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Nr. 30

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Biophysiologische Interfaces in der Mensch-Maschine-Interaktion

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Die 1. Berliner Fachtagung zu Biophysiologischen Interfaces in der Mensch-Maschine-Interaktion adressiert das global wachsende Forschungsinteresse an physiologischen Schnittstellen und wendet sich an Wissenschaftler in diesem Bereich. Der Anspruch der Tagung ist es, die Grundlagen aus der Biophysiologie nicht nur isoliert zu betrachten, sondern diese mit Perspektive auf reale Anwendungsfelder in der angewandten Mensch-Technik-Interaktion zu reflektieren und zu diskutieren. Die in diesem Band erschienenen Beiträge spiegeln nicht nur den Querschnitt der eingereichten Beiträge. Vielmehr werden auch die Diskussionen und Anmerkungen aus den einzelnen thematischen Sitzungen aufgegriffen und von den Sitzungsmoderatoren in eigens verfassten Artikeln zusammengefasst.

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Vorwort

Die Interaktion von Menschen mit technischen Systemen wird sich durch die Online-Erfassung biophysiologischer Parameter grundlegend und nachhaltig verändern. Emotionale Interfaces adaptieren an kurz- oder mittelfristige emotionale Zustände der Nutzer. Ambient-Assisted-Living-Systeme unterstützen ihre Nutzer in Abhängigkeit von ihren Leistungsvoraussetzungen und momentanen Zuständen. Automationsstufen werden sich der menschlichen Beanspruchung anpassen. Durch Brain-Computer-Interfaces werden gedankenschnelle Steuerungen technischer Systeme und deren Funktionen möglich.

Die Erforschung dieser neuen, natürlichen und effizienten Interaktionstechnologien ist Gegenstand aktuellster Forschung im Bereich der Mensch-Maschine-Interaktion. Die Erfassung von Veränderungen der Physiologie des Menschen stellt dabei in diesem Kontext eine Vielzahl reichhaltiger Informationsquellen bereit, wenn es gelingt das Potential solcher Signale zu heben um diese in Konzepte der Mensch-Maschine-Interaktion einzubetten.

Durch den Wunsch die unterschiedlichen daran beteiligten Forschungsdisziplinen zusammen zu bringen und durch unsere Faszination an diesem Forschungsgegenstand entstand der Wunsch, eine Arbeitstagung als Forum für intensiven Gedanken- und Erfahrungsaustausch erstmalig zu veranstalten. In Zusammenarbeit des Fachgebietes Mensch-Maschine-Systeme der Technischen Universität Berlin, der HFC Human-Factors-Consult GmbH und dem IEF, Institut für Ergonomieforschung e.V. konnte diese Idee in eine entsprechende Tagung umgesetzt werden.

Die 1. Berliner Fachtagung zu Biophysiologischen Interfaces in der Mensch-Maschine-Interaktion adressiert das global wachsende Forschungsinteresse an physiologischen Schnittstellen und ist als Arbeitstagung konzipiert. Ihr Anspruch ist es, die Grundlagen aus der Biophysiologie nicht nur isoliert zu betrachten, sondern diese mit Perspektive auf reale Anwendungsfelder in der angewandten Mensch-Technik-Interaktion zu reflektieren und zu diskutieren. Daher werden Forschungsergebnisse zusammengetragen und aktuelle Arbeiten beleuchtet, aber auch Zukunftsperspektiven für die Entwicklung von experimentellen und neuen Anwendungsgebieten erarbeitet.

Die Unsicherheit bezüglich des generellen Interesses und der Annahme einer solchen ersten Fachtagung, wich der Überraschung und Freude der Veranstalter über die unerwartet hohe Anzahl und Vielfalt der eingereichten Beiträge. An den eingereichten Beiträgen zeigt sich, dass ein großes Interesse an der Online-Erfassung und Interpretation von Hirnsignalen in diesem Kontext besteht. Die schnell voranschreitende Entwicklung von algorithmischen Verfahren der Mustererkennung macht es möglich, Korrelate menschlicher Kognition in diesen Daten zu erschließen und somit für die Interaktion vom Menschen mit Technik nutzbar zu machen.

Die in diesem Band erschienenen Beiträge reflektieren nicht nur den Querschnitt der eingereichten Beiträge. Vielmehr werden auch die Diskussionen und Anmerkungen aus den einzelnen thematischen Sitzungen aufgegriffen und von den Sitzungsmoderatoren in eigens verfassten Artikeln zusammengefasst.

VR as Promising Tool for Experimental Research on Human Spatial Navigation

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Spatial navigation constitutes a core element for human survival. It describes a complex ensemble of cognitive processes that enable us to reach relevant locations as fast and as energy-conserving as possible. In order to control for the relative contributions of sensory inputs (bottom-up) as well as cognitive strategies and environmental learning (top-down) on navigation performance, virtual reality [VR] has evolved as novel medium in experimental research on human responses to spatial structures, allowing the precise control of experimental stimuli. The present work aimed at disentangling the influence of individual proclivities in the use of distinct reference frames and environmental factors on homing accuracy after path integration. In a VR navigation study participants traversed virtual tunnels constructed from sparse visual flow and were asked to perform a homing task ('point to origin') after passages through tunnels with one or two turns bending into different directions. High-density electroencephalography [EEG] was recorded continuously and co-registered with parameters of trial-to-trial behavioral performance. The results demonstrate that subjects were able to navigate the environment based on distinct but interacting reference frames. The preferred use of a specific reference frame (egocentric or allocentric) was reflected in differential homing patterns and response times as well as EEG dynamics for both strategy groups during navigation. The results demonstrate the advantage of VR-technology for spatial cognition research and can help designing adaptive navigational tools and applications in order to effectively support spatial navigation.

1 Theoretical Background

1.1 Introduction

Humans and other mobile organisms perceive, act upon and think about space. They localize threats, rewards and other agents in their proximal and distal surroundings by extracting spatial information from perceptual systems. This information is used to build up enduring spatial representations comprising information regarding the relative location of starting points, landmarks and destinations, of routes, and environmental layouts. They are also capable to derive information regarding their own position and orientation with respect to the represented entities. This, further, enables humans to locomote within real and virtual environments of varying scale and complexity as well as to interact with objects and other social agents in their surroundings (Etchamendy & Bohbot, 2007; Tversky, 1993). These activities would barely be possible without *spatial cognition*, a complex cognitive function defined as the capacity to acquire, organize, utilize, and revise knowledge about spatial environments in order to achieve a wide variety of goals fundamental to survival. Spatial navigation, as one among other spatial cognitive processes, is defined as planning of travel through the environment by 'determining and maintaining a course or trajectory from one place to another' (Gallistel, 1990, p. 35) following specific evolutionary constraints such as shortest distance, minimal travel time, or maximal safety (Golledge, 1997).

1.2 Spatial Updating – Piloting and Path Integration

As the navigator moves, he has to update his position and orientation with respect to the environment. The information used for updating can be based on position ('*piloting*'), or velocity and acceleration ('*path integration*') (Loomis et al., 1993). Piloting requires the presence of visible, audible or otherwise perceivable exteroceptive cues, so-called 'landmarks', in combination with a map of the surroundings in order to infer one's position and orientation with respect to the environmental entities (Golledge, 1999). Additionally, path integration allows to infer one's current displacement from a given starting point of an excursion by integrating the translational and rotational variation along a traversed trajectory based on external cues, e.g., skylight polarization or the geomagnetic field, *and/or* internal signals, such as vestibular and kinesthetic information, proprioceptive signals from muscles, tendons, and joints, as well as optic and acoustic flow (Mittelstaedt & Mittelstaedt, 1982).

1.3 Spatial Reference Frames

Sensory input, information about the momentary position of the navigator, and long-term enduring action-plans have to be continuously updated, consolidated and integrated into more or less coherent and accurate mental representations. Spatial representations vary in their elaborateness, ranging from rather inflexible route-based sequences of left and right turns to more map-like representations comprising metric parameters and inter-landmark distances. Current research coincides that these representations can be mounted within distinct but interacting spatial reference frames, being defined as a 'means of representing the locations of entities in space' (Klatzky, 1998, p. 1).

Most generally, a distinction is made between a self-centered *egocentric* reference frame and an environment-centered *allocentric* reference frame (Klatzky, 1998). Within the former, space is coded based on the three intrinsically defined axes of the navigator: front–back, right–left, and up–down (Bryant & Tversky, 1999). Distances and directions of entities in space are represented independent of each other, solely related to the navigator's current position and axis of orientation (Aguirre & D'Esposito, 1999). In other words, the world constantly changes around the spatially fixed navigator (Wang & Spelke, 2000). Since this *egocentric locational representation* (Klatzky, 1998) has to be updated with each translation and/or rotation, the resulting spatial representation, comprising *egocentric distances and bearings*, can be characterized as being highly dynamic and instable. By contrast, an *allocentric reference frame* establishes a coordinate system with an origin external to the navigator and an external reference direction (Burgess, 2006; Mou et al., 2006). Within the resulting *allocentric locational representation* inter-object relations are represented independent of the navigator's current position and/or orientation, exclusively related to the external reference properties, implying a map-like survey view of the surroundings with coordinate axes corresponding to the cardinal directions, or the global layout of the environment (Shelton & McNamara, 2004). Also, the navigator himself is represented solely in terms of position, but without any orientation – comparable to a 'you are here'-spot commonly encountered in man-made survey maps of spatial structures (Klippel et al., 2006). Therefore, applying an allocentric reference frame requires the moving navigator to constantly update positional but not orientation-related information, since all *allocentric object-to-object distances and bearings* remain stationary as the navigator proceeds.

Most importantly, humans are able to learn and utilize different reference frames in a flexible way, either in isolation or in combination (Aguirre & D'Esposito, 1999). But whereas some studies suggested that the choice of either reference frame is obligatorily determined by task demands or external features, e.g., the perspective from which an environment is initially experienced (Shelton & Gabrieli, 2002), recent investigations have substantiated the existence of stable individual preferences for coding space within distinct spatial reference frames (Gramann et al., 2005). Behavioral and electroencephalographic (EEG) studies have further supported the assumption of reference frame proclivities and have shown that distinct brain areas subserve the computation and use of an allocentric or an egocentric reference frame (Gramann et al., 2006; Plank, 2009; Seubert et al., 2008).

1.4 Benefits of Virtual Environment Technology

Importantly, these personal affinities for specific reference frames only come to bear when experimental conditions are carefully set up. In order to disentangle the relative contributions of bottom-up perceptual inputs as well as top-down cognitive strategies on navigation performance, virtual reality [VR] has evolved as novel medium in experimental research on human responses to spatial structures, implying several benefits as compared to traditional experimental approaches in real 3D environments or when confronted with 2D stimulation in the lab (Gillner & Mallot, 1998; Peruch et al., 2000).

First, VR allows precisely controlling experimental stimuli and conditions without destructing the 3D characteristics of the presented stimuli (Christou & Bülthoff, 2000). Further, and in contrast to real environments with changing weather conditions, using VR guarantees comparable experimental settings (e.g., constant levels of illumination) for all participants. Second, VR allows for generating stimuli in a flexible and personalized way, dependent on individual performance and other behavioral properties of the observer (e.g., the preference for egocentric or allocentric reference frames). Also, the increased ecological validity of VR facilitates to monitor the process of *natural problem solving* in a continuous manner, being 'more informative than verbal responses in forced-choice paradigms' (Christou & Bülthoff, 2000, p. 321). In this context, VR has opened the way for psychophysiological and neuroscientific research on human spatial navigation. Due to technical constraints, it is, hitherto, not possible to apply imaging techniques (such as functional magnetic resonance imaging, fMRI) or magneto- and electroencephalographic (MEG, EEG) measurements in real environments beyond the laboratory. Since subjects are required to lie in a scanner or sit in a chair, VR permits unconstrained movement within large-scale virtual environments (Bowman et al., 1999). Finally, VR qualifies by its modularity. In contrast to real constructions and mazes, virtually simulated environmental configurations can be built with minimal computational effort.

In the following section, we will present a VR spatial navigation task suitable for the investigation of behavioral and electrocortical correlates of human visual path integration based on individual proclivities for spatial updating within an egocentric or an allocentric reference frame.

2 An Experimental Paradigm – The Tunnel Task

The Tunnel task provides participants with visual flow stimulation of 3D virtual turning tunnels consisting of straight and curved segments (seamless transition between segments; no vestibular input). After the tunnel passages subjects have to adjust a virtual 2D rendering (using perspective depth cues) of a 3D-arrow to point directly back to the starting point of the passage (homing task, see Figure 1). Therefore, the navigator does not only receive spatial movement information, but is also able to respond within virtual space.

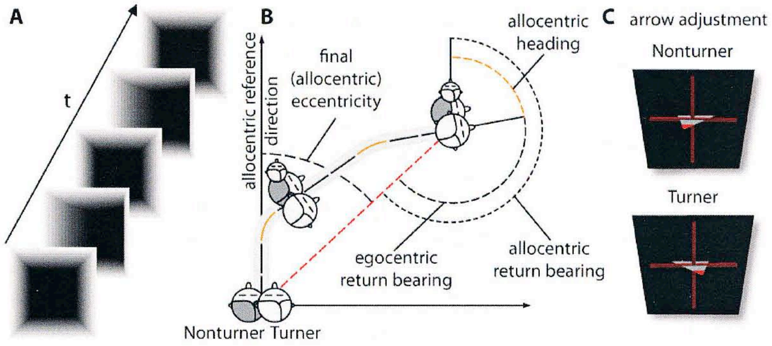

*Figure 1: **(A)** Snapshot of the tunnel with straight and curved segments; **(B)** Return bearings of Turners (using an egocentric reference frame) and Nonturners (using an allocentric reference frame) are initially aligned, but diverge with orientation changes along the trajectory by the angular sum of all turns encountered during the passage; **(C)** Based on the return bearing of the respective reference frames, arrow adjustments of Nonturners and Turners differ. Whereas Nonturners adjust this arrow to point to the left side and back, for Turners the correct solution is an arrow pointing to their right side and back (adapted and modified from Gramann et al., 2006).*

Despite identical experimental stimulation with virtual tunnels and identical task instructions, subjects were found to apply distinct strategies based on the reference frame chosen for updating the homing vector back to the starting point. *Turners*, using an egocentric reference frame, update their *egocentric return bearing* with successive rotations and translations. After a tunnel passage with a rightward turn, their homing arrow typically points to their right behind them. By contrast, *Nonturners*, using an allocentric reference frame, base their arrow adjustment on the *allocentric return bearing* (for further definition of terms see Klatzky, 1998). Since this group establishes a heading-independent allocentric representation of the environment, and all orientation changes of the tunnel passage are set in relation to the reference direction, their final arrow adjustment after the very same rightward-turning tunnel passage points to the left behind them.

In other words, the allocentric homing arrow overestimates the egocentric angular adjustment by the summed angles of rotations encountered along the outbound trajectory (see Figure 1.B, marked in light grey):

'*allocentric return bearing*' = '*egocentric return bearing*' + '*angular sum of turns*' (**eq. 1**)

Although both groups differ in their homing response, it has been shown that the resulting spatial representations are of comparable accuracy (Gramann et al., 2005).

2.1 Aims of the Current Study

Bringing together the excellent temporal resolution of high-density EEG recordings, seminal progress in utilizing scalp EEG recordings for intracortical source reconstruction, as well as VR technology for building up outbound paths of varying complexity, the current study aimed at the identification of generator sources of brain activity as well as macroscopic oscillatory dynamics during egocentric and allocentric path integration at various complexity levels. The central question was whether representational accuracy and response latency of subjects preferentially using an allocentric or an egocentric reference frame diverge as path complexity is increased. Path complexity was operationalized as the number and directions of successive turns (of varying angularity) along an outbound trajectory, and representational accuracy was captured in terms of homing accuracy as well as response latency (time to initiate the homing response).

3 Methods

3.1 Participants

Nineteen male students recruited from the Ludwig-Maximilians-University Munich, Germany, participated in Experiment 1 (age (M±SD) = 23.74 ± 3.62 years), of which ten subjects were categorized as Turners and nine as Nonturners in a pre-experimental session. Participants were either paid 8€ per hour or received course credit for taking part in the experiment. All subjects had normal or corrected to normal vision and reported no history of neurological disorder. All Turners were right-handed, one Nonturner was left-handed.

3.2 Task, Materials, and Procedure

The simulation provided the navigator with sparse visual flow information on translational and rotational changes. Subjects had to keep up orientation while traversing 160 experimental tunnels of modular structure: Each tunnel consisted of several segments (with duration of approx. 1880 ms each), which were either straight or curved. 80 experimental trials consisted of five segments with the turn of varying angularity placed in the third segment [condition '*1 turn*']. Additionally, tunnels with 9 segments were presented with turns (bending into the same direction) placed in segment 3 and segment 7 [condition '*2 turns*'] (see Figure 2). Therefore, subjects could not determine if traversing a tunnel with one or with two turns until either the end of the passage showed up or the tunnel continued with a second turn.

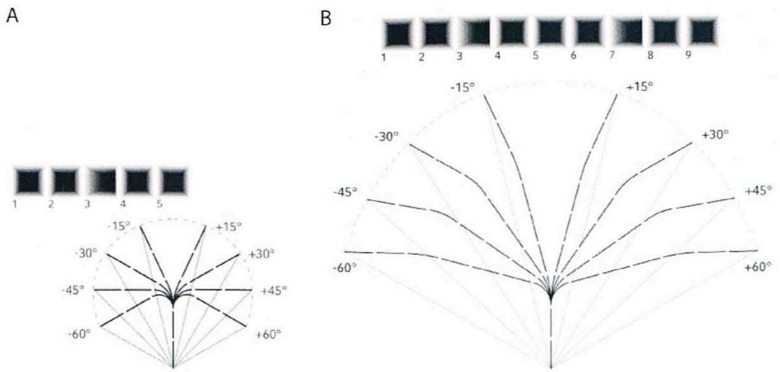

*Figure 2: Tunnel layouts ending at end positions of 15°, 30°, 45°, and 60° eccentricity (± 2° deviation to avoid categorical reactions when adjusting the homing vector) to the left and right with respect to the starting position: **(A)** Condition* 'one turn' *(5 segments, turn located in segment 3), turning angles of 30°, 60°, 90°, and 120°, respectively; **(B)** Condition* 'two turns' *(9 segments, turns located in segments 3 and 7), summed turning angles of 25°, 61°, 80°, and 89°, respectively.*

There were 10 tunnels for each eccentricity of end position to either side. At the end of each passage a 3D homing arrow cue was presented with the arrowhead pointing into the depth of the screen. The task of the subjects was to adjust this homing arrow to point as accurately as possible directly back to the starting point of the passage (pressing and holding left or right mouse button caused the arrow to rotate counterclockwise or clockwise, respectively). When the participant adjusted the subjectively correct homing vector, the setting was confirmed by pressing the middle mouse button, and after a short interval the next trial was initiated.

3.3 EEG Recordings and Analysis

High-density 128-channel EEG recordings were analyzed using Independent Component Analysis (ICA) as implemented in the MATLAB-based EEGLAB toolbox developed at the Swartz Center for Computational Neuroscience, UCSD (Makeig et al., 2004). Generator sources of the obtained independent component (IC) processes were localized within the cortical source domain based on equivalent current dipole model reconstruction (Anemüller, Sejnowski, &Makeig, 2003; Makeig et al., 2004). Event-related spectral perturbations (ERSP) of independent component processes provide insights into continuous brain dynamics covering a wide range of frequencies (ranging from at least 3 to 45 Hz). Individually reconstructed IC sources were clustered using a *K-means* cluster algorithm (Onton & Makeig, 2006).

4 Results

4.1 Behavioral Data

Subjects committed only few side errors (less than 0.95% for all trials) and displayed pronounced correlations ('angular fit') between adjusted and (strategy-specific) expected homing responses (Nonturners vs. Turners: $r_{NT}(144) = .956$, $p < .0001$, vs. $r_T(220) = .923$, $p <$

.0001). Overall angular fit indices of Turners and Nonturners differed significantly ($p < .01$), primarily caused by differences for one-turn tunnels ($p < .02$). Whereas for Nonturners angular fit for tunnels with one turn was higher as compared to tunnels with two turns (Nonturners: $r_{1\text{-turn}}(72) = .976$; $r_{2\text{-turns}}(72) =.937$; ps< .0001; difference: $p < .004$), within the group of Turners, no statistically significant difference was obtained ($r_{1\text{-turn}}(80) = .950$; $r_{2\text{-turns}}(140) = .924$; ps< .0001).

Analysis of response latencies as well as signed error scores was accomplished by means of mixed-design ANOVAs in order to reveal effects of the following factors: 'Number of Turns' (one vs. two), 'Eccentricity of End Position' (15°, 30°, 45°, or 60°, respectively), as well as the between-subjects factor 'Preferred Strategy' (Turners vs. Nonturners). Significant terms were further analyzed with post-hoc tests using the iterative *Holm-Bonferroni* adjustment.

Response latencies to initiate the homing arrow adjustment were found to be affected by the number of successive turns [main effect of Number of Turns; $F(1, 17) = 10.125$, $p < .005$, $\eta_G^2 = .016$], replicating results of Loomis et al. (1993): The more complex the pathway the longer participants took to initiate the homing response. This pattern was more pronounced in Turner subjects [interaction of Preferred Strategy × Number of Turns; $F(1, 17) = 8.432$, $p < .01$, $\eta_G^2 = .013$]. By contrast, Nonturners' responses after traversing tunnels with one turn and two turns were found to be comparable.

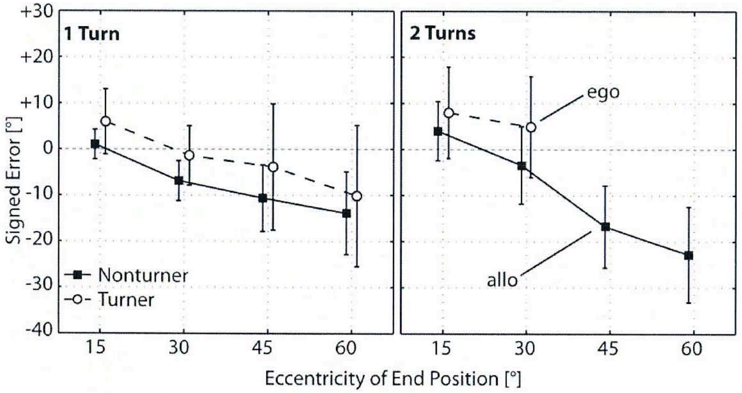

Figure 3: Mean signed error (± 1 SD, depicted by the error bars) of the adjusted homing vector for tunnels with one and two turns, as a function of eccentricity of end position (aggregated over left and right end positions of equal eccentricity), separately for Nonturners (solid line) and Turners (dashed line). Due to (eq. 1) and characteristics of the stimulus material (see description of Figure 2), egocentric and allocentric eccentricities were equivalent for tunnels with one turn only, whereas for tunnels with two turns no equivalence of egocentric and allocentric eccentricities was given. In detail, tunnels with two turns ended at categorical allocentric eccentricities of 15°, 30°, 45°, and 60°, but within an egocentric reference frame laterality was reduced to end positions varying between 10° and 35° eccentricity.

Analysis of signed error (over- and underestimations) revealed a significant main effect of Strategy [$F(1, 17) = 13.086$, $p < .002$, $\eta_G^2 = .224$], and Eccentricity of End Position [$F(1.29, 51) = 27.629$, $p < .0001$, $\eta_G^2 = .175$].

Further, statistical significance was obtained for the interaction of Preferred Strategy × Number of Turns [$F(1, 17) = 5.290$, $p < .034$, $\eta_G^2 = .056$], as well as Preferred Strategy × Eccentricity of End Position [$F(1.29, 51) = 7.532$, $p < .008$, $\eta_G^2 = .058$]. Additionally, the interaction of Preferred Strategy × Number of Turns × Eccentricity of End Position was found to take impact on signed error scores [$F(2.14, 51) = 13.767$, $p < .0001$, $\eta_G^2 = .064$] (see Figure 3). Whereas Nonturners displayed a comparable pattern of overestimating inner and underestimating more lateral end positions for tunnels with one turn and two turns, Turners displayed this regression for tunnels with one turn only. When confronted with tunnels with two turns, their signed error scores were no longer determined by the allocentric eccentricity of end position. Instead, they displayed a comparable level of overestimation at all tested eccentricities. However, when error scores of Turners were computed dependent on the *egocentric eccentricity of end position* (with categorical eccentricities of 15°, and 30°, respectively), a marginally significant trend in signed error was obtained comparable to tunnels with one turn ($p \leq .065$).

4.2 Electroencephalographic Data

A total of 323 IC source processes were obtained. The number of functional ICs in Nonturners and Turners (148 vs. 175) was found to be comparable [$F(1, 312) = 0.364$, $p = .547$]. 22 clusters were computed, with two clusters comprising horizontal and vertical eye movement, respectively, and 20 clusters reflecting cortical generator sources (see Figure 4).

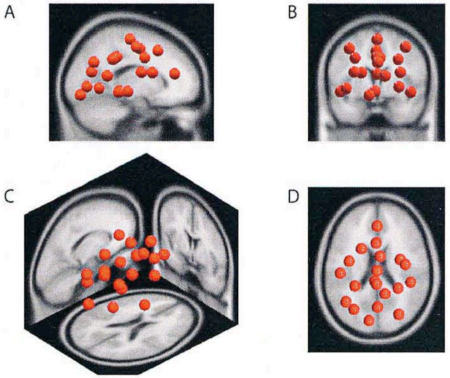

Figure 4: Cluster centroids of 20 reconstructed IC clusters overlaid on the MNI-brain for ***(A)*** *sagittal,* ***(B)*** *coronal,* ***(D)*** *top, and* ***(C)*** *3D view. Cluster locations closely resembled areas previously identified as being crucial for spatial processing within egocentric and allocentric reference frames.*

Analysis of mean event-related spectral perturbation (ERSP) for an IC cluster located in or near midline precuneus (parietal cortex, BA 7/31) revealed strategy-specific patterns of (de-) synchronization as apparent from the significant difference between strategy groups during the second turn (see Figure 5, panel NT-T, black oval frame), since Turners displayed more pronounced (9 – 13 Hz) alpha blocking (desynchronization) when approaching the curved segment.

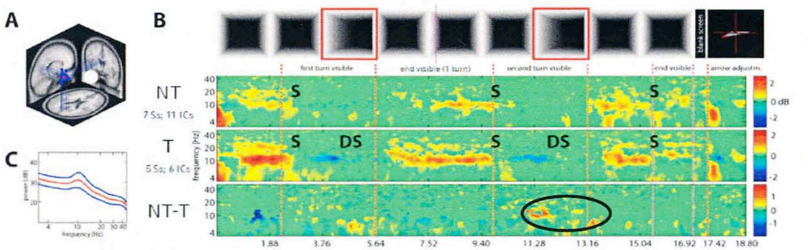

Figure 5: Mean event-related spectral perturbation (ERSP) images for an independent component cluster located in or near midline precuneus (parietal cortex, BA 7/31, panel A) revealing task-dependent changes in spectral power during spatial navigation through tunnel passages containing two turns (panel B) and subsequent homing arrow adjustment. Cluster centroid mean ERSPs are plotted in log-spaced frequencies from 3 – 45 Hz for IC processes of Nonturners (NT), *and Turners* (T). *ERSP difference between Nonturners and Turners is shown in panel* NT-T. *Grey colors indicate no significant (p > 0.001) difference in mean log power (dB) from baseline (mean baseline power [M±SD] depicted in panel C). Darker grey/black indicates significant increases (synchronizations, S) and decreased (desynchronizations, DS) in log power from baseline. Important time points of the tunnel passage are marked with dashed lines, indicating the period when participants perceived the approaching turn and the time period during the stimulus turn (from 3.76 s); the time period during which the subjects were approaching the end of the tunnel, as well as the time point when the virtual homing vector was displayed.*

Mean event-related spectral perturbation (ERSP) images for an IC cluster located in or near medial frontal gyrus (BA 32, not depicted) revealed task-dependent increases (synchronizations) in spectral power during spatial navigation through tunnel passages containing one turn, two turns, and subsequent homing arrow adjustment. For both Turners and Nonturners, a final (4 – 8 Hz) theta burst during tunnels with one turn appeared upon viewing the end of the passage. However, for tunnels with two turns this pattern was temporally shifted. Here, the final theta complex already appeared upon viewing the second turn.

5 Discussion

By utilizing VR technology it was possible to investigate the behavioral and electrocortical correlates of human path integration within egocentric and allocentric reference frames on different levels of pathway complexity. Analysis of behavioral data provided evidence for participants being generally able to not only coarsely distinguish between tunnels ending at the left or right side, but also to accurately adjust the homing vector within their preferred reference frame according to the eccentricity of end position based on the acquisition, maintenance and retrieval of spatial knowledge. Both strategy groups displayed a comparably declining pattern in signed error scores with increasing laterality of end position, which suggests that navigators not only update overall return bearing (a single value that is refreshed in constant intervals irrespective of the path layout) but also store a more or less comprehensive record of the previously traversed pathway on the representational level (i.e., in spatial memory), which, in turn, takes impact on the encoding of novel visuo-spatial information. This is further supported by the analysis of response latency. Particularly for Turners, spatial updating might have been cognitively more demanding during paths of higher complexity as compared to Nonturners, since within an egocentric frame all self-to-object relations have to be constantly updated independent of each other. By contrast, within an allocentric reference frame, the navigator moves in a spatially fixed environment. The present behavioral results support the conceptualizations of Klatzky et al. (1999). In their view, based on trial history, navigators build up route expectancies, so-called 'average pathways', that are retrieved from the representational level in a top-down manner whenever cognitive demands or memory-loss constrain a purely bottom-up encoding of incoming spatial information.

Consistent with recent imaging studies on spatial navigation (Committeri et al., 2004; Galati et al., 2000; Maguire et al., 1998; Wolbers et al., 2007) and processing of visual flow information (Culham et al., 2001; Sunaert et al., 1999), the present investigation resembled a wide-ranging cortical network of IC source with spectral dynamics mirroring the processing of translational and rotational information during curved tunnel segments from a first-person perspective, including bilateral activity in premotor cortices (BA 4/6). These were accompanied by alpha (near 10 Hz) blocking in occipito-parietal areas and lateral temporal/frontal midline theta (near 6 Hz) activation. Turners encoded spatial information primarily within occipito-parietal and parietal cortices subserving the construction of the egocentric reference frame, whereas for Nonturners ventral activation was increased, complemented by retrosplenial activation, the transition zone between reference systems (Maguire, 2001). In addition to the reference-frame-specific activation patterns in the depicted regions, both Turners and Nonturners displayed increased frontal midline theta activity when traversing tunnels with two turns. These results replicate and extend previous findings on electrocortical activity during path integration (Gramann et al., 2006; Riccobon, 2007).

Future research has to address how the present results transfer to more general navigation tasks in realistic 3D virtual environments, e.g., when additional ideothetic information from the vestibular system is present, or allothetic cues such as landmarks are available. Spatial encoding should be significantly altered, as suggested by Foo and colleagues (2007). However, these near-real-world tasks require the precise control of experimental stimulation as well as the integration of data obtained by motion-capture technology in order to examine the impact of movement planning and execution on EEG dynamics. Immersive VR systems utilizing mobile brain imaging (Makeig et al., in press) might constitute the seminal basis for further investigation of complexity effects on behavioral and electrocortical correlates of allocentric and egocentric navigation under more natural conditions.

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