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Research Report

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

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ABSTRACT

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

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1. Introduction

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

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

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

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

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

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

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

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

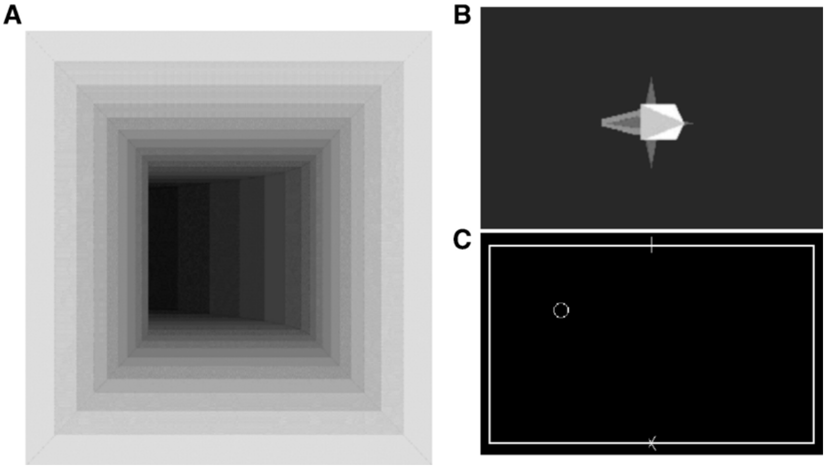

Fig. 1 – (A) View into a tunnel with a turn to the left; (B and C) depiction of the two reaction formats used in the experiment with (B) the homing arrow after rotation pointing towards the navigator, in the example indicating a position to the right of the navigator, and (C) the map-like reaction format with a cross indicating the origin of a path and a line at the end position of a (possible) tunnel without turn. The circle, which the subject had to move to the tunnel's end position, indicates a possible end position on the left side relative to the origin.

associated with the computation of an ego- and, respectively, an allocentric spatial representation. Since the representation of spatial information differs between the egocentric and allocentric reference frames after imagined body rotation (see Fig. 2 for a detailed description), distinct activation patterns dependent on the trajectory would be expected at two stages during the passage: (1) at the onset of the tunnel movement, where a straight segment is presented, there should be no differences between the ego- and allocentric frames of reference (because the underlying coordinate systems do not differ during the initial segment); (2) during the turn, however, differences between turners and nonturners would be expected to emerge, because the coordinate systems underlying the ego- and allocentric reference frames diverge at this point; (3) finally, differences in cortical activation patterns would also be expected for straight segments after a turn,

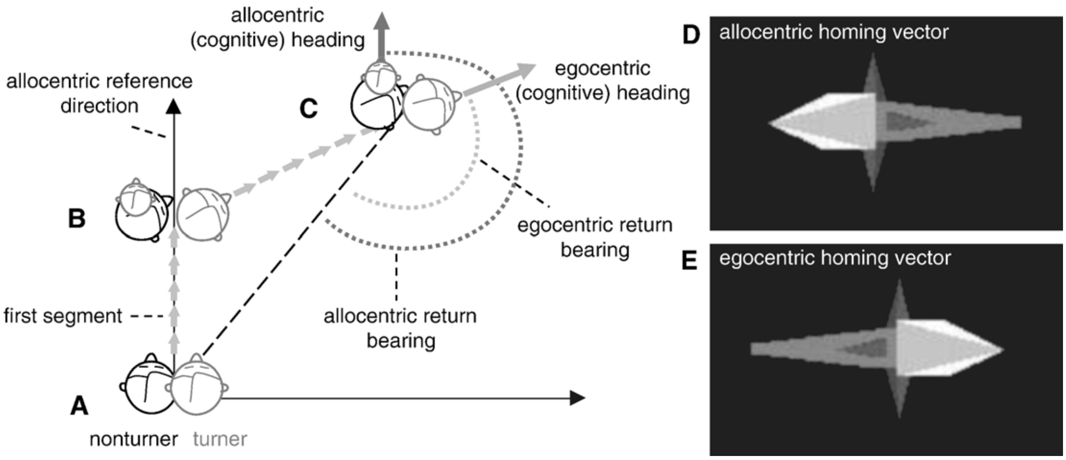

Fig. 2 – Depiction of a passage through a tunnel with a turn to the right, with nonparallel start and end segments. The left-side displays a nonturner (dark grey head representing the perceived heading and the small light grey head representing the cognitive heading) using an allocentric frame of reference, with the navigator's heading during the first segment (A), during the turn (B), and during the last segment (C) of the tunnel passage. 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, the axis of orientation changes (B). At the end of the tunnel, the turner's cognitive heading is different from that of a nonturner. Note that turners build up an additional allocentric frame of reference if they are forced to react based on an allocentric frame. There is no depiction of an additional allocentric reference frame for turners 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 nonturners, and panel E that for turners.

because the egocentric reference system would be rotated relative to the initial segment, whereas the allocentric frame would still be aligned.

2. Results

2.1. Behavioral results

2.1.1. Performance measures

For investigating homogeneous cognitive processes, it is crucial to distinguish between correct and incorrect solutions of the tunnel task and to omit trials on which the navigator might have lost orientation from further analysis.

2.1.2. Side errors

One simple criterion for a correct solution is provided by valid indication of the side of the tunnel's end position, left or right, relative to the origin. Reactions indicating the wrong side will be referred to as 'side errors'. Such errors might reflect simple confusion of left and right or total loss of orientation. Side errors were analyzed separately and eliminated from further analysis.

2.1.3. Angular fit

As a criterion of the accuracy of the spatial representation, participants should be able to differentiate between varying eccentricities of end position within the virtual environment. As an indicator of a participant's ability to discriminate among these eccentricities, the correlation between the adjusted homing vector and the true angular vector for the various eccentricities of end positions was calculated.

The behavioral data were analyzed separately for responses with the homing arrow and the map-like reaction formats (for more extensive analyses, see Gramann et al., 2005).

2.1.4. Side errors—homing vector

Only few side errors were made with the homing arrow (<1.6%), independently of the eccentricity of end position and the preferred reference frame (turners versus nonturners). The frequency of side errors was too small for further statistical analysis.

2.1.5. Angular fit—homing vector

Increasing eccentricity of end position was associated with a corresponding increase in the adjusted homing vectors. Separate correlations of eccentricity of end position with angular adjustment for both strategy groups' preferred reference frame revealed this relationship to be significant, for both turners and nonturners: $r(48) = 0.948$, $p < 0.0001$, and $r(46) = 0.977$, $p < 0.0001$, respectively.

2.1.6. Side errors—map format

Hardly any side errors were made when adjusting the end positions with the map-like reaction format (<0.4%).

2.1.7. Angular fit—map format

Furthermore, with the map-like reaction format, participants' angular adjustments were significantly correlated with the eccentricities of end position, $r(92) = 0.975$, $p < 0.0001$. This was the case for both turners and nonturners: $r(46) = 0.971$, $p < 0.0001$, and $r(46) = 0.985$, $p < 0.0001$, respectively.

2.2. Electrophysiology

The question at issue was whether the use of differential orientation strategies (using an ego- or an allocentric frame of reference) would be reflected by activation within distinct cortical structures. Fig. 3 presents the superimposed grand average data, separately for the five selected turners and the five nonturners. With the onset of the tunnel movement (Fig. 3A), several peaks of activity can be discerned, which were similar for both strategy groups. Fig. 3B presents the grand average waveforms related to the onset of a turn in the tunnel passage. Compared to tunnel movement onset, the peak amplitudes are clearly reduced. However, since the turn was not accompanied by an abrupt luminance change or movement onset, these data represent averaged activity in the absence of a clearly marked stimulus onset. The same holds true for the onset of the first straight segment after a turn (Fig. 3C). The superimposed average waveforms show variations in amplitude, but no clear peaks, again due to the absence of a luminance change or movement onset. Note that the visual flow information provided by tunnel 'events', such as the onset of a turn or a straight segment after a turn, cannot be locked to a distinct point in time and information processing is likely to vary to a substantial degree among different participants. Therefore, we refrained from further analyzing event-related potentials.

2.3. Source reconstruction

2.3.1. Onset of tunnel movement

First, cortical areas activated with the onset of the tunnel movement (straight segments only) were identified. For turners and nonturners, the following areas revealed activity of at least 75% of the maximum strength in three or more of the five participants who used an ego- and, respectively, an allocentric reference frame for navigation (see Table 1).

The use of an *egocentric* frame (turners) activated a bilateral occipito-temporal network, with additional activation in frontal cortex. This network included a set of occipital regions, comprising the cuneus as well as the inferior, middle, and superior occipital gyri, with dominance over the right hemisphere. Activation within temporal cortex ranged from the posterior part, including the parahippocampal and fusiform gyri, to the more anterior part, including the middle temporal gyrus. Activation within frontal cortex was observed within the medial part of the insula and the more anteriorly located middle frontal gyrus.

In contrast, the use of an *allocentric* frame of reference (nonturners) was accompanied by activation within a bilateral temporo-occipital network that included the anterior occipital regions and the fusiform gyrus at the border to the temporal cortex, and the middle temporal gyrus over both hemispheres. Substantial overlap in activation patterns was found for both strategy groups bilateral within extrastriate cortex (BA 19) and temporal gyri (BA 20 and BA 21). However, only turners revealed dominant activation within the left and right cuneus

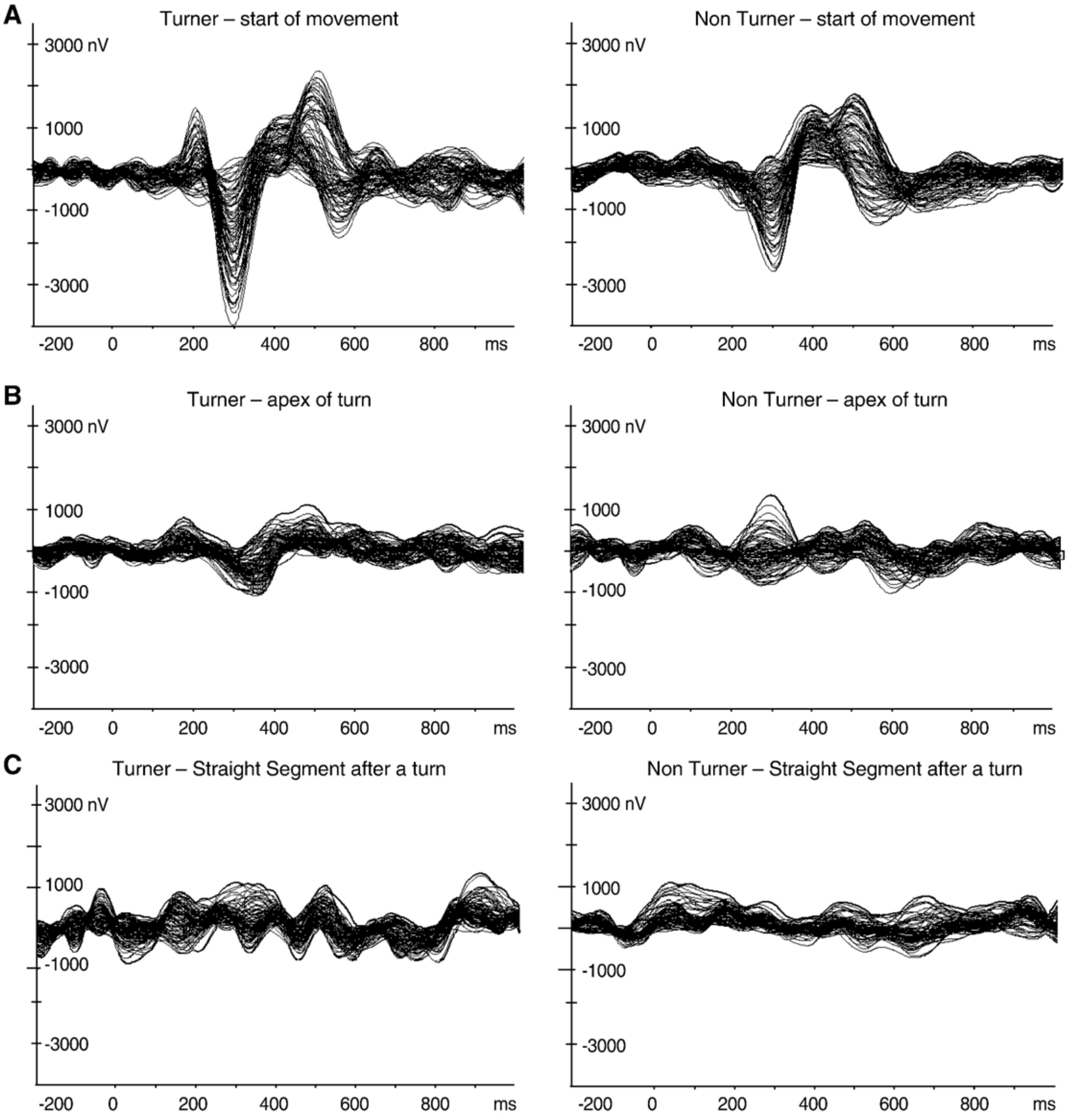

Fig. 3 – Superimposed grand average waveforms from 96 channels time-locked to the onset of tunnel movement (A), the apex of turns in the tunnel passage (B), and the onset of straight segments following turns (C). The left and right columns display grand average waveforms for turners and nonturners, respectively.

and, in addition, within the left middle frontal gyrus. No such frontal activity was observed for nonturners by means of the above described criteria (Fig. 4).

2.3.2. *Apex of turn*

The second set of comparisons, for the turn in the tunnel passage, revealed differences in cortical activation between turners and nonturners, who used an ego- and an allocentric reference frame, respectively. During the turn, the egocentric and allocentric coordinate systems started to diverge, due to the rotation of the egocentric system. Dominant activity was observed within in the following regions (see Table 2).

For *turners* (egocentric frame), a fronto-parietal network, with dominance over the left hemisphere, was activated. This included a set of posterior parietal regions, comprising the left and right precunei and the paracentral lobule. In the frontal lobe, smaller regions were activated in lateral premotor cortex, near the intersection of the precentral and superior frontal sulci, as well as bilateral activations in the medial frontal gyrus. In contrast, *nonturners* (allocentric frame) exhibited major activation only within the left anterior cingulate gyrus in three out of five participants. No other regions displayed significant activation in terms of the criteria described above.

2.3.3. *Straight segment after turn*

For the straight segment after a turn, the reconstruction revealed the following activation patterns for turners and nonturners, respectively (see Table 3).

Turners (egocentric frame) exhibited prevailing activity bilaterally within a fronto-parietal network including regions that were activated both with the onset of the tunnel movement and during the turn in the tunnel passage. The posterior parietal network included a set of regions comprising the precuneus and the postcentral gyrus over the left hemisphere.

Table 1 – Brain areas activated with the onset of the tunnel movement, separately for turners and nonturners

Regions	x	y	z	BA	Max strength	Participants
Turners						
Right cuneus	13	−102	−1	BA 18	1.00	3/5
Right cuneus	8	−90	17	BA 18	0.86	4/5
Left cuneus	−14	−101	−3	BA 18	0.85	3/5
Right superior occipital gyrus	41	−82	28	BA 19	0.81	5/5
Right middle occipital gyrus	56	−63	−5	BA 19	0.75	5/5
Right inferior occipital gyrus	37	−80	−1	BA 19	0.77	5/5
Left fusiform gyrus	−45	−21	−15	BA 20	0.81	5/5
Right middle temporal gyrus	56	−35	−11	BA 20	0.77	5/5
Right superior temporal gyrus	51	−27	3	BA 22	0.77	5/5
Right Insula	43	10	−2	BA 13	0.80	5/5
Left middle frontal gyrus	−29	42	−5	BA 11	0.75	3/5
Nonturners						
Left inferior occipital gyrus	−42	−77	−2	BA 19	0.88	5/5
Right inferior occipital gyrus	35	−74	−4	BA 19	0.75	3/5
Right fusiform gyrus	48	−66	−10	BA 19	0.81	5/5
Left fusiform gyrus	−46	−64	−15	BA 37	0.77	5/5
Right middle temporal gyrus	56	−42	−14	BA 20	0.90	5/5
Left middle temporal gyrus	−35	−7	−30	BA 20	0.85	5/5
Left middle temporal gyrus	−53	−40	−14	BA 20	0.85	4/5
Left middle temporal gyrus	−46	−18	−22	BA 20	0.81	5/5
Right middle temporal gyrus	53	−33	−6	BA 21	0.79	4/5

The frontal network comprised a set of regions ranging from premotor cortex to the middle portion of the frontal gyrus. Additionally, a set of temporal regions was activated bilaterally, including the middle and superior temporal gyri. In contrast, *nonturners* (allocentric frame) displayed a right-hemispheric activation pattern comprising the temporal cortex, ranging from the more lateral surface to the medial insula and the right premotor regions. There were no regions exhibiting dominant activation within the left hemisphere.

2.3.4. *Statistical comparison of source activity*

The source reconstruction results presented above describe activation patterns for the two strategy groups in a rather qualitative manner, with the brain areas identified exhibiting dominant activity during the various stages of the tunnel passage dependent on participants' preferred strategy. To permit comparison of all active brain areas, including those that were not identified by the above selection criteria, the data were further analyzed with respect to the mean activity

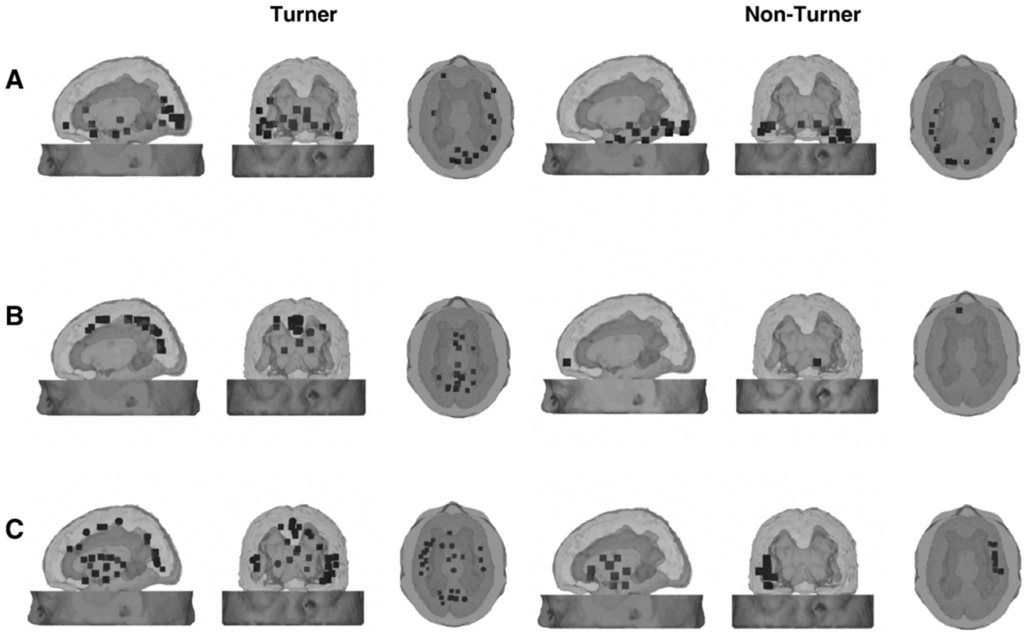

Fig. 4 – Source activity after clustering of relevant sources for turners (left column) and nonturners (right column) for the onset of the tunnel movement (A), the apex of turns (B), and straight segments after turns (C). The figures display all reconstructed clusters exhibiting ≥75% of the maximum source activity for ≥60% of the participants in a strategy group (see text for details).

Table 2 – Brain areas activated with the apex of turns in the tunnel passage, separately for turners and nonturners

Regions	x	y	z	BA	Max strength	Participants
Turners						
Left cuneus	−4	−83	25	BA 18	0.90	5/5
Left precuneus	−18	−80	39	BA 19	0.84	3/5
Right precuneus	6	−63	53	BA 7	1.00	5/5
Left precuneus	−3	−58	53	BA 7	0.99	5/5
Left precuneus	−1	−74	41	BA 7	0.97	5/5
Left paracentral lobule	−1	−41	56	BA 5	0.94	3/5
Left medial frontal gyrus	0	−12	56	BA 6	0.87	5/5
Left medial frontal gyrus	−5	−3	56	BA 6	0.81	5/5
Right medial frontal gyrus	6	7	46	BA 32	0.75	3/5
Nonturners						
Left anterior cingulate gyrus	−13	45	−4	BA 32	1.00	3/5

of all clusters. That is, individual mean cluster activity was computed for clusters within defined Brodmann areas (BAs), resulting in two values, one for the left- and one for the right-hemisphere, for each subject and reconstructed condition (first straight segment, turn, straight segment after a turn). These data were then entered into a mixed-design ANOVA, with the within-subject factors Side of BA (left versus right hemisphere) and tunnel Segment (first straight segment, turn, straight segment after a turn) and the between-subject factor preferred Strategy. As regions (BAs) of interest, all clusters displaying dominant source activity independently of the strategy group were selected (all areas listed in Tables 1–3, irrespective of whether both groups or only one group exhibited dominant source activity within an area). Only statistical effects involving the factor Strategy and, respectively, Segment were considered further. — This analysis revealed significant strategy differences only within BAs 7 and 32 [$F(1,8)=5.396$, $p<0.049$, and $F(1,8)=12.847$, $p<0.007$, respectively].

As can be seen from Fig. 5, nonturners exhibited significantly stronger activation of sources within BA 32 compared to turners, whereas turners displayed stronger activation in BA 7

Table 3 – Brain areas activated with the onset of straight segments following turns, separately for turners and nonturners

Regions	x	y	z	BA	Max strength	Participants
Turners						
Right cuneus	19	−86	9	BA 17	0.85	3/5
Left cuneus	−5	−84	24	BA 18	1.00	5/5
Left superior temporal gyrus	−45	−22	6	BA 22	0.99	5/5
Left superior temporal gyrus	−50	−8	−3	BA 22	0.99	3/5
Right superior temporal gyrus	46	−21	3	BA 22	0.87	3/5
Left middle temporal gyrus	−54	−43	8	BA 21	0.83	3/5
Left fusiform gyrus	−45	−21	−11	BA 20	0.98	3/5
Right middle temporal gyrus	50	−33	−10	BA 20	0.75	3/5
Right superior temporal gyrus	51	−36	14	BA 29	0.81	5/5
Left postcentral gyrus	−52	−28	17	BA 40	0.90	5/5
Right precuneus	7	−73	37	BA 7	0.81	3/5
Left precuneus	−3	−73	44	BA 7	0.80	5/5
Left medial frontal gyrus	−2	3	49	BA 6	0.88	5/5
Right medial frontal gyrus	1	−14	56	BA 6	0.87	5/5
Right precentral gyrus	46	−1	6	BA 44	0.85	5/5
Left middle frontal gyrus	−34	13	30	BA 9	0.81	5/5
Right Insula	46	−20	17	BA 13	0.85	5/5
Left Insula	−45	−3	16	BA 13	0.95	5/5
Left cingulate gyrus	−6	25	28	BA 32	0.82	4/5
Left anterior cingulate gyrus	−2	37	16	BA 32	0.75	3/5
Nonturners						
Right superior temporal gyrus	46	−20	−3	BA 22	1.00	5/5
Right middle temporal gyrus	55	−35	3	BA 22	0.94	4/5
Right fusiform gyrus	46	−33	−15	BA 20	0.84	3/5
Right fusiform gyrus	42	−18	−15	BA 20	0.82	4/5
Right inferior temporal gyrus	56	−44	−15	BA 37	0.77	4/5
Right precentral gyrus	46	−5	20	BA 6	0.81	4/5
Right insula	46	−13	11	BA 13	1.00	4/5
Right insula	45	10	5	BA 13	0.93	5/5
Right insula	46	−23	20	BA 13	0.84	4/5

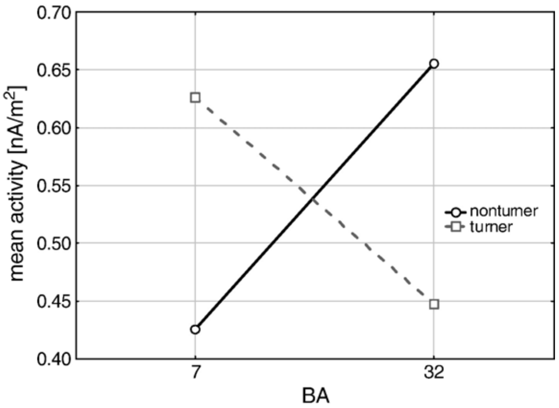

Fig. 5 – Mean source activity for Brodmann areas 7 and 32 separately for turners (egocentric reference frame) and nonturners (allocentric reference frame) in the tunnel task.

compared to nonturners. There were no further interaction effects (involving side of BA and/or tunnel segment) for either area. That is, statistically, there was stronger source activation within BA 32 for nonturners and, respectively, stronger activation in BA 7 for turners throughout the tunnel passage. In addition to the above main effects of preferred Strategy, a Strategy × Segment interaction was observed for BA 19 [$F(2,16) = 4.811$; $p < 0.023$]. Within this extrastriate area, source activity was comparable for the two strategy groups for straight segments prior to and after the turn. However, during the turn, nonturners displayed significantly less cluster activity compared to turners. No other BA derived from the source reconstruction for either strategy group revealed any differential effects of preferred Strategy and/or tunnel Segment.

3. Discussion

The present study was designed to identify brain regions associated with the use of an ego- and, respectively, an allocentric frame of reference during passages through a virtual tunnel. The reference frames differed with respect to the dynamics of the underlying coordinate system: the egocentric frame was rotated during the turn of the passage, whereas the cardinal direction of allocentric reference was kept constant. The frame of reference used by individual participants during the simulated passage could be identified in advance: distinct reaction patterns in adjusting the homing arrow from the end point of a tunnel passage back to the origin indicated that turners used an egocentric and nonturners an allocentric reference frame (Gramann et al., 2005). The point in time at which differences in cortical activation emerged between turners and nonturners was derived theoretically. During the initial, straight, tunnel segment, the ego- and allocentric reference frames did not differ with respect to the navigator's heading direction and bearing from the origin. The first divergence between the two reference systems emerged during the turn, where the egocentric coordinate system rotated in accordance with the angle of the turn, whereas the allocentric coordinate system stayed the same. For the segments after the turn, the differences between the two strategy groups persisted. In the present experiment, participants were presented unpredictably with one of two different reaction formats at the end of a tunnel passage: a homing vector that could be adjusted using an ego- or an allocentric reference frame, or a map-like reaction format that had to be answered using an allocentric frame. Thus, the performance data provided insights into the accuracy associated with either reaction format *after* the tunnel passage. However, it is likely that both strategy groups built up more than one spatial representation *during* the passage, so as to be able to adequately respond with either reaction format.

Turners' and nonturners' homing arrow reactions revealed characteristic differences in the represented mental heading at the end of the tunnels. Turners adjusted the homing arrow as if they had adopted the new heading in the course of and after the turn, whereas nonturners' adjustments indicated that their heading remained the same as in the initial segment. When turners' homing arrow adjustments were recalculated in terms of an allocentric reference system, their accuracy turned out to be comparable to that of nonturners. The same holds true for turners' reactions with the map-like format, even though this format was based explicitly on an allocentric frame of reference. Indeed, turners' accuracy was comparable to that of nonturners, although the reaction format was unpredictable on a trial (see Gramann et al., 2005, for details of the relevant performance data). There is no evidence that turners (egocentric frame), when presented with the map-like reaction format, re-computed their egocentric bearing from the origin into an allocentric reference frame. Such an additional computation should have led to increased errors or at least greater variability in performance, which was, however, not observed. Therefore, this set of findings may be taken as supporting the idea that turners use multiple frames of reference in parallel for their reaction. Further support for this hypothesis is provided by the stCDR results discussed below.

3.1. *Source reconstruction*

With tunnel movement onset, dominant activation within a bilateral occipito-temporal network was observed for both strategy groups. *Turners* (egocentric frame) revealed activation within a set of areas comprising the left and the right cuneus as well as the superior, middle, and inferior occipital cortex. The latter areas include V5, an area concerned with the processing of visual motion information. Furthermore, areas in temporal cortex, located bilaterally, exhibited increased activity with tunnel movement onset. These regions are associated with the computation of survey knowledge during navigation and episodic memory (Aguirre et al., 1996, 1998; Ghaem et al., 1997; Maguire et al., 1998; Burgess et al., 2002). Finally, two activation clusters within frontal cortex were reconstructed, which can be associated with central-executive processes (Owen et al., 1996a,b; Belger et al., 1998).

Similar areas were reconstructed for *nonturners* (allocentric frame). Dominant activation was reconstructed bilaterally within extrastriate regions, most likely reflecting activity within functional area V5. One cluster was located within the left fusiform gyrus, part of a network involved in object identification in tasks with spatial structures (Lacquanti et al., 1997; Owen et al., 1998). Finally, there was bilateral activation within a set of temporal areas, comprising the left and right middle temporal gyri, which resembles the activation pattern reconstructed for turners.

In summary, with the onset of the tunnel movement, similar regions were found to be activated for both turners and nonturners, who prefer to use an ego- and allocentric frame of reference, respectively. This is as expected, because the underlying coordinate systems would be congruent for the initial (straight) segment. Thus, the similar activation patterns in medial temporal cortex exhibited by the two strategy groups are most likely associated with the computation of a map-like representation that includes a reference point (starting position) and direction (direction of the first segment) for the following passage (acquisition of survey knowledge).

In a second step of analysis, the activation strengths within identified brain areas were directly compared statistically. Note that these areas were not determined according the selection procedure used for the qualitative description of source activity (criterion: 75% of maximum strength in at least 60% of the members of a strategy group). This procedure focused on the reconstruction of strategy-specific activity separately for the two strategy groups (and the three different tunnel segments), permitting brain areas with dominant activity to be determined for each group. By contrast, the statistical comparison of all active sources independently of the preferred strategy and individual source magnitudes permitted source strengths to be compared directly across participants even if a cluster was not dominantly active in either strategy group. This comparison revealed differences between the two groups for the first (straight) segment within BAs 7 and 32. While both strategy groups exhibited activity within BA7, the activation was significantly stronger for *turners* than for nonturners. Similarly, both strategy groups exhibited activity in BA32, which was, however, stronger for *nonturners* than for turners. Thus, both turners and nonturners showed evidence of parietal activation with the onset of the tunnel movement, likely reflecting the involvement of an egocentric reference frame in the computation of visuo-spatial information perceived from a first-person perspective. The same is true for frontal executive functions that are initiated with the onset of the tunnel passage. Both brain areas are relevant for the navigation process, and differences in activation strengths may reflect the relevance of either area for the respective preferred strategy.

Differences between the two strategy groups were expected for segments with a turn, which was confirmed by the reconstruction results. During the apex of a turn, *turners* (egocentric frame) exhibited prevailing activation within a network that comprised parietal and premotor areas. This network resembles that observed in visuo-spatial tasks involving spatial attention and working memory (Corbetta et al., 1993; Smith et al., 1995; Nobre et al., 1997), as well as in navigation tasks (Ungerleider and Haxby, 1994; Aguirre et al., 1996; Aguirre and D'Esposito, 1997; Maguire et al., 1998; Mellet et al., 2000; Shelton and Gabrieli, 2002; Iaria et al., 2003) and studies demonstrating parietal activation with the use of an egocentric frame of reference (Vallar et al., 1999; Galati et al., 2000; Committeri et al., 2004). Additional sources were reconstructed within extrastriate cortices and within frontal cortex. The former sources can be associated with the processing of visuo-spatial information (Haxby et al., 1994; Kohler et al., 1995; Aguirre and D'Esposito, 1997). The latter activation, within dorsolateral prefrontal cortex, is likely associated with executive processes (Petrides et al., 1993; Goldman-Rakic, 1996; Owen et al., 1996a; Belger et al., 1998), arising from the computational demands of updating changes in imagined heading direction and bearing from the origin. In marked contrast, only one region was revealed to be dominantly active for *nonturners* (allocentric frame). This source, reconstructed within the left medial part of the dorsolateral prefrontal cortex, is most likely associated with executive processes involved in the computation of rotational and translational changes during the turn with bearing remaining unchanged when an allocentric reference frame is used (Gramann et al., 2005).

Direct statistical comparison of the activation strengths within the BAs described for the turn revealed significant differences between the strategy groups in BAs 19, 7, and 32. In BA19, activation was stronger for turners (relative to nonturners), likely reflecting enhanced processing of visuo-spatial information in extrastriate areas for participants who mentally adopt the heading change during the turn. Moreover, activation was stronger for turners in BA7, while nonturners exhibited stronger activation in BA32. Recall that BA7 was identified as one of the dominant sources only for turners; their stronger activation in this area during turns underlines the importance of posterior parietal cortex in the egocentric processing of visuo-spatial information associated with changes in heading direction. However, nonturners did also show activation within this area during turns, though to a significantly weaker degree. Increased activation in anterior cingulate cortex (ACC, BA32) for both strategy groups during the turn (compared to the first, straight, segment) corresponds to the finding that over 60% of the participants in each group showed dominant activity in ACC during this critical stage of the tunnel passage. As for the first straight segment, nonturners showed significant stronger activation within the ACC as compared to turners. In contrast to the above areas, source strengths during turns were comparable for the two strategy groups within medial frontal areas and extrastriate areas close to the primary visual cortex (BAs 5, 6, and 18).

Taken together, these results support a distinction between the ego- and allocentric frames of reference for tunnel segments with a turn. Use of an egocentric reference frame gives rise to dominant activity within a posterior parieto-premotor network, consistent with activation patterns associated with the use of an egocentric frame in line bisection (Vallar et al., 1999; Galati et al., 2000) and complex virtual reality environments encoded in a viewer-centered manner (Committeri et al., 2004). The additional activation within dorsolateral prefrontal cortex might reflect executive processes involved in the updating of imagined heading and/or bearing from the origin of the tunnel passage. Importantly, the use of an allocentric reference frame was found to dominantly activate components of the parieto-premotor network, though the strongest activation was located within anterior cingulate cortex. This dominance of prefrontal activation for nonturners may be taken to reflect the critical role of executive processes for the updating of translational and rotational changes within an (dominant) allocentric frame of reference. That is, stronger ACC activation for nonturners (as compared to turners) might reflect enhanced frontal control processes associated with the preferential use of an allocentric representation, which has to be computed on-line while visual information is encoded from a first-person perspective.

The finding that, with the absence of salient landmarks in the present task, there was only partial overlap in the group activation patterns is at variance with Shelton and Gabrieli (2002). Given this, the overlapping activation patterns reported by Shelton and Gabrieli might reflect navigation based on visual landmarks using an egocentric or an allocentric encoding strategy.

Further support for distinct cortical networks underlying the ego- and allocentric reference frames in simulated navigation is provided by the stCDR for straight tunnel segments following a turn. After mental rotation of the midsagittal plane, *turners* displayed activation within occipital and temporal areas and, additionally, in a parieto-frontal network. The activation of the temporal areas might reflect the activation of hippocampus and parahippocampus transforming egocentric information into an observer-independent representation in combination with the updating of episodic memory (Wolbers and Büchel, 2005; Aguirre et al., 1998; Maguire et al., 1998; Burgess et al., 2002). The latter network included the same areas that were active during turns in the tunnel passage. In addition, turners displayed more regions in frontal cortex to be active during straight segments following a turn. This additional activation is most likely associated with executive processes, reflecting the increased computational demands in updating the momentary heading and bearing from the origin for this strategy group. *Nonturners*, by contrast, exhibited prevailing activation within a temporo-frontal network that was much less extensive and confined to the right hemisphere. This agrees with neuropsychological data suggesting a major contribution of the right hemisphere to the computation of an allocentric reference frame, such as when judging the mid-point of a line (Schenkenberg et al., 1980). And it agrees with imaging studies that have consistently linked the medial temporal area with the storage of 'cognitive maps' (Aguirre et al., 1996, 1998; Ghaem et al., 1997; Maguire et al., 1998; Burgess et al., 2002; Iaria et al., 2003).

The direct statistical comparison of source strengths within the described areas disclosed no significant differences between the two strategy groups with respect to the activated networks for the last, straight, segment after a turn. The only differences found were located in the posterior parietal and the anterior cingulate cortex. Thus, largely comparable networks were active with both turners and nonturners during the final tunnel segments. This agrees with the assumption that both strategy groups built up and make use of more than one frame of reference during spatial navigation—at least under conditions in which participants do not know in advance which reference frame they would have to use to respond accurately at the end of the tunnel (recall that the reaction format presented at the end varied unpredictably across trials).

Since trials with large EOG and EMG artefacts were excluded from the analyses, only small-amplitude and nonstereotypical eye movements and muscle artefacts may have contributed to the present findings. Eye movements were expected to be made during the course of tunnel passage, especially turns, when the visual flow pattern changed in an informative way over time. However, rather than being 'artefacts', such eye movements may be a potential source of difference between the two strategy groups, and eliminating eye movement trials prior to source reconstruction may have 'biased' the results. This possibility remains to be examined in future studies.

Another problem stems form the lack of a control condition to be subtracted from the experimental condition in the present study. Without subtracting baseline activation from activation during the navigation process, the specificity of identified brain regions for navigational processes remains tentative. However, due to the absence of any salient stimulation during the navigation process, any reconstruction based on transient stimulation before the navigation (e.g., fixation) would distort the results due to an imbalance in signal-to-noise ratio of the different signals entered in the reconstruction. This problem has to be solved in future studies by incorporating control conditions with similar visual stimulation, but without any navigational demands.

In summary, the identification of brain areas, by means of stCDR, for turners and nonturners revealed a network of dominant activation that reflects the strategy-specific importance of different cortical areas during distinct stages of the virtual tunnel passage. By contrast, direct comparisons of source strengths disclosed significant differences only in a small number of brain areas, thus demonstrating a large overlap in the cortical network activated in both strategy groups. This is in line with largely similar surface potentials that would result from overlapping source configurations.

Thus, the present results revealed turners and nonturners to exhibit a widely distributed and overlapping network of brain areas involved in the (parallel) computation of an ego- and an allocentric frame of reference. Turners exhibit dominant activation within a network comprising posterior parietal and premotor areas in combination with prefrontal activity. By contrast, nonturners show prevailing activation within an occipito-temporal network involving activity within the ventral visuo-perceptual stream. However, the dominance of one or the other cortical network represents only a relative difference between the two strategy groups, dependent on the preferred frame of reference. A direct comparison of all activated areas revealed a widespread overlapping cortical network for turners and nonturners alike to be involved in spatial navigation. In line with the performance data, this lends further support to the idea (e.g., Wickens, 1993; Redish and Touretzky, 1997; Sholl and Nolin, 1997; Aguirre and D'Esposito, 1999; Redish, 1999; Sholl, 2001; Mou et al., 2004) of multiple frames of reference being active in parallel in both strategy groups.

4. Experimental procedure

4.1. *Participants*

The tunnel task was presented as one task in an experiment that used electroencephalography to differentiate among spatial, visual, and verbal working memory processes. The different tasks were blocked to avoid any switching costs between different experimental conditions (Gramann, 2002). Because of gender-specific differences in the neural substrate underlying navigation (Sandstrom et al., 1998; Grön et al., 2000; Shelton and Gabrieli, 2004), ten male participants (aged between 22 and 34 years; mean age 25.83 years) were selected for the analyses. Performance data of all participants in the tunnel task of this experiment, including the ten participants presented here, are published in Gramann et al. (2005). All subjects had normal or corrected-to-normal vision and were paid for their participation. In a pre-experimental session, participants were categorized with respect to their preferential use of an allo- or an egocentric reference frame, resulting in two groups. Five subjects with individually recorded electrode positions preferentially using an ego- or an allocentric frame of reference were selected from all categorized subjects. The categorization task was applied prior to the main experiment (note that this task was validated in an earlier study by Schönebeck et al., 2001). In a separate session, turners and nonturners had to traverse tunnels with one turn of varying angle. At the end of each tunnel, two arrows were displayed representing the correct response within an ego- and an allocentric reference frame, respectively (see Fig. 2D). Participants had to decide which one of the displayed arrows pointed back to the origin of the traversed tunnel path (see Gramann et al., 2005 for the instruction). That is, subjects did not adjust, but rather chose one out of two simultaneously displayed homing vectors. Since tunnels included only one turn, the arrows differed clearly. The tunnels were chosen such that, within 3 blocks of 10 tunnel trials, alternative solutions differed clearly at the beginning and then became increasingly difficult to discriminate between. To take part in the main experiments, participants had to consistently (i.e., in ≥70% of the trials)[3] select one or the other homing-vector solution to be classified as a turner or nonturner, respectively.

4.2. Stimuli, task, and procedure

Participants were seated in a dimly illuminated room in front of a 19-in. display monitor. A computer screen was placed 110 cm in front of the subject so that the fixation cross was in the subjects horizontal straight ahead line of sight. Each trial started with an asterisk for 500 ms, followed by presentation of the first tunnel segment for 1000 ms. Then, tunnel movement started, with total traversal time depending on the length of the tunnel (14 and 21 s for tunnels with 4 and 6 segments, respectively). Each segment was composed of 16 subsegments with increasing gray values (see Fig. 1A) providing depth perspective. The movement speed was determined by the number of subsegments added in the depth of the tunnel with 4.6 subsegments per second. This speed was held constant for all segments, including turns. At the end of each tunnel, the last segment was displayed for 500 ms as a static image, followed by a second asterisk presented for 4 s, marking the retention interval.

Tunnels consisted of four or six segments and included only one turn, placed in the second or third segment, with varying degrees of angular acuteness. At the end of each passage, participants were presented with a “three-dimensional” arrow or, unpredictable on a trial, a map-like reaction format in the display center (Figs. 1B and C, respectively). In the former format, the arrowhead pointed away from the navigator into the depth of the monitor. By pressing the left or right mouse button, it was rotated towards the navigator, representing the homing vector. When the right angle setting was reached, the setting was confirmed by pressing the middle mouse button, and the next trial started after a short interval. Since the orientation of the arrow was initially aligned with the navigator’s axis of orientation, it could be interpreted as a prolongation of the navigator’s heading. The latter reaction format, the map-like format, was introduced that presented an outline square (white line drawing) with a cross marking the starting point of the tunnel and a line at the point where tunnels without turns would have ended. The task was to mark the end position of a given tunnel relative to its origin, by moving a mouse-controlled cursor circle to the appropriate location. Because this map-like reaction format displays *x*- and *y*-axes from a “bird’s-eye-view”, the coordinate system lies outside the navigator. Thus, the map format can only be answered using an allocentric reference frame. Pressing the middle mouse button confirmed the position, and the next trial was initiated.

The navigators’ task was to maintain orientation during the tunnel passage and to indicate their location either by adjusting a homing vector or the end point of the passage within the map-like reaction format. In total, there were 109 ‘experimental’ tunnels to be solved (there were also ‘filler’ trials without turns or with turns of an angle greater than 90°, which were randomly interspersed amongst the experimental trials). Eccentricity of end positions of relevant trials (no filler trials varied between 60° to the left and 60° to the right relative to the origin of the passage. For statistical analysis, these were grouped into six end positions to either side of the origin (5°, 15°, 25°, 35°, 45°, and 55°).

4.3. EEG recording

The electroencephalogram (EEG) was recorded continuously, at a sampling rate of 500 Hz, using 96 Ag/AgCl electrodes including those corresponding to the international ten–twenty system (American Electroencephalographic Society, 1991). Vertical and horizontal eye movements were monitored by means of electrodes placed at the outer canthi of the eyes and the superior and inferior orbits. Electrophysiological signals were amplified using a 0.1–100 Hz bandpass filter via SynAmps (NeuroScan). All electrodes were referenced to Cz. Trials with EOG artefacts, excessive peak-to-peak deflections (>100 μV or <−100 μV), or bursts of electromyographic activity were excluded from analyses. After fitting of the electrode cap (EasyCap, FMS), a digitizing system (Zebris, CMS20S) was used to individually determine the positions of the 96 channels for later current density reconstruction.

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[3] One subject was excluded because he switched strategy from turner to nonturner after his first exposure to the map-like reaction format.

4.4. *Head model*

Current density reconstruction was computed using the Electro-anatomical Source Imaging Software (EaSI, BrainProducts). EaSI incorporates a head model based on the T1 template image provided by the Montreal Neurological Institute, which is thought to be representative of a normal brain. The surfaces of the inner and outer skull and the skin were segmented on the basis of the gray values of the T1 image and used for creating a Finite Elements Model (FEM). The region of the T1 template image that corresponded to the average gray value of the cortex, was segmented and served as source space. Source analysis was performed using a regular grid normalized to the AC–PC line (anterior and posterior commissures) and placed within the source space with points 10 mm apart, resulting in 1523 possible source locations. The individually measured electrode positions were transformed to the surface of the T1 template image by rotating them using three anatomical landmarks (nasion and left and right preauricular points) and eighteen landmarks according to the international 10–20 system.

4.5. *Source reconstruction*

For source reconstruction, the LORETA algorithm (Pasqual-Marqui and Biscay-Lirio, 1993) was applied using the variant of the L2 norm for both the data and the model term. In addition, to obtain more stable results, a temporal coupling was applied (for a detailed description of the model, see Darvas et al., 2001). The introduction of temporal coupling is based on the assumption that neuronal population do not change their activity pattern abruptly over a given time interval. Source configurations that reveal a smooth development of activity over time are favored over configurations with abrupt changes in the source time series. The integration of temporal coupling demonstrates robustness against noise and better reconstruction results with respect to the spatial and temporal resolution in spherical as well as in realistic head models (Darvas et al., 2001). Source reconstruction was performed on three relevant epochs computed individually for each subject and data set. The following conditions were of particular interest: (1) onset of tunnel movement, (2) segments including a turn, and (3) straight segments after the turn. For each subject epochs of 1000-ms duration were segmented and averaged for onset of tunnel movement, onset of turns, and onset of straight segments after a turn, as demarcated by the markers that were set with onset of each new segment during a passage in the EEG data. Source activity was performed over a window of 1000 ms for each condition and participant and included activity for identical temporal and path durations. Next, the source magnitudes were normalized by dividing them by the maximum source amplitude for each participant and condition. Then, mean and standard deviation of the source magnitudes at each point of the regular grid were calculated. Regions with source activity at corresponding points across participants were determined for the three conditions (tunnel movement, tunnel turn, straight segment after turn). For all participants, a matrix representing all distances between source strength maxima was computed, and maxima with a distance less than 20 mm were combined into one cluster. The clustering procedure searches for local maxima of the current density distribution over all available time slices. Local maxima that are spatially closer than the defined distance of 20 mm were classified as cluster. The result is a list of regions of interest which exhibit locally increased activity (Darvas, 2002). Only clusters exhibiting ≥75% of maximum source strength in at least three participants per strategy group (i.e., 60% of the participants) were considered relevant. In this way, the mean location of a relevant cluster and the mean source magnitude within this cluster across participants were determined. With this restriction to relevant sources revealing peak activity (with 1523 possible sources locations) and a defined number of subjects (at least 60%) per strategy group this procedure provides an estimates of brain regions likely to be important for explaining differential effects resulting from the use of an ego- and, respectively, an allocentric reference frame. All reconstructed clusters for each condition were anatomically specified by means of Talairach and Tournoux coordinates using the Talairach demon software (http://ric.uthscsa.edu/td_applet/) returning the coordinates of the nearest grey-matter point[4].

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[4] The determination of coordinates for nearest grey-matter points in the Talairach demon algorithm might lead to overlap of the clusters defined by the cluster algorithm in EaSI. Therefore, clusters with distances less than 20 mm might result from the search algorithm implemented in the Talairach demon software. In addition, for the same reason, clusters without positive or negative values in the *x*-coordinate might be assigned to one or the other hemisphere.

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