P300). Proceedings of the 2000 IEEE International Workshop on Robot and Human Interactive Communication, pp. 235–240.

Ullsperger, P., Gille, H.-G., Pietschmann, M., & Neumann, U. (1986). P300 component of the ERP as an index of processing difficulty. In F. Klix & H. Hagendorf (Eds.), *Human memory and cognitive capabilities*. North-Holland, Amsterdam.

van Boxtel, G. J. M. v. (1998). Computational and statistical methods for analyzing event-related potential data. *Behavior Research Methods, Instruments, & Computers*, **30**, 87-102.

Vidal, M., Amorim, M.-A., & Berthoz, A. (2004). Navigating in a virtual three-dimensional maze: how do egocentric and allocentric reference frames interact? *Cognitive Brain Research*, **19**, 244-258.

Vidal, M., Lipshits, M., McIntyre, J., & Berthoz, A. (2003). Gravity and spatial orientation in virtual 3D-mazes. *Journal of Vestibular Research: Equilibrium and Orientation*, **13**, 273-286.

Vogel, E. K., & Luck, S. J. (2000). The visual N1 component as an index of a discrimination process. *Psychophysiology*, **37**, 190-203.

Vogel, E. K., Luck, S. J., & Shapiro, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance*, **24**, 1656-1674.

von Stein, A., & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, **38**, 301-313.

Wang, R. F., & Simons, D. J. (1999). Active and passive scene recognition across views. *Cognition*, **70**, 191-210.

Wang, R. F., & Spelke, E. S. (2000). Updating egocentric representations in human navigation. *Cognition*, **77**, 215-250.

Wang, R. F., & Spelke, E. S. (2002). Human spatial representation: Insights from animals. *Trends in Cognitive Sciences*, **6**, 376-382.

Witmer, B. G., Bailey, J. H., Knerr, B. W., & Parsons, K. C. (1996). Virtual spaces and real world places: Transfer of route knowledge. *International Journal of Human Computer Studies*, **45**, 413-428.

Wolfe, J. M., Cave, K. R., & Franzel, S. L. (1989). Guided search: An alternative to the feature integration model for visual search. *Journal of Experimental Psychology: Human Perception and Performance*, **15**, 419-433.

Wraga, M. (2003). Thinking Outside the Body: An Advantage for Spatial Updating During Imagined Versus Physical Self-Rotation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, **29**, 993–1005.

CURRICULUM VITAE

Davide Riccobon

born on October 10th 1975 in Trieste (Italy)

Academic Education

1994 – 2001	Diploma in Psychology (University of Padova, Italy)
1997 – 1998	Erasmus-Program (Ludwig–Maximilians-University, Munich, Germany)
2002 – 2007	Ph.D. in Psychology (Ludwig–Maximilians-University, Munich, Germany)

Professional Experience

2002 – 2004	Italian Consulate, Munich, employee
2004 – 2007	Department of Psychology, Ludwig–Maximilians-University in Munich, researcher