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Evidence of Separable Spatial Representations in a Virtual Navigation Task

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Three experiments investigated spatial orientation in a virtual navigation task. Subjects had to adjust a homing vector indicating their end position relative to the origin of the path. It was demonstrated that sparse visual flow was sufficient for accurate path integration. Moreover, subjects were found to prefer a distinct egocentric or allocentric reference frame to solve the task. "Turners" reacted as if they had taken on the new orientation during turns of the path by mentally rotating their sagittal axis (egocentric frame). "Nonturners," by contrast, tracked the new orientation without adopting it (allocentric frame). When instructed to use their nonpreferred reference frame, both groups displayed no decline in response accuracy relative to their preferred frame; even when presented with reaction formats based on either ego- or allocentric coordinates, with format unpredictable on a trial, both groups responded highly accurately. These findings support the assumption of coexisting spatial representations during navigation.

Keywords: spatial navigation, reference frames, path integration, spatial strategy, virtual reality

Spatial cognition plays an important role for the adequate interaction with humans' environment. Raubal and Egenhofer (1998) defined the processes that subserve orientation and navigation in space as the subject of human way-finding research. In accordance with this definition, we conceive of spatial orientation as a cognitive function that comprises the construction and use of a mental representation of the environment. Within this spatial representation, incoming information from multiple modalities, the momentary location of the navigator, as well as action plans have to be aligned and integrated. Thus, spatial cognition refers to a complex ability that involves many different processes. One approach to differentiate these processes is the systematic analysis of single and double dissociations pursued in neuropsychological research (e.g., Ellis & Young, 1991). According to Kerkhoff's (2000) systematic analysis of disorders of orientation, the relevant subprocesses of spatial orientation include (a) the intake and integration of modality-specific input information, (b) the further processing of the spatial information within an ego- or allocentric frame of reference, and (c) the computation of a spatial representation of the traversed environment.

Of particular interest for the present investigation is the choice of the reference frame for the further processing of spatial information and the resulting spatial representation in human navigation. Various methods can be used when navigating in the environment, for example, *piloting* and *path integration* (Loomis, Klatzky, Golledge, & Philbeck, 1999). During *piloting*, or *position-based navigation*, the navigator updates his or her current position within an environment and orients by using landmarks in conjunction with a map. Position-based navigation relies on external signals indicating the navigator's position, such as significant landmarks in the environment (church towers, intersections, etc.). By contrast, *path integration*, or *velocity-based* navigation, refers to the updating of position and orientation within an environment based on internal (idiothetic) or external (allothetic) information of velocity and acceleration (Mittelstaedt & Mittelstaedt, 1982). In the present article, we use *path integration* in terms of Loomis et al. (1999), which includes visual input as an additional or exclusive source of information. Path integration provides an estimate of current location and directional orientation by integrating local translations and rotations into a larger spatial framework. Integration of translational and rotational changes can be based on an ego- or an allocentric frame of reference. The use of an ego- or allocentric reference frame as "a means of representing the locations of entities in space" (Klatzky, 1998, p. 1) leads to distinct spatial representations conveying different types of information (representational primitives). However, which factors determine the use of a certain frame of reference during navigation remains an open issue.

Frames of Reference in Spatial Orientation

Several studies have demonstrated that the choice of an ego- or an allocentric reference frame is dependent on the kind of information provided. For example, Thinus-Blanc and Gaunet (1997) showed that learning a map, in contrast to self-exploring navigation, yields distinct spatial representations in terms of survey and route knowledge based on allo- and egocentric coordinates, respectively. Other studies have revealed differences in the representation of heading changes dependent on the kind of information provided during the task. In everyday life, spatial representations are updated on the basis of various sources of information, including proprioceptive, vestibular, and visual information when actively changing one's own position in the environment. In the present context, the focus is on studies that have used visual,

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proprioceptive, and vestibular information sources, or combinations of these, for updating spatial representations. Under experimental conditions, the amount and quality of information can be controlled, permitting the relative contributions of the three types of information to spatial updating to be examined. Klatzky, Loomis, Beall, Chance, and Golledge (1998) demonstrated that when all three sources of information about changes in space were available in a path integration task, subjects were able to reliably update their internal representation of heading (i.e., the angle between the navigator's axis of orientation and a reference direction). In contrast, when subjects heard a description of the path layout, updating of heading failed. The latter condition represents the other extreme with respect to the amount and quality of relevant information provided during navigation (complete lack of proprioceptive, vestibular, and visual information about changes in heading), with the updating being entirely reliant on imagining one's own translations and/or rotations in the absence of visual (and other perceptual) cues.

Subjects have been shown to be able to update their position and orientation relative to landmarks that they had learned before, even without vision (Klatzky et al., 1998; Loomis, Da Silva, Fujita, & Fukusima, 1992; Loomis et al., 1993; Rieser, Guth, & Hill, 1986; Sholl, 1989). In contrast, when subjects are required to update their position and orientation over the course of an imagined movement, impaired performance is observed in comparison with real motion (Klatzky et al., 1998; Loomis et al., 1993; Rieser et al., 1986). Other studies have demonstrated that subjects are able to respond in accordance with imagined heading changes, though reactions are much slower and less accurate compared with physical rotation of the body (Easton & Sholl, 1995; Farrell & Robertson, 1998; May, 1996; Presson & Montello, 1994). This decline in response speed and accuracy has been attributed to effortful cognitive processing required to recalculate egocentric bearing (i.e., the angle between the navigator's axis of orientation and the axis of orientation of an object) because of a lack of updated heading. It seems evident that under imagery conditions, subjects fail to compute an egocentric (locational) representation, which, by definition, includes egocentric bearing from an origin (see also Klatzky, 1998, for definition of terms). In contrast, construction of an allocentric locational representation containing the pathway layout does not require the updating of heading changes during navigation (Klatzky et al., 1998). In this kind of spatial representation, the navigator is represented without orientation, that is, as one point among others. Neuropsychological studies support the idea of a functional dissociation between the allo- and egocentric reference systems (Pizzamiglio, Guariglia, & Cosentino, 1998; Woodin & Allport, 1998) and individual preferences for the use of either system (Just & Carpenter, 1985).

Studies using virtual environments or desktop-based simulations for testing spatial orientation have consistently shown that when proprioceptive cues are unavailable, subjects display impaired performance in updating their heading during turns; as a result, they misjudge their bearing from reference points, that is, the origin of the path (Chance, Gaunet, Beall, & Loomis, 1998; Klatzky et al., 1998). Nonetheless, virtual environments that include self-locomotion (Bakker, Werkhoven, & Passenier, 1999; May & Klatzky, 2000; May, Wartenberg, & Peruch, 1997; Péruch, May, & Wartenberg, 1997; Steck, Mochnatzky, & Mallot, 2003) or passive reception of movement (Christou & Bülthoff, 2000; Foreman & Wilson, 1996; Höll, Leplow, Schönfeld, & Mehdorn, 2003; Kirschen, Kahana, Sekuler, & Burack, 2000; Mallot, Gillner, van Venn, & Bülthoff, 1998; Nadel et al., 1998; Péruch & Gaunet, 1998; Waller, Beall, & Loomis, 2004) provide sufficient information for spatial orientation. Yet, it remains unclear whether a further reduction of the sensory input by means of a simple computer-based simulation is sufficient to allow for accurate spatial orientation.

In summary, the substantially impaired updating of heading observed under conditions of imagination and pure visual information (real or virtual) suggests that subjects fail to compute an egocentric spatial representation (which, by definition, includes egocentric bearing from an origin). Proprioceptive information appears crucial for computing such a representation: Whenever proprioceptive information is unavailable, subjects exhibit impaired performance on tasks that require updating of heading changes; when proprioceptive information is available, heading is updated automatically (see, e.g., Farrell & Robertson, 1998, for proprioceptive information about rotational changes).

However, the work reviewed above has, hitherto, given little consideration to individual strategies in spatial orientation—despite the fact that individual differences are known to exist in the use of reference frames during navigation (Lawton, 1994, 1996; Tversky, 1996) and the fact that individuals use differential strategies when they have to learn new environments, including spatial and nonspatial (such as verbal coding of a route) processes.

Strategies in Spatial Learning

In the present study, the focus is on spatial strategies. According to Lawton (1994), two types of (spatial) strategy can be distinguished: route and orientation, which preferentially use information about the route to be followed and about global reference points such as compass directions, respectively. Orientation-based and route-based strategies can be identified in outdoor and indoor way-finding tasks, and subjects seem to prefer the same strategy in both environments (Lawton, 1996). Another distinction made by Denis, Pazzaglia, Cornoldi, and Bertolo (1999; Pazzaglia & De Beni, 2001) refers to the preferred use of survey perspective as opposed to visual memory of landmarks. Denis et al. showed that subjects' preference for either spatial representation is revealed in differences in the way they process visuospatial information. However, common to both distinctions is the assumption that there are two separate ways of orienting within the environment: one based on an allocentric and the other on an egocentric spatial representation.

Further support for differential strategies during spatial learning stems from studies that have attempted to determine the neural substrates underlying the different types of spatial representation. Most often, virtual environments have been used to present subjects with ground-level and survey-level spatial information of the same environment within the same task (Mellet et al., 2000; Shelton & Gabrieli, 2002, 2004). The results support the distinction between ego- and allocentric representations of space with partially distinct underlying neural networks. Moreover, subjects were revealed to spontaneously adopt differential strategies, which were modified during learning (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003).

Aims of the Present Study

In summary, on the basis of the studies reviewed above, the lack of proprioceptive information leads to failures in updating egocentric representation; furthermore, individuals differ with respect to their preferential use of ego- or allocentric spatial representations. The present study was designed to bring both factors together: individuals' preference for a particular reference frame and the influence of the kind of information provided for spatial orientation.

In more detail, the present study used a desktop-simulated tunnel that provided visual information only (Schönebeck, Thanhäuser, & Debus, 2001) to examine whether path integration could be achieved solely on the basis of simulated visual movement without landmarks. Because the evidence reviewed above suggests that under the absence of proprioceptive and vestibular information, subjects fail to update heading or display impaired path integration, we asked whether the tunnel simulation is sufficient to permit a spatial representation to be built up and, if so, whether the resulting representation accurately depicts locations of varying eccentricity. A related question concerned the frame of reference used during spatial navigation. If idiothetic information is needed to update heading and build up an egocentric representation, subjects in the tunnel task should display a systematic overturn in adjusting a homing vector from the end position back to the origin of the path. Furthermore, subjects were forced to use different frames of reference during navigation in order to permit performance differences to be evaluated dependent on the underlying spatial representation and the individual preference for one or the other representation.

Description of Tunnel Task

In the simulated-tunnel task, subjects have to navigate through a route (path) of straight and curved segments. The simulated passage provides the navigator with visual information on translational and rotational changes only through the rate of optic (floor and wall texture) flow (see Figure 1). Their task is to indicate the end position relative to the origin of the path, which can only be achieved by computing spatial relations among reference points. Given that these reference points are no longer visible at the end of the passage, the task can only be solved on the basis of an internal spatial representation. The notion of a simple association of reference point and action to be performed is difficult to maintain if the navigational task is a purely passive one that does not afford any action sequence and is placed within a perceptually reduced environment that does not provide any reference points.

The optic flow during the passage through a tunnel provides spatial information that is directly perceptible, whereas other information (e.g., the eccentricity of end position relative to the origin of the passage) has to be derived because it is not visible. *Perceptible spatial variables* were, among others, the angle of a turn (turn of defined angle vs. straight segments), the orientation of segments (straight ahead, left, right, upward, downward), and the length of the tunnel (number of segments). During rotation, the rate of optic flow from the surround specifies the angular speed as

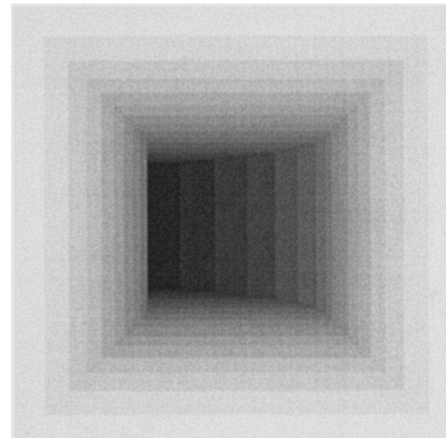

Figure 1. View into a tunnel with a turn to the left. Note that in the beginning of each trial, a static picture of the tunnel entrance always displaying a straight segment was presented.

well as the direction of rotation (Warren, 1995). Therefore, the navigator can determine the traversed angle by integrating the optic flow over time. The same holds true for translational information, with optic flow specifying the direction and speed of translation (Kearns, Warren, Duchon, & Tarr, 2002). *Nonperceptible variables* were the eccentricity of end position (in degrees), the relative heading during the last segment compared with the initial segment (parallel heading or heading of defined angle), and the distance of the end position from the origin.

In the tunnel task, the initial segment was always straight ("north" direction). Because subjects were seated in front of the monitor, their axis of orientation was aligned with the first segment that defined the reference direction and, therefore, determining the navigator's heading direction during the first segment (Mou, McNamara, Valiquette, & Rump, 2004; Shelton & McNamara, 2001).

Because the egocentric frame of reference is defined by the axis of the navigator, the reference direction was always aligned with the navigator's orientation. For an allocentric frame of reference, a reference direction is needed (see Klatzky, 1998). Because the orientation of the first segment could be perceived within an allo- or an egocentric reference frame, the task left it open which frame of reference to use during the passage (see Figure 2A). Moreover, the ego- and allocentric coordinate systems were aligned at this point of the task, and differences in heading evolved only at later stages (see Figure 2B). If task performance is based on an allocentric frame of reference, the navigator's axis of orientation remains unchanged. In contrast, if an egocentric frame of reference is used, the navigator's axis of orientation changes over the course of a turn (see Figure 2B).

Tunnels with parallel start and end segments are again identical with respect to the heading direction of the navigator, independently of the use of an ego- or an allocentric frame of reference. Only tunnels that end with nonparallel segments can reveal differences in heading directions. In this case, a navigator using an allocentric reference frame exhibits the same heading direction as that during the initial segment. In contrast, when an egocentric reference frame is used, the navigator's heading with respect to the heading direction at the start of the tunnel differs (see Figure 2C).

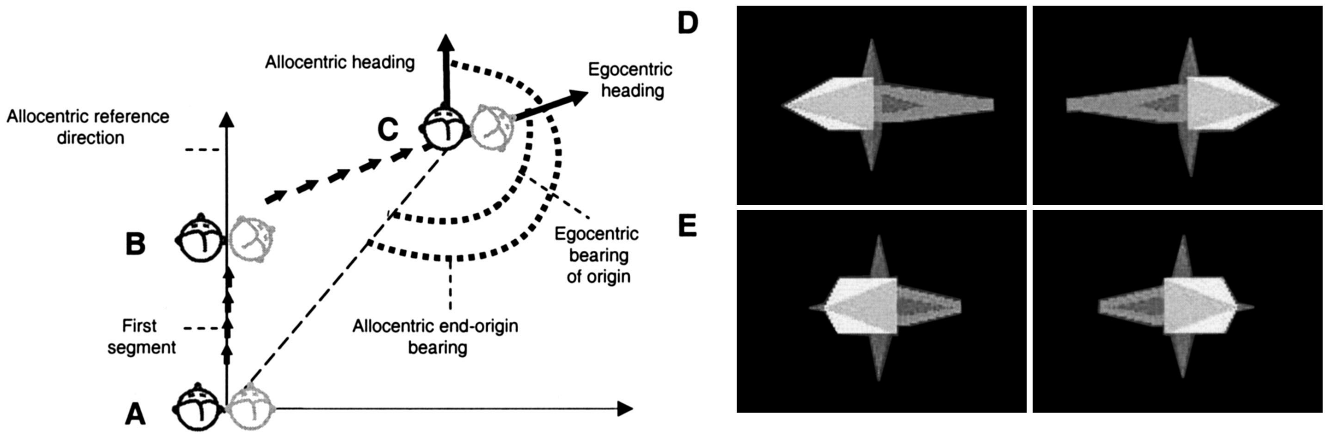

Figure 2. Depiction of a passage through a tunnel with a turn to the right, with nonparallel start and end segments. The left side displays a nonturner using an allocentric frame of reference, with the navigator's axis of orientation during the first segment (A), during the turn (B), and during the last segment (C) of the tunnel passage. On the right, a turner is displayed who uses an egocentric frame of reference. During the first segment (A), the turner's axis of orientation is identical with that of a nonturner. During the turn, the axis of orientation changes (B). At the end of the tunnel, the turner's axis of orientation is different from that of a nonturner. To the right side examples for homing vectors are displayed with the correct angular adjustment for a tunnel with one turn of 60° to the right with the correct homing vectors for nonturners (allocentric reference frame) on the left and turners (egocentric reference frame) on the right side (D) and examples of the correct homing vector for a tunnel with one turn of 30° with the correct homing vectors for nonturners and turners to left and right side, respectively (E).

At the end of each trial, a three-dimensional arrow[1] was presented in the display center aligned with the sagittal axis of the navigator, with the arrowhead pointing away from the subject into the depth of the simulated space (i.e., the subject saw a foreshortened view of the arrow's tail side). By pressing the left or right mouse button, the navigator could rotate the arrowhead toward him- or herself, representing the homing vector. When the subjectively correct angle setting was reached, the navigator confirmed the setting by pressing the middle mouse button, and the next trial started after a short interval. Because 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.

Concerning the first process involved in spatial orientation (in terms of Kerkhoff, 2000), the intake and integration of modality-specific information, the tunnel task imposes constraints on the integration processes, because the available input information is reduced to optic flow (no self-locomotion, no landmarks). The tunnel task therefore provides the possibility to compare the use of allo- and egocentric reference frames for the further processing of spatial information. And, with respect to the third process of spatial orientation, computation of a spatial representation is needed to solve the task, because the tunnel is never seen as a whole nor is any directly perceptible information provided as to the relation between the end position and the origin of the path (e.g., bearing and distance).

Overview of the Experiments

In a preliminary study, Schönebeck Thanhäuser, and Debus, (2001) showed that subjects differ with respect to the reference frame they used during the passage through a virtual tunnel. Empirically, subjects can be classified into two groups: the first group, which we will refer to as *turners* henceforth, displays systematic differences in adjusting a homing vector for tunnels with parallel start and end segments compared with routes that involve a different heading direction in the end of the traversed path compared with the initial direction (nonparallel segments). The second group, which we will refer to as *nonturners*,[2] does not show any differences in adjusting a homing vector for tunnels with parallel and nonparallel start and end segments. Theoretically, the numerical value of the homing vector depends on the reference frame used during the tunnel passage. For turners and nonturners using an egocentric and an allocentric reference frame, respectively, the initial segment of each tunnel defines the external reference direction. The required homing vector can be readily calculated for nonturners as the numerical value of the angle between the reference direction and a line connecting the start and end position of the tunnel. By contrast, for turners, the change of their axis of orientation during a turn leads to a different homing vector: The egocentric bearing of the start from the end point of a tunnel is equivalent to the angle between the reference direction and the line connecting the start and end positions plus the angle of turns during the passage. This difference allows a categorization of subjects with respect to the reference frame they use during the task.

[1] More precisely, the displayed arrow was a two-dimensional rendering (using perspective depth cues) of a three-dimensional arrow.

[2] We thank Roberta L. Klatzky for her very helpful comments (in particular concerning nomenclature and statistics) on a previous version of this article.

On the basis of these findings, we devised a categorization task that permitted the identification of the preferred use of an allo- or an egocentric reference frame prior to the main experiment (note that this task was validated in an earlier study by Schönebeck et al., 2001). In a separate session before the main experiments, 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 Figures 2D and 2E). Subjects had to decide which one of the displayed arrows pointed back to the origin of the traversed tunnel path (see the Appendix for the instruction). That is, subjects did not adjust but rather chose one out of two simultaneously displayed homing vectors. Because 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, subjects had to consistently (i.e., in $\geq$ 70% of the trials)[3] select one or the other homing-vector solution to be classified as a turner or nonturner, respectively.

A simple means of verifying the individual categorization based on the experimental data is to compute the correlation between eccentricity of end position and angular adjustment separately for each subject. For nonturners, the correct angular adjustment is derived directly from the eccentricity of the end position. Therefore, angular adjustment will be positively correlated with eccentricity of end position. In contrast, turners adopting a new heading direction during the turns will exhibit a negative relationship between angular reaction and eccentricity of end position. Imagine, for example, a tunnel with six segments and an end position of an eccentricity of 30° to the left side relative to the origin (see Figure 3 for an illustration). To reach an eccentricity of 30°, a turn with an angle of 60° was placed within the third segment of the tunnel. Now assume that deviations from the allocentric reference direction (0°) to the left are signed positive (+60° turn and +30° eccentricity). Nonturners, tracking the angular changes without adopting the new heading, interpret the homing arrow as the prolongation of their sagittal axis, which is still aligned with the allocentric reference direction (0°). This strategy group adjusts the homing arrow as a direct vector from the end position to the origin, that is, they produce a homing vector of 30°. In contrast, turners mentally adopt the new heading direction during the turn (0° plus 60° heading) and they also interpret the homing arrow as the prolongation of their sagittal axis. Accordingly, the resulting homing vector for turners within their preferred frame of reference will be, ideally, −30° (allocentric eccentricity of 30° minus 60° egocentric heading). Besides the magnitude of the correlation coefficient as an indicator of the subjects' strategy, the significance of the coefficient reflects the consistent use of either strategy.

On the basis of the findings of impaired path integration in the absence of proprioceptive and vestibular information, the aim of Experiment 1 was to explore whether reducing the sensory input to a simple visual (computer-based) simulation would be sufficient to allow for accurate spatial orientation. If visual-flow information by itself is sufficient to permit a spatial representation to be built up, then subjects should be able to correctly perform the task. A second hypothesis concerned the frame of reference used during spatial navigation. If body senses are needed to build up an egocentric representation, then subjects in the tunnel task should display a systematic overturn in adjusting the homing vector. The results revealed subjects to be able to solve the task and, furthermore, to prefer a distinct, egocentric (turners) or allocentric (nonturners) reference frame. Both groups of subjects solved the task with similar accuracy in their homing-vector adjustments.

Experiment 2 was designed to examine whether the two strategy groups would be able to learn the use of their nonpreferred reference frame during the tunnel passage, that is, for turners an allocentric frame and for nonturners an egocentric frame. If the choice of one or the other frame of reference is preferential and not habitual in nature, then subjects should be able to learn to solve the task using their nonpreferred reference frame. The two strategy groups displayed no decline in accuracy when instructed to use their nonpreferred, rather than their preferred, reference frame throughout an experimental session (in fact, turners even showed some improvement).

This flexible availability of the two reference frames to subjects in both groups was investigated further in Experiment 3. In this experiment, a second reaction format based on allocentric coordinates (maplike format) was presented, randomly interspersed with the homing-vector format (already used in Experiments 1 and 2). If subjects navigate using exclusively one frame of reference, then turners (using an egocentric frame of reference) should display impaired performance when confronted with an allocentric reaction format. Despite the particular reaction format on a given trial being unpredictable, subjects in both strategy groups achieved high response accuracy. This was true even for turners (who prefer to use an egocentric reference frame) when forced to respond with the maplike reaction format (requiring an allocentric frame). Taken together, these findings (especially those of Experiments 3) support the assumption of coexisting spatial representations during navigation.

Experiment 1

Experiment 1 was designed to explore whether the two strategy groups, turners and nonturners, would display equivalent performance (accuracy) on the basis of the respective spatial representations built up during the tunnel passage. One might expect differences in the characteristics of the spatial representation dependent on the acquisition processes. In particular, by rotating their axis of orientation with each change of direction, turners would be expected to be more prone to orientation loss (i.e., display an increasing number of side errors) with increasing number of turns over the course of a tunnel; nonturners, by comparison, would be less affected by this factor.

Method

Subjects

Twelve subjects (3 women) of the Technical University of Aachen, Aachen, Germany, took part in Experiment 1. Their ages ranged from 18

[3] One subject had to be excluded because of this criterion in Experiment 1. There were no exclusions in Experiment 2 and none in Experiment 3. Nonetheless, in Experiment 3, 1 subject was excluded because he switched strategy from turner to nonturner after his first exposure to the maplike reaction format.

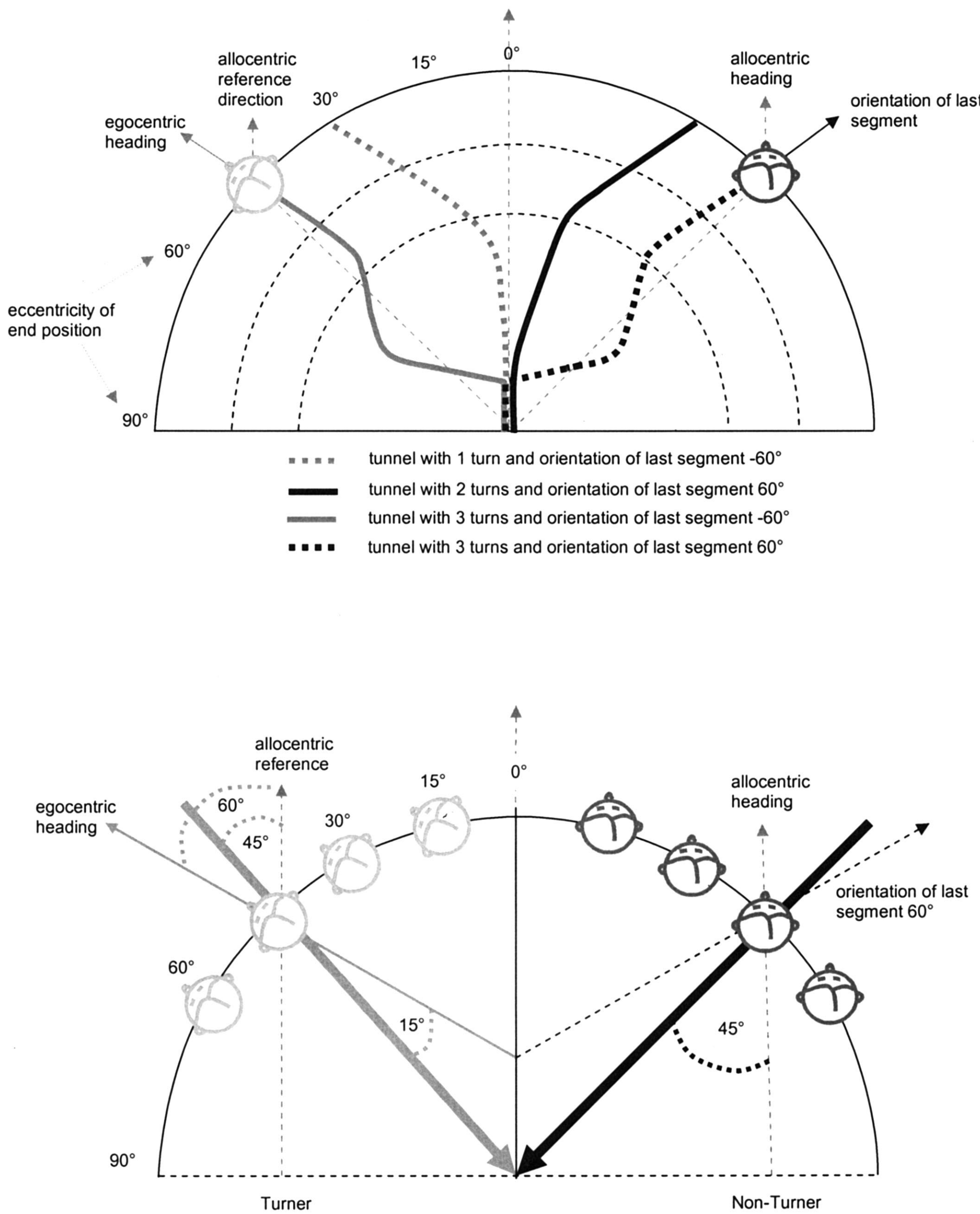

Figure 3. Illustration of spatial material in Experiment 1. The upper panel displays four different tunnels with varying numbers of turns with the same length ending on a virtual semicircle with end positions with eccentricities of 0°, 15°, 30°, 45°, 60°, and 90° to the left side of the origin. The same eccentricities are present but not pictured to the right side of the origin. The allocentric reference direction is equivalent to the orientation of the first segment. To the left, a turner is pictured at the end of a tunnel displaying a heading direction of 60°. To the right, a nonturner is pictured displaying a heading direction of 0° at the end of the tunnel. Four different tunnels display possible configurations of the material, with the first tunnel including one turn with an angle of 60° to the left, placed within the third segment of the passage. The second tunnel displays a passage with two turns, placed within the second and the fifth segment of the tunnel. Tunnel 3 displays a passage with three turns, placed within the second, the fourth, and the sixth segment, with a mirror image as Tunnel 4. The lower panel displays turners to the left (gray lines) and nonturners to the right (black lines). For turners, the heading in the end of a passage is equivalent to the heading direction of the last segment (constant heading of 60°). For nonturners, the heading direction in the end of the passage is equivalent to the allocentric reference direction (0°). The expected angular reaction for a subject using an egocentric reference frame during the passage (turner) for an end position with an eccentricity of 45° is calculated as follows:

$$\text{expected reaction} = \text{allocentric eccentricity} - \text{orientation of the last segment}.$$

Because the allocentric eccentricity is 45° and the orientation of the last segment is 60°, the expected angular reaction for a turner is −15°. For a subject using an allocentric frame of reference (nonturners), the expected angular reaction is calculated as the angle of the allocentric eccentricity of end position. A turner ending at 45° to the left of the origin would have to adjust the homing arrow with 45°.

to 35 years ($M = 23.5$ years). Subjects were either paid (€8 or $9.63 per hour) or received course credit for participating. Prior to the main experiment, subjects were categorized with respect to their preferred use of an allo- or an egocentric reference frame. Five subjects were categorized as turners and 7 as nonturners.

Task, Materials, and Procedure

Subjects were seated in a dimly illuminated room in front of a 19-in. display monitor. The monitor was surrounded by black cardboard to eliminate additional reference information. The experiment was performed in two sessions on consecutive days. On the first day, subjects were informed of the purpose of the experiment and the procedure for the following day. Afterward, subjects were categorized for their preferred strategy. Two training blocks of 48 trials each followed, and subjects received strategy-specific feedback about their performance. On each trial, the subject adjusted her or his strategy-specific homing arrow, and we gave feedback on the accuracy of the angular adjustment by presenting the correct answer together with the subject's reaction on the screen. The main experimental session, conducted on the second day, included four trial blocks with breaks after each block.

The subject's task was to keep up orientation during the passage through the tunnels. On each trial, subjects started the tunnel by pressing one of the mouse buttons. After doing so, an asterisk appeared for 500 ms, followed by the static display of the entrance into a tunnel for another 500 ms. Then, the tunnel movement commenced. Having traversed the preselected straight and curved segments, the tunnel movement ended with the display of the last frame for 500 ms. Subsequently, an asterisk was presented for 1,000 ms, followed by the onset of the response arrow. Subjects had to react by using the mouse to adjust the arrow so as to represent the homing vector. Feedback was given randomly about the accuracy of the adjustment.

Task difficulty was varied in terms of the number of turns during the paths, whereas tunnel length was kept constant. All tunnels consisted of seven segments and included one, two, or three turns. Each tunnel started and ended with a straight segment. For tunnels with one turn, the bend was located between Segments 3 and 5. For tunnels with two turns, bends were located in Segments 2 and 5; for tunnels with three turns, bends were located in Segments 2, 4, and 6. Turns were always placed between straight segments. The eccentricity of end positions was systematically varied, with eccentricities of 15°, 30°, 45°, or 60° to each side relative to the origin. To keep the heading direction constant, tunnels with more than one turn always exhibited an orientation of the last segment of 60° relative to the initial segment (see Figure 3 for an illustration of possible tunnel passages with varying numbers of turns). The design therefore included the following factors: number of turns (one, two, or three), side of end position (left or right relative to starting point), and eccentricity of end position (15°, 30°, 45°, or 60°). There were six trials for each combination of this $3 \times 2 \times 4$ factorial design, giving a total number of 144 tunnels to be performed. Additional filler trials were included that ended up somewhere in between the eccentricities of interest, in order to prevent subjects from categorizing classes of eccentricity.

Performance Measures

The tunnel paradigm follows the logic of analyzing cognitive processes during spatial orientation using psychophysiological measures. For analyzing homogeneous cognitive processes, it is crucial to distinguish between correct and false solutions. The latter, that is, trials on which the navigator loses orientation during the task, have to be omitted from further analysis, whereas only correct reactions can be analyzed.

Side Errors

The simplest criterion for a correct solution of the tunnel task is provided by valid indications of the side of the end position, left or right, relative to the origin.[4] Reactions indicating the wrong side of end position are labeled *side error*. Such side errors might reflect a simple mixing up of left and right or a total loss of orientation. Therefore, side errors were analyzed separately and eliminated from further analysis.

Angular Fit

As one basic criterion for a correct spatial representation, the subject should be able to differentiate among varying eccentricities of end position within the virtual environment. A correlation coefficient for the adjusted homing vector for each eccentricity of end position and the objective angular vector reflects the subject's ability to discriminate among varying eccentricities (after elimination of side errors).

Absolute Error

The absolute difference between the subject's reaction and the expected reaction provides a measure of the absolute error. Eccentricity of end position is defined in allocentric coordinates, just as the reaction of nonturners using an allocentric frame of reference. For this strategy group, the absolute error is computed as the difference between eccentricity of end position and angular adjustment. For subjects using an egocentric reference frame, the numerical value of the subject's reaction is composed of the (allocentric) eccentricity of end position and the angle between the (allocentric) reference direction and the heading direction of the last segment. For tunnels with parallel start and end segments, this difference is zero. Because of the absolute nature of this error, over- and underestimations sum up and, therefore, give an unrefined description of error tendencies. To analyze the absolute error scores, we conducted several analyses of variance (ANOVAs), the design of which is described in the respective experimental sections. If necessary, the Greenhouse–Geisser correction was applied.

Relative Error

The computation of the relative error follows the same rationale as described for the absolute error. However, by analyzing the signed error, we considered possible differences in angular adjustments between turners and nonturners with respect to the direction of error (under- or overestimation). It is important to note that the direction of the error in angular reaction dependent on the eccentricity of end position is accounted for by this measure. To analyze the relative error scores, we conducted identical ANOVAs as for the absolute error (applying the Greenhouse–Geisser correction if necessary).

Results

Subjects demonstrated a spontaneous and stable preference for choosing an ego- or allocentric frame of reference. This preference on Day 1 was maintained throughout the experiment, as evidenced by consistent reactions within the chosen frame of reference. The number of side errors was small overall, and angular reactions increased with increasing eccentricity of end position for both

[4] Side errors are defined solely as responses indicating the wrong side of end position within the preferred frame of reference. For end positions that require a reaction close to 0°, the possibility of side errors is increased, because small deviations to the wrong side might already cross the vertical meridian.

strategy groups. Errors in angular adjustment also increased with increasing eccentricity (tendency to overestimate positions of low eccentricity and underestimate positions of high eccentricity) and differed only slightly between the two strategy groups. In more detail, the results were as follows.

Side Errors

Figure 4 presents the mean number of side errors dependent on the number of turns, separately for turners and nonturners. Side errors were rare overall, likely because of the extensive number of practice trials. A mixed-design ANOVA of the side error scores, with preferred strategy (turner, nonturner) as the between-subjects factor and number of turns (one, two, three) as the within-subject factor, revealed the main effect of number of turns, $F(2, 20) = 13.29$, $p < .002$, $\varepsilon = .672$, and the Preferred Strategy × Number of Turns interaction, $F(2, 20) = 5.36$, $p < .014$, to be significant. For turners, side errors increased with increasing number of turns, $F(2, 8) = 8.73$, $p < .010$. Nonturners, by contrast, were only marginally affected by the number of turns, $F(2, 12) = 2.06$, $p < .084$.

Angular Fit

Taking into consideration the different coordinate systems used by the two strategy groups, the analysis of the adjusted homing vectors revealed comparable performance for turners and nonturners. Correlations of observed angular response with strategy-specific expected angular response revealed highly significant interrelationships for both turners, $r(56) = .976$, $p < .0001$, and nonturners, $r(45) = .961$, $p < .0001$. Taking the number of turns into account, both groups displayed significant interrelationships between expected and observed angular responses. For nonturners, equivalent correlations were obtained for tunnels with one, two, and three turns (rs = .977, .947, and .966, respectively, ps < .0001). Turners displayed slightly decreasing correlations with increasing number of turns (rs = .965, 935, and .903 for tunnels with one, two, and three turns, respectively, ps < .0001).

Absolute Error

The absolute error scores are presented in Figure 5. Because turners' orientation performance is influenced by the heading defined by the last segment of the tunnel (Schönebeck et al., 2001), only tunnels with constant heading in the last segment were presented in Experiment 1—with the exception of tunnels with just one turn, for which this is not possible (in this case, heading is confounded with eccentricity of end position). Therefore, the analyses of absolute error scores were performed separately for tunnels with one turn and those with two or three turns. Mixed-design ANOVAs were conducted, with preferred strategy (turner, nonturner) as the between-subjects factor and side of end position (left or right relative to starting point), eccentricity of end position (15°, 30°, 45°, 60°), and, additionally for tunnels with more than one turn, the number of turns (two or three) as the within-subject factors.

For tunnels with one turn (see Figure 5A), the absolute error was revealed to be significantly influenced by the eccentricity of end position, $F(3, 30) = 5.29$, $p < .014$, $\varepsilon = .665$. Subjects made comparable absolute errors for end positions of 15° and 30° eccentricity and increasing errors when eccentricity of end position increased to 45° and 60°.

For tunnels with two and three turns (see Figure 5B), none of the factors were revealed to have a significant effect on absolute error. Nonetheless, there appeared to be some differences between the two strategy groups. To examine for these differences, we performed separate ANOVAs for tunnels with two and three turns.

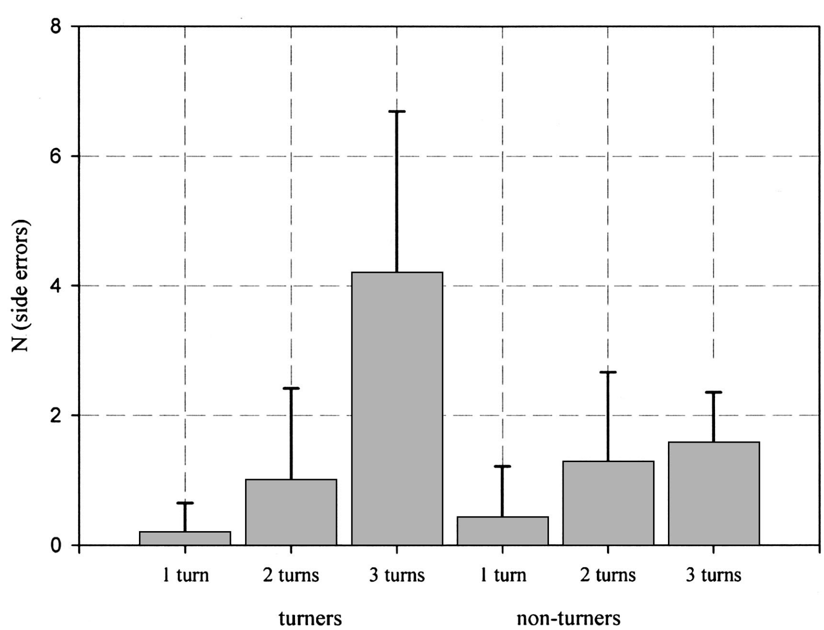

Figure 4. Mean number of side errors (+ 1 *SD*, depicted by the error bars) for turners (left bars) and nonturners (right bars) for tunnels with one, two, and three turns.

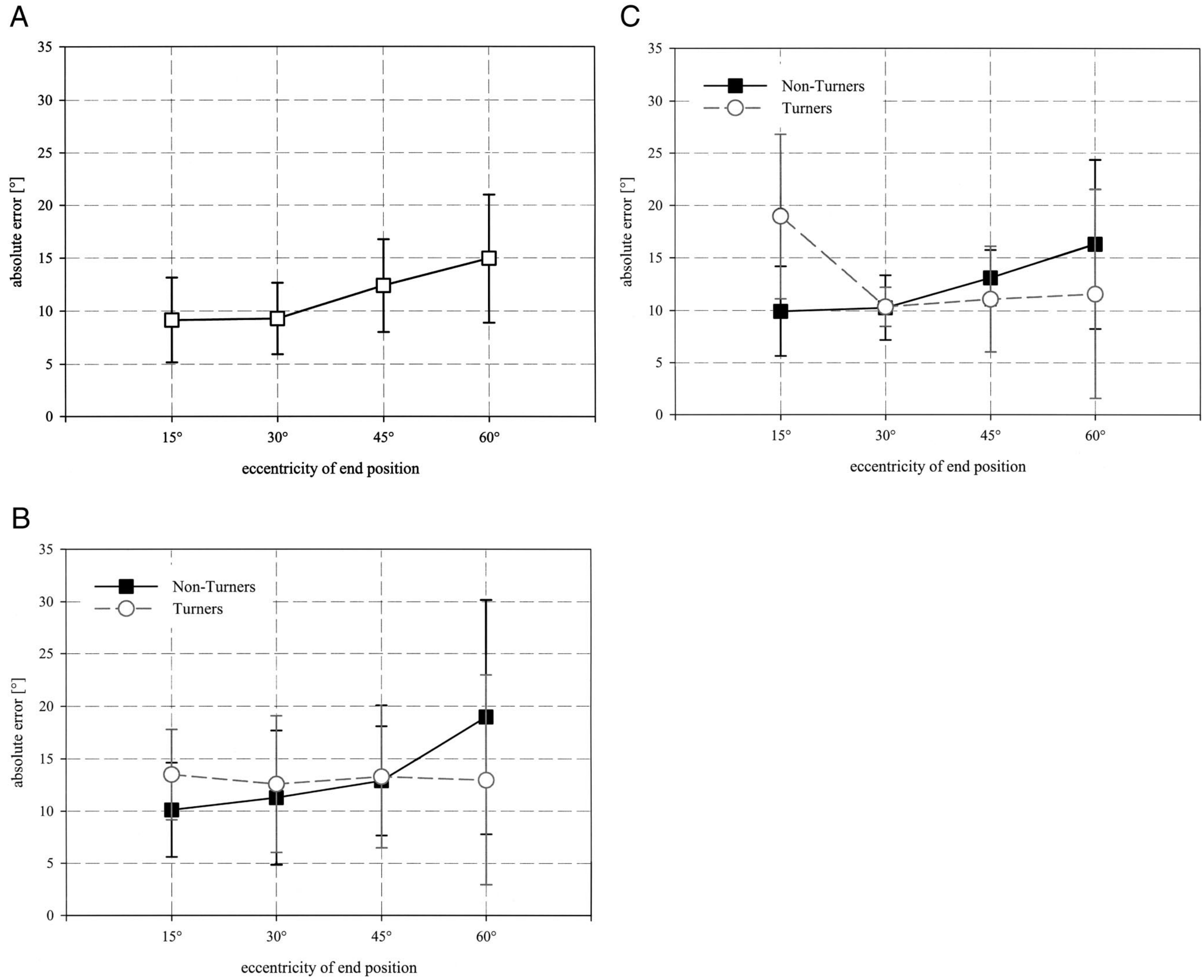

Figure 5. A: Mean absolute error (± 1 *SD*, depicted by the error bars) of the adjusted homing vector for tunnels with one turn dependent on the eccentricity of end position relative to the origin of the path, averaged over turners and nonturners. B: Mean absolute error (± 1 *SD*, depicted by the error bars) for tunnels with two turns dependent on the eccentricity of end position relative to the origin of the path, separately for turners (dotted line) and nonturners (continuous line). C: Mean absolute error (± 1 *SD*, depicted by the error bars) for tunnels with three turns dependent on the eccentricity of end position relative to the origin of the path, separately for turners (dotted line) and nonturners (continuous line).

For tunnels with two turns, again, there were no significant effects. However, for tunnels with three turns, the Preferred Strategy × Eccentricity of End Position interaction was marginally significant, $F(3, 30) = 2.88$, $p < .052$.

For tunnels with three turns, nonturners displayed an increase in absolute error with increasing eccentricity of end position. For turners, by contrast, absolute error did not increase with increasing eccentricity of end position; rather, absolute errors were highest for end positions of 15° eccentricity. However, these differences have to be interpreted with caution. For both strategy groups, errors are depicted within an allocentric coordinate system. For tunnels with parallel orientation of the initial and the last segment, the egocentric and allocentric coordinate systems are aligned, so that a direct comparison is straightforward. But in the absolute-error data reported above, the last segment always diverged in orientation from the reference direction defined by the first segment. Therefore, ego- and allocentric coordinate systems differ with respect to their alignment at the end of the last segment, and turners' reactions have to be transformed into an allocentric coordinate system.

Relative Error

The signed error scores, presented in Figure 6, were examined in separate analyses for tunnels with one turn (and therefore varying heading directions defined by the orientations of the last segment) and tunnels with two and three turns (with constant heading). A

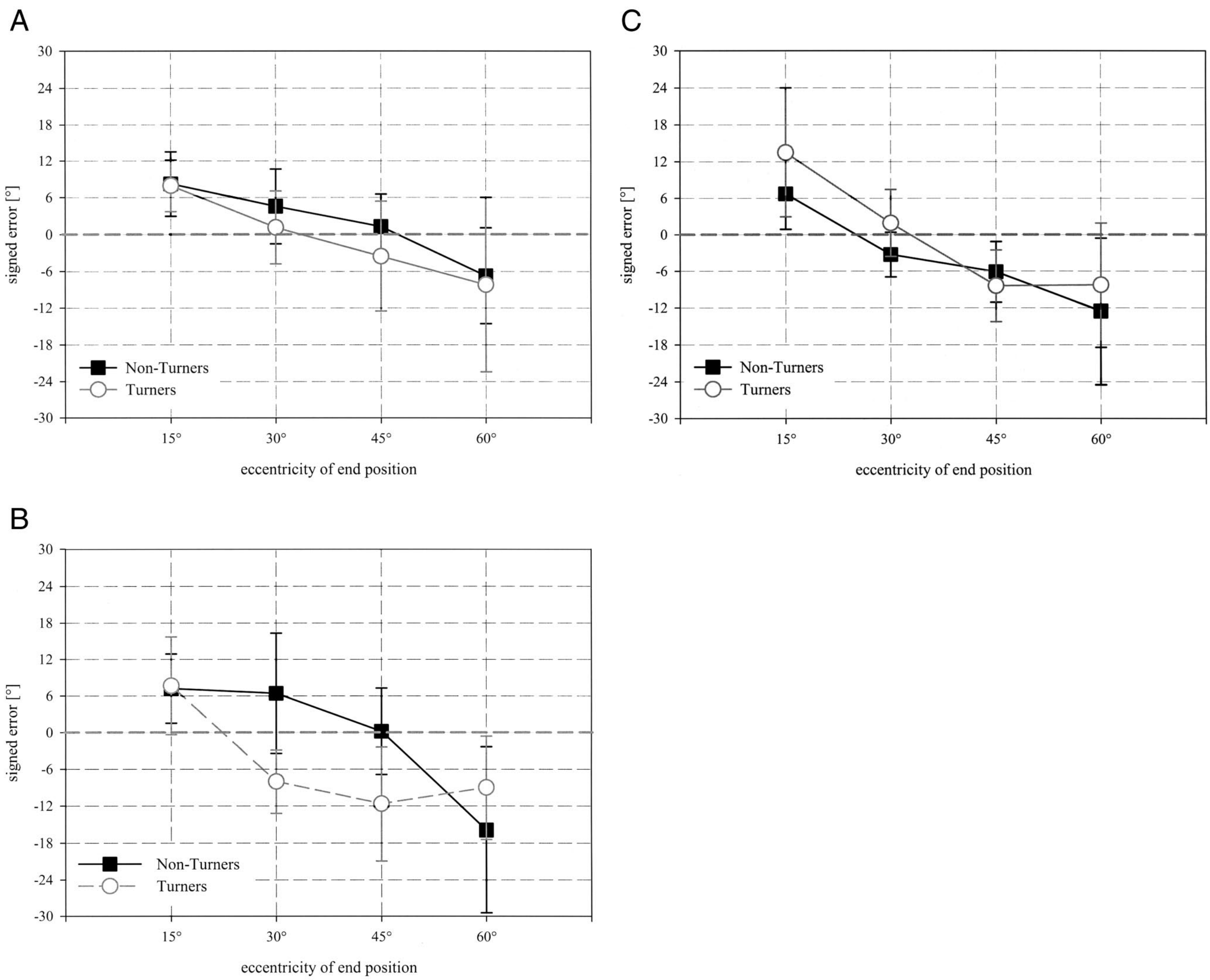

Figure 6. Mean signed error (± 1 *SD*, depicted by the error bars) of the adjusted homing vector dependent on the eccentricity of end position relative to the origin of the path, separately for turners (dotted line) and nonturners (continuous line), for tunnels with one (A), two (B), and three (C) turns.

mixed-design ANOVA was conducted for tunnels with one turn, with preferred strategy (turner, nonturner) as the between-subjects factor and side of end position (left or right relative to starting point) and eccentricity of end position (15°, 30°, 45°, 60°) as the within-subject factors. The results revealed only the main effect of eccentricity to be significant, $F(3, 30) = 16.26$, $p < .0001$. As can be seen from Figure 6A, which presents the signed errors for turners and nonturners separately, both strategy groups tended toward an overestimation of end positions up to 30° and an underestimation of more eccentric end positions.

For tunnels with more than one turn, a mixed-design ANOVA was conducted, with preferred strategy (turner, nonturner) as the between-subjects factor and number of turns (two, three), side of end position (left or right relative to starting point), and eccentricity of end position (15°, 30°, 45°, 60°) as the within-subject factors. This analysis revealed the main effect of eccentricity, $F(3, 30) = 13.56$, $p < .0001$, as well as the Preferred Strategy × Number of Turns interaction, $F(1, 10) = 14.38$, $p < .004$, the Preferred Strategy × Number of Turns × Eccentricity interaction, $F(3, 30) = 4.64$, $p < .009$, and the Preferred Strategy × Side of End Position × Eccentricity interaction, $F(3, 30) = 3.13$, $p < .040$, to be significant. Figures 6B and 6C present the error patterns for turners and nonturners, separately for tunnels with two and three turns.

For tunnels with two and three turns, the two strategy groups displayed some dissimilarity in the signed error patterns. For tunnels with two turns (see Figure 6B), nonturners overestimated end positions up to 30° eccentricity while adjusting the homing vector for end positions of 45° eccentricity relatively precisely. In contrast, turners underestimated eccentricity for all end positions greater than 15°. For tunnels with three turns (see Figure 6C), however, both strategy groups again displayed a similar pattern of signed errors. There was a tendency to overestimate end positions of low eccentricity and underestimate end positions of high eccentricity. The effect of the side of end position resulted from more extreme underestimation of 30° and 45° end positions on the left, compared with the right, side for turners.

Discussion

The aim of Experiment 1 was to determine whether the information provided in a desktop-simulated tunnel task, with only visual flow and without any proprioceptive or vestibular information, would be sufficient to allow for spatial orientation. The results clearly indicate that the tunnel task is solvable. That is, subjects showed little difficulty in building up an adequate spatial representation when presented with a simple, computer-simulated homing task. In line with studies that attest to computer-simulated environments being a promising tool for studying cognitive processes (Annoshian & Seibert, 1996; May et al., 1997; Wartenberg, May, & Péruch, 1998), even a simple desktop virtual environment is sufficient to permit subjects to establish a spatial representation.

Given that the tunnel was not seen as a whole and did not provide any visual landmarks, the task could be solved only if subjects built up a spatial representation. The good orientation performance, as evidenced by the highly significant correlations of angular reaction with eccentricity of end position, reflects the experimental variation of the nonperceptible spatial variable eccentricity of end position independently of the side of end position (left or right). This supports the conclusion that the underlying spatial representation is symmetrical. There were general tendencies to overestimate end positions of low eccentricity and underestimate end positions of high eccentricity, reflecting a tendency toward the middle. This seems to be a stable tendency, which is independent of the frame of reference used during the task (it was observed in both strategy groups for tunnels with different numbers of turns).

Compared with other studies, the absolute error magnitudes were small. Thorndyke and Hayes-Roth (1982) reported errors ranging from 16.9° to 39.3° depending on the task, Loomis et al. (1992) reported errors ranging from 10° to 15°, and May et al. (1997) reported errors ranging from 15° to 30°. In contrast to the study of May et al., in the present study, subjects displayed a mean absolute error of just 6.28°, even though the traversed tunnels included a higher number of turns. This indicates the high resolution of the underlying spatial representation. Thus, the tunnel task provides sufficient information to build up a spatial representation, and this representation contains information that allows for relatively accurate path integration.

The second question examined in Experiment 1 concerned the frame of reference used during navigation in the tunnel task. If body senses are needed to update heading as a prerequisite for recalculating egocentric bearing, then subjects in the tunnel task should constantly work within an allocentric reference frame. The results clearly demonstrate that subjects react differentially to the task at hand, using either an egocentric or an allocentric frame of reference. The tunnel task does not necessitate the use of a certain type of reference frame; rather, the decision to use one or the other is based on spontaneous but intraindividually consistent preferences. Even without proprioceptive or vestibular information during navigation, one half of the subjects chose an egocentric frame of reference for spatial orientation. This is in marked contrast to other studies that have concluded that in the absence of real body rotation, a recalculation of egocentric bearing leads to impaired accuracy because of a lack of updated heading (Chance et al., 1998; Easton & Sholl, 1995; Farrell & Robertson, 1998; May, 1996; Presson & Montello, 1994). Instead, the present study points to an individual preference to choose an ego- or an allocentric frame of reference for navigation, independently of the fact that only visual information was provided. For nonturners, the use of an allocentric frame of reference in the tunnel task did not necessitate the updating of heading, because the homing vector could be adjusted without a recalculation of egocentric bearing from the starting position. But turners, using an egocentric frame of reference during navigation, clearly updated heading changes as well as egocentric bearing even in the absence of proprioceptive or vestibular information. Thus, idiothetic information is not necessary for successfully updating heading and egocentric bearing (i.e., for building up an egocentric representation); rather, an individual preference to use an ego- or an allocentric frame of reference is likely to be one important factor in navigation.

The results clearly demonstrate that the tunnel task is a convenient tool for studying spatial orientation within a sparse computer-generated environment. Under such conditions of reduced visual information, subjects reveal a stable preference in using an ego- or an allocentric frame of reference. Because no proprioceptive or vestibular information is available from active movement, there are no cues other than visual information for changes in heading direction. This raises the question whether the choice of one or the other frame of reference during navigation is preferential or habitual in nature; that is, whether subjects would be able to use the nonpreferred reference frame without impairment in performance. (We refer to the subjects' bias to use one frame of reference rather consistently from the very first exposure to the tunnel task as the *preferred strategy*; analogously, we refer to the use of the nonpreferred reference frame as *nonpreferred strategy*.)

Experiment 2

This question was examined in Experiment 2, in which subjects had to use the nonpreferred reference frame. The most difficult part in encouraging subjects to use their nonpreferred strategy was to find an instruction that allowed them to understand and apply their nonpreferred frame of reference. This was achieved by instructing subjects to imagine walking through the tunnel while seeing themselves from the bird's-eye view (allocentric frame of reference) or imagining that they were driving a bike leaning themselves into the turns of the tunnel (egocentric frame of reference).

Method

Subjects

Eight students of the Technical University of Aachen took part in Experiment 2 (6 men and 2 women; mean age = 25 years; age range = 21–30 years; all with normal or corrected-to-normal vision). They received either payment (€8 or $9.63 per hour) or course credit for their participation. In a preexperimental session, subjects' preferred use of an ego- or an allocentric frame of reference was determined (for procedure, see above). Four subjects were categorized as turners and 4 as nonturners.

Task and Procedure

Subjects had to perform the same tunnel task as described above (see Experiment 1, *Method* section). The experiment was conducted over 2 separate days, with subjects using their preferred strategy on Day 1 and their nonpreferred strategy on Day 2. Prior to the experimental task on Day 1, subjects' preferred strategy was identified by using the forced-choice categorization task described above. Immediately afterward, subjects performed 4 blocks of 42 tunnels each using their preferred strategy. On Day 2, subjects were informed that the tunnel task could also be solved by using a different strategy: that which they had not used on Day 1 (i.e., their nonpreferred strategy). This strategy was explained to them, and they then performed a number of practice trials using this strategy until they felt comfortable with it. Following practice, they again performed 4 blocks of 42 tunnels using the nonpreferred strategy.

In each strategy condition, preferred and nonpreferred, subjects had to traverse a total of 168 tunnels. The tunnels ended up at positions ranging from 100° to the left to 100° to the right of the starting point. Performance was analyzed, by means of ANOVAs, only for tunnels that ended at positions of 15°, 30°, or 45° eccentricity (with a range of 2° to each side of the end position) to either side of the starting point (70% of the tunnels). The other tunnels served as filler trials (30%).

Results

For both strategy groups, the number of side errors was small, and angular adjustment significantly correlated with eccentricity of end position. The patterns of absolute and signed errors were more similar overall when both strategy groups used the same frame of reference (i.e., the preferred frame for one group and the nonpreferred for the other) compared with the error patterns of each strategy group within different frames of reference (the preferred and nonpreferred for turner and nonturner). In more detail, the results were as follows.

Side Errors

Turners made fewer side errors using their nonpreferred (allocentric reference frame) compared with their preferred strategy (egocentric frame): 0.8% versus 2.8%, respectively. Nonturners, by contrast, displayed no difference in side errors between their preferred and nonpreferred strategies (2.9% vs. 3.1%, respectively). A mixed-design ANOVA of the side error scores, with preferred strategy (turners, nonturners) as the between-subjects factor and instructed strategy (preferred, nonpreferred) and number of turns over the course of the tunnel (one, two, three) as the within-subject factors, revealed the Preferred Strategy × Instructed Strategy × Number of Turns interaction to be significant, $F(2, 12) = 7.30$, $p < .008$. Turners, using their preferred strategy, made more side errors for tunnels with three turns compared with tunnels with one and two turns. When using their nonpreferred reference frame, turners made fewer side errors overall, with error rate independent of the number of turns. In contrast, nonturners, when using their preferred strategy, displayed the highest number of side errors for tunnels with two turns; when using their nonpreferred strategy, their error rate was constant across tunnels with varying number of turns.

Angular Fit

Using their preferred strategy, both turners and nonturners adjusted the homing vector in line with increasing eccentricity of the tunnels' end positions. Pearson product–moment correlations revealed significant relations of eccentricity of end position with angular vector: $r(48) = .939$, $p < .0001$, for turners, and $r(34) = .956$, $p < .0001$, for nonturners. Significant correlations were also observed when subjects used their nonpreferred strategy: $r(34) = .972$, $p < .0001$, for turners, and $r(48) = .933$, $p < .0001$, for nonturners. This indicates that both strategy groups were able to build up a spatial representation independently of the reference frame, preferred or nonpreferred, used during task performance.

Absolute Errors

Figure 7 presents the absolute error dependent on the eccentricity of end position and the reference frame used, separately for turners and nonturners using their preferred and nonpreferred reference frames on Day 1 and Day 2, respectively.

To examine for differences in accuracy depending on the reference frame that had to be used, we performed a mixed-design ANOVA, with preferred strategy (turners, nonturners) as the between-subjects factor and instructed strategy (preferred, nonpreferred strategy), number of turns (one, two, three), and eccentricity of end position (15°, 30°, 45°) as the within-subject factors. This analysis revealed significant main effects of number of turns, $F(2, 12) = 5.07$, $p < .007$, and eccentricity of end position, $F(2, 12) = 10.09$, $p < .015$, $\varepsilon = .560$. There was also a marginally significant Preferred Strategy × Instructed Strategy interaction, $F(1, 6) = 4.50$, $p < .078$, and the Preferred Strategy × Instructed Strategy × Eccentricity of Position interaction was significant, $F(2, 12) = 6.84$, $p < .010$.

Absolute errors were larger for tunnels with two and three turns compared with tunnels with just one turn, and there was an increase in absolute error with increasing eccentricity of end position (significant differences for 45° compared with 15° and 30° eccentricity). Accuracy was improved overall on Day 2 because of an improvement of turners using their nonpreferred strategy (marginally significant Preferred Strategy × Instructed Strategy interaction), $F(1, 6) = 4.50$, $p < .078$. The Preferred Strategy × Instructed Strategy × Eccentricity of Position interaction was due to nonturners displaying an increased absolute error for 45° end positions when using their nonpreferred (compared with their preferred) strategy, whereas for end positions of 15° eccentricity, they showed larger absolute errors when using their preferred strategy. Turners, by contrast, displayed a significant improvement for 15° end positions when using their nonpreferred strategy (i.e., on Day 2).

As can be seen from Figure 7, turners showed a substantial improvement from Day 1 to Day 2 of the experiment. A comparison between turners using their preferred strategy and nonturners using their nonpreferred strategy (i.e., with both using an egocentric reference frame) revealed no striking differences in absolute error. Comparing turners using their nonpreferred strategy and nonturners using their preferred strategy (i.e., with both using an allocentric reference frame) revealed slight advantages in accuracy for the former group (turners).

Repeated measures ANOVAs of the absolute error scores were performed separately for turners and nonturners, with strategy (preferred, instructed), number of turns (one, two, three), and

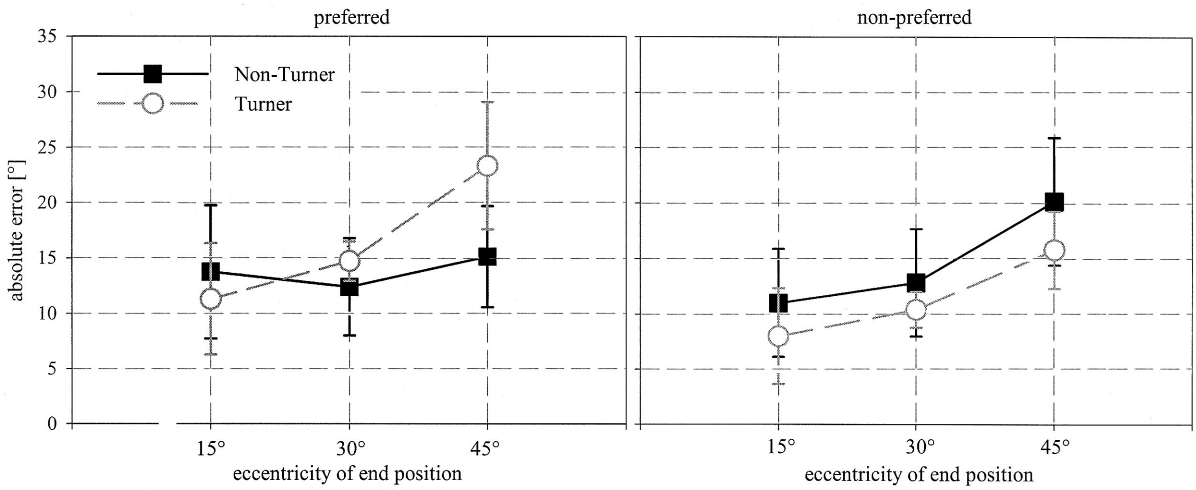

Figure 7. Mean absolute error (± 1 *SD*, depicted by the error bars) of the adjusted homing vector dependent on the eccentricity of end position and the reference frame used, separately for turners (dotted line) and nonturners (continuous line) using their preferred and nonpreferred reference frames on Day 1 and Day 2, respectively.

eccentricity of end position (15°, 30°, 45°) as factors. For turners, the ANOVA confirmed improved performance on Day 2 (main effect of instructed strategy, $F[1, 3] = 19.32$, $p < .022$), besides replicating the main effects of number of turns and eccentricity of end position, $F(2, 6) = 5.94$, $p < .038$, and $F(2, 6) = 7.30$, $p < .025$, respectively. For nonturners, by contrast, only the Instructed Strategy × Eccentricity of End Position interaction was revealed to be significant, $F(2, 6) = 5.34$, $p < .047$.

Relative Error

Figure 8 presents the signed error dependent on the eccentricity of end position and the reference frame used, separately for turners and nonturners using their preferred and nonpreferred reference frames on Day 1 and Day 2, respectively.

The signed error scores were examined in a mixed-design ANOVA, with preferred strategy (turners, nonturners) as the between-subjects factor and instructed strategy (preferred, nonpreferred), number of turns (one, two, three), and eccentricity of end position (15°, 30°, 45°) as the within-subject factors. This ANOVA revealed significant main effects of number of turns and eccentricity of end position, $F(2, 12) = 7.37$, $p < .008$, and $F(2, 12) = 9.74$, $p < .015$, $\varepsilon = 5.79$, respectively. Moreover, the following interactions were significant: Number of Turns × Eccentricity of End position, $F(4, 24) = 6.56$, $p < .001$; Preferred

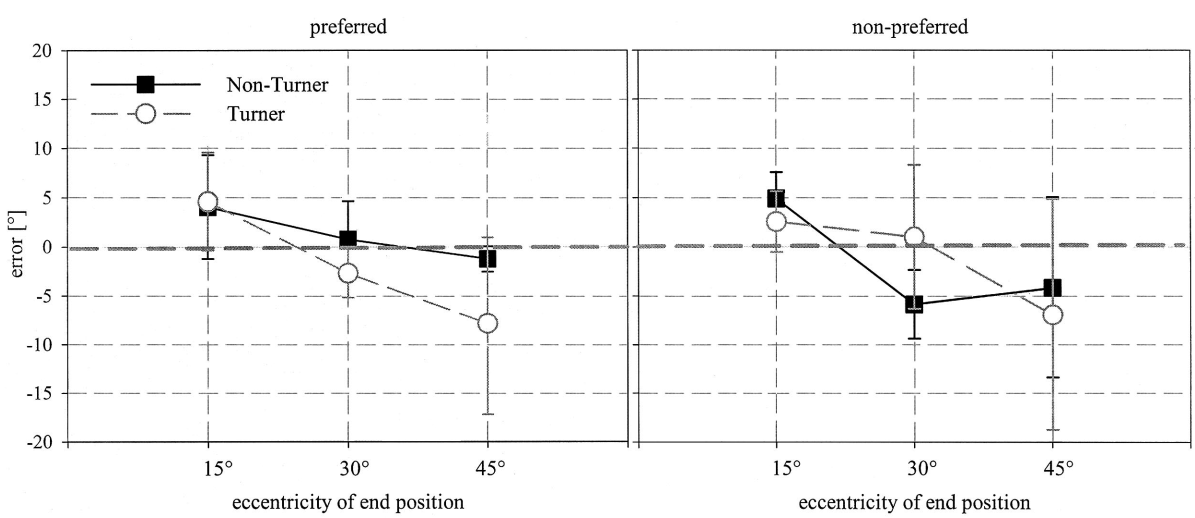

Figure 8. Mean signed error (± 1 *SD*, depicted by the error bars) of the adjusted homing vector dependent on the eccentricity of end position and the reference frame used, separately for turners (dotted line) and nonturners (continuous line) using their preferred and nonpreferred reference frames on Day 1 and Day 2, respectively.

Strategy × Number of Curves × Eccentricity of End Position, $F(4, 24) = 3.35$, $p < .026$; and the interaction among all four factors, $F(4, 24) = 5.12$, $p < .004$.

There was a slight overestimation of eccentricity for tunnels with one turn, a near-exact estimation of eccentricity for tunnels with two turns, and a slight underestimation for tunnels with three turns (main effect of number of turns). Furthermore, there was an overestimation for end positions of low eccentricity (15°) and an underestimation for end positions of higher eccentricity (main effect of eccentricity of end position).

As can be seen from Figure 8, turners and nonturners displayed comparable error tendencies for tunnels with different number of turns when using their preferred, compared with their nonpreferred, frame of reference: overestimation of end positions for tunnels with one and two turns, underestimation for tunnels with three turns. The Number of Turns × Eccentricity of End Position interaction was due to a greater overestimation of 15° end positions with tunnels with three turns, whereas end positions of higher eccentricity were more markedly underestimated with three turns.

To decompose the higher order interactions involving preferred strategy, we conducted separate repeated measures ANOVAs for turners and nonturners, with instructed strategy (preferred, nonpreferred), number of turns (one, two, three), and eccentricity of end position (15°, 30°, 45°) as factors. For turners, the Number of Turns × Eccentricity of End Position interaction, $F(4, 12) = 4.29$, $p < .022$, and the interaction among all three factors, $F(4, 12) = 9.53$, $p < .001$, were significant. For nonturners, the main effects of number of turns, $F(2, 6) = 11.88$, $p < .008$, and eccentricity of end position, $F(2, 6) = 7.35$, $p < .072$, $\varepsilon = .505$, as well as the interaction between these two factors, $F(4, 12) = 3.45$, $p < .045$, were significant.

Turners displayed stronger overestimation for 15° end positions with tunnels with three turns and stronger underestimations with tunnels with three turns when eccentricity of end position was 30° or greater (accounting for the Number of Turns × Eccentricity interaction). However, these patterns were partly reversed for the preferred relative to the nonpreferred strategy (accounting for the three-way interaction). Nonturners displayed a monotonic increase in underestimation with tunnels with increasing number of turns: 1.8° (i.e., slight overestimation), −6.9°, and −20° for tunnels with one, two, and three turns, respectively. For tunnels with one or two turns, the error scores were moderate, ranging from 5° underestimation to 5° overestimation for different eccentricities.

Discussion

The aim of Experiment 2 was to evaluate whether turners and nonturners would be able to use their nonpreferred frame of reference during spatial navigation. The ability to use the nonpreferred reference system without performance deterioration can be regarded as evidence in favor of a preference for, rather than the habitual use of, a certain representation of space. In terms of absolute error, turners showed improved performance on Day 2 of the experiment on which they used their nonpreferred strategy, that is, an allocentric frame of reference. In contrast, nonturners' performance did not differ significantly between Day 1 and Day 2, when they used their preferred (allocentric reference frame) and nonpreferred strategies (egocentric frame). The analysis of signed errors for turners and nonturners revealed comparable performance for the use of the preferred and the nonpreferred strategy. This pattern supports the hypothesis that subjects are able to solve the task using their nonpreferred frame of reference. Most important, though, neither turners nor nonturners showed performance deterioration on Day 2. Therefore, it is safe to conclude that both turners and nonturners are able to learn navigating within a virtual environment using their nonpreferred frame of reference and that they can achieve comparable accuracy using their nonpreferred frame.

The question remains why subjects chose either an ego- or an allocentric frame of reference. Bryant (1992) suggested that the choice of one specific coordinate system is dependent on the task at hand. He argued that subjects would choose an allocentric frame when the navigator's task is to judge object-to-object relations within a stable environment. Our results clearly demonstrate that this is not the case. When presented with the tunnel task, subjects used differential reference systems even though the environment was the same. Other studies have attempted to relate the use of one or the other reference frame to peculiarities of the task environment. For example, Heft (1979) reported that, if environments with sparse visual landmarks were to be traversed, subjects tended to choose an allocentric reference frame. This was disconfirmed in the present study: The tunnels eliminated visual landmarks and, yet, the task was solved by using differential frames of reference. On the basis of the present findings, it seems more plausible that multiple representations of space may be active simultaneously (Aguirre & D'Esposito, 1999; Bridgeman, Peery, & Anand, 1997; Milner & Goodale, 1995; Mou et al., 2004; Paillard, 1991; Perrig & Hofer, 1989; Redish, 1999; Redish & Touretzky, 1997; Sholl, 2001; Sholl & Nolin, 1997; Touretzky & Redish, 1996; Wickens, 1992) and that subjects are able to learn to use different strategies of processing and representing spatial information.

The experiments reported thus far have shown that turners and nonturners use differential reference frames for spatial navigation and that these frames differ with respect to the dynamics of the underlying coordinate system. Taking a reference frame as a means of representing locations of objects in space (Klatzky, 1998), the data indicate a stable preference to use an ego- or an allocentric spatial representation but also the ability to learn navigating using the nonpreferred representation of space. If instructed to do so, subjects are just as accurate using their nonpreferred (compared with their preferred) representation to solve the task. This suggests that the use of an ego- or an allocentric frame of reference is preferential rather than obligatory in nature.

Because the primitive parameters differ between ego- and allocentric representations, it is implausible to assume that subjects relied on their preferred representation exclusively. Imagine, for instance, nonturners using their preferred spatial representation but reacting within an egocentric frame of reference. Because the egocentric bearing of the end position from the origin is not a primitive within the allocentric representation, it requires computation. This additional computational step should lead to more and larger errors or at least greater variance in the responses. This was clearly not observed. It seems more plausible that subjects were able to operate within different reference frames in parallel. However, because subjects in Experiment 2 worked with their preferred and nonpreferred reference frame on two separate days, it cannot be decided whether there was just one reference frame that was used or whether there were multiple frames coexisting in parallel.

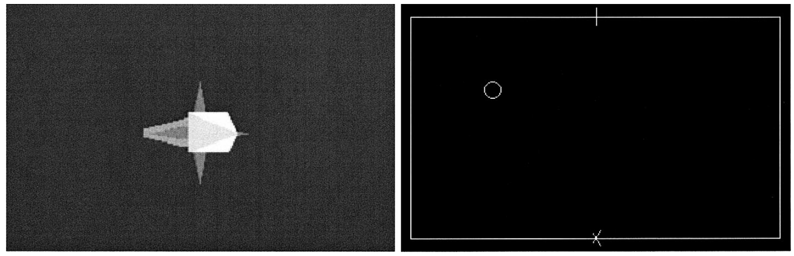

Figure 9. Depiction of the two reaction formats used in Experiment 3. Left panel: Homing arrow after rotation pointing toward the navigator, indicating a position to the right of the navigator. Right panel: Maplike reaction format with an *x* indicating the origin of a path and a vertical line at the 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.

Experiment 3

Experiment 3 was designed to further examine the possibility of coexisting reference frames. In the previous experiments, the reaction format (adjusting a homing vector) left it open which frame of reference to use to solve the task. In Experiment 3, a second maplike reaction format was introduced (in addition to the homing-vector format), which forced subjects to use an allocentric frame of reference. It is important to note that which of the two alternative formats was presented at the end of a tunnel was varied randomly across trials within a given block (in contrast to Experiment 2, in which the instructed strategy, preferred or nonpreferred, was blocked).

Because nonturners prefer an allocentric reference frame, this strategy group should display little difficulty to react within the second format. In contrast, assuming that turners prefer working with an egocentric representation by default and no other spatial representation coexists in parallel, this strategy group should display impaired performance when, unpredictably on a trial, they are presented with an allocentric reaction format (because the computation of derived parameters would lead to impaired accuracy for each computational step, possibly including distortions of the spatial layout). The aim of Experiment 3 was to examine whether there would be differences in response accuracy when different reaction formats with distinct underlying coordinate systems (i.e., allo- and egocentric) are used.

In summary, two different reaction formats were presented in Experiment 3. The formats differed with respect to the reference frame used for response. The first format was the homing vector described above (Experiments 1 and 2). A second maplike reaction format was introduced that presented an outline square (white line drawing) with an *x* marking the starting point of the tunnel and a vertical line at the point where tunnels without turns would have ended (see Figure 9). 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 maplike 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. If turners, by default, build up an egocentric representation only, then this strategy group should display impaired performance when being presented with an allocentric reaction format.

Method

Subjects

The tunnel task was presented as part of a more complex experimental design that used electroencephalography to differentiate among spatial, visual, and verbal working memory processes. Because of gender-specific differences in the neural substrate underlying navigation (Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000), only male subjects, 23 in number (aged between 22 and 34 years; mean age = 25.83 years), were selected to participate in Experiment 3 (to exclude an additional factor in the analysis of ongoing brain electrical activity).[5] All subjects had normal or corrected-to-normal vision and were paid (€8 or $9.63 per hour) for their participation. In a preexperimental session, subjects were categorized with respect to their preferred use of an allo- or an egocentric reference frame. Twelve subjects were identified as nonturners and 11 as turners. The main experiment was then conducted after a delay of at least 3 days.

Task, Materials, and Procedure

Tunnels in Experiment 3 contained only one turn to keep the task as simple as possible (in order to be able to track the various processing components of working memory; Gramann, 2002). Turns were placed within the second or third segment, with varying angles of the turn. Additionally, filler trials without turns or with turns greater than 90° were presented interspersed with the experimental trials. Two different tunnel lengths were used: tunnels of four and of six segments. End positions ranged from 70° to the left to 70° to the right side relative to the origin of the passage. Trials with end positions of more than 60° eccentricity were excluded from the analysis (i.e., they served as filler trials). The first and the last segments were always straight. In total, 55 tunnels had to be solved using the homing-vector reaction and 54 using the map-format reaction. For purposes of data analysis, end positions were grouped into six positions of 5°, 15°, 25°, 35°, 45°, and 55° eccentricity to either side of the origin. At the end of a tunnel, one of the two reaction formats, homing vector or map, was displayed at random.

[5] The existence of gender differences is supported by animal studies (e.g., Isgor & Sengelaub, 1997; Roof, 1993; Roof, Zhang, Glasier, & Stein, 1993; Williams & Meck, 1991) and studies with human subjects that have revealed gender-specific differences in the use of landmarks (Beatty & Troster, 1987; Galea & Kimura, 1993; Goodrich, Damin, Ascione, & Thompson, 1993; Johnson & Meade, 1987; Kerns & Berenbaum, 1991; Lawton, 1994; Sandstrom, Kaufman, & Huettel, 1998; Ward, Newcombe, & Overton, 1986).

Results

The data were analyzed separately for responses with the homing-arrow and the maplike reaction format. With both reaction formats, turners and nonturners displayed negligible numbers of side errors and significant correlations of angular adjustment and eccentricity of end position. Differential task performance between turners and nonturners was evident only with the homing-arrow format but not with the maplike format. Finally, both absolute and relative errors were increased for short, relative to long, tunnels for end positions of small, but not large, eccentricities. The detailed results are presented below, first for the homing vector and then for the maplike reaction format.

Homing-Vector Reaction

Side errors. With the homing-arrow reaction format, side errors (less than 1.6%) were too few to permit further statistical analysis. Small numbers of side errors were observed under all experimental conditions for both strategy groups.

Angular fit. Subjects' adjusted homing vectors were significantly correlated with the expected angular responses, $r(104) = .954$, $p < .0001$. Increasing eccentricity of end position was associated with corresponding increases in homing vectors. Separate correlations for reactions within both strategy groups' preferred frame of reference revealed this correlation to be significant for both turners and nonturners, respectively: $r(58) = .949$, $p < .0001$, and $r(46) = .971$, $p < .0001$.

Absolute errors. The absolute errors in the homing-arrow adjustments were examined by a mixed-design ANOVA, with preferred strategy (turner, nonturner) as the between-subjects factor and side of end position (left or right relative to starting position), eccentricity of end position (5°, 15°, 25°, 35°, 45°, 55°), and tunnel length (four or six segments) as the within-subject factors. The results revealed the main effect of eccentricity of end position, $F(5, 105) = 10.19$, $p < .0001$, and the following interactions to be significant: Preferred Strategy × Eccentricity of End Position, $F(5, 105) = 4.42$, $p < .001$; Preferred Strategy × Tunnel Length, $F(1, 21) = 9.53$, $p < .006$; Side × Eccentricity of End Position, $F(5, 105) = 2.49$, $p < .036$; Preferred Strategy × Tunnel Length × Eccentricity of End Position, $F(5, 105) = 2.43$, $p < .040$ (see Figure 10); and Tunnel Length × Side × Eccentricity of End Position, $F(5, 105) = 2.78$, $p < .044$, $\varepsilon = .640$.

For both strategy groups, absolute errors were smallest for end positions of 5° and increased in magnitude with increasing eccentricity. Whereas absolute errors were comparable for nonturners and tuners with long tunnels (11.26° and 10.95°, respectively), they were greater for nonturners than for turners with short tunnels (11.97° and 9.38°, respectively; Preferred Strategy × Tunnel Length interaction). Further, absolute errors were greater for end positions of 15° and 25° and smaller for end positions of 35° and 45° to the left compared with the right side of the origin (Side × Eccentricity of End Position interaction). However, the absolute difference between the left and right sides amounted to maximally 2.43° and showed no influence of preferred strategy.

Both strategy groups displayed an increase in absolute error with increasing eccentricity of end position (eccentricity main effect). However, for turners, absolute errors differed between end positions of 5° and all positions of larger eccentricity. Nonturners, by contrast, showed similar absolute errors for end positions up to 35° eccentricity; absolute errors were significantly increased only for the most eccentric positions. These differential error patterns account for the Preferred Strategy × Eccentricity interaction.

Additionally, the Preferred Strategy × Tunnel Length × Eccentricity of End Position interaction reflected distinct error patterns for the two tunnel lengths (see Figure 10, which presents the absolute error as a function of eccentricity of end position, separately for turners and for nonturners, for short and for long tunnels). The most striking difference between the two strategy

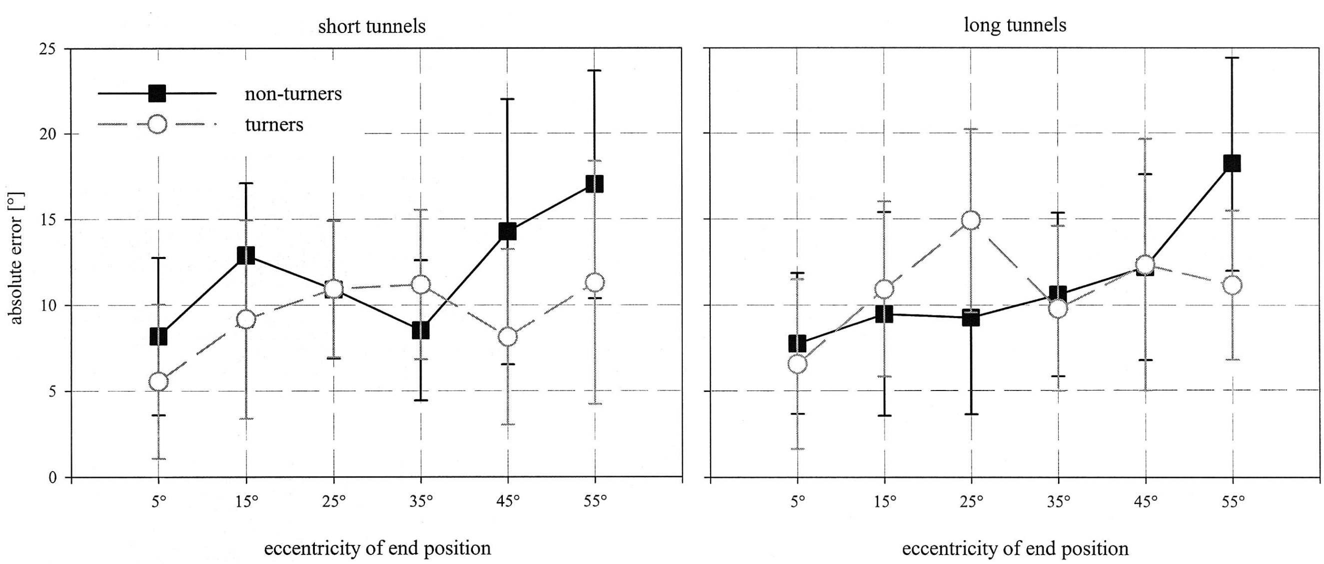

Figure 10. Mean absolute error (± 1 *SD*, depicted by the error bars) of angular adjustment with the homing arrow dependent on the eccentricity of end position, separately for turners (dotted line) and nonturners (continuous line) in short and long tunnels.

groups was the monotonic increase in absolute error for nonturners with long tunnels, with the largest errors for end positions of 55° eccentricity; with short tunnels, nonturners displayed slightly raised absolute errors for positions of 15° eccentricity and the largest errors again for the most eccentric positions. Turners, by contrast, showed increased errors for all eccentricities compared with 5° end positions. This was the case for both short and long tunnels, with the highest absolute error for end positions of 25° eccentricity with long tunnels.

Relative error. The relative errors in the homing-arrow adjustments were examined by an analogous (mixed-design) ANOVA, which revealed the main effects of preferred strategy, $F(1, 21) = 8.42$, $p < .009$, tunnel length, $F(1, 21) = 14.81$, $p < .001$, and eccentricity of end position, $F(5, 105) = 18.55$, $p < .0001$, to be significant. Furthermore, the following interactions were significant: Tunnel Length × Eccentricity of End Position, $F(5, 105) = 3.83$, $p < .003$; Preferred Strategy × Tunnel Length, $F(1, 21) = 22.56$, $p < .0001$; Preferred Strategy × Eccentricity of End Position, $F(5, 105) = 14.94$, $p < .0001$; and Preferred Strategy × Tunnel Length × Eccentricity of End Position, $F(5, 105) = 4.67$, $p < .001$.

Figure 11 presents the relative error as a function of eccentricity of end position, separately for turners and for nonturners, for short and for long tunnels (Preferred Strategy × Tunnel Length × Eccentricity interaction). As can be seen, nonturners tended to overestimate the eccentricity of end positions up to 25°, whereas more eccentric end positions were underestimated with both short and long tunnels. In contrast, turners displayed an overestimation for (almost) all eccentricities with both tunnel lengths; however, with short tunnels, they made minimal errors for end positions of 25° and 35° eccentricity.

Maplike Reaction Format

Side errors. With the maplike reaction format, subjects made hardly any side errors (less than 0.3%).

Angular fit. Again, subjects' angular adjustments were significantly correlated with the end positions' eccentricities, $r(104) = .975$, $p < .0001$. This was the case for both turners, $r(59) = .973$, $p < .0001$, and nonturners, $r(46) = .979$, $p < .0001$.

Absolute error. The absolute error scores were examined by a mixed-design ANOVA, with preferred strategy (turner, nonturner), side of end position (left, right), eccentricity of end position (5°, 15°, 25°, 35°, 45°, 55°), and tunnel length (four or six segments) as factors. This analysis revealed the main effect of tunnel length, $F(1, 21) = 17.68$, $p < .0001$, and the Tunnel Length × Eccentricity of End Position interaction, $F(5, 105) = 10.79$, $p < .0001$, to be significant. Furthermore, the Preferred Strategy × Eccentricity of End Position interaction was significant, $F(5, 105) = 2.47$, $p < .0001$.

Figure 12 presents the absolute error as a function of eccentricity of end position, separately for turners and for nonturners (Preferred Strategy × Eccentricity of End Position interaction). As with the homing-arrow format, nonturners displayed a near-monotonic increase in absolute error with increasing eccentricity of end position, with the largest errors for positions of 55° eccentricity. In contrast, turners showed absolute errors of similar magnitude for all eccentricities.

Figure 13 presents the absolute error as a function of eccentricity of end position, separately for short and for long tunnels (Tunnel Length × Eccentricity of End Position interaction). There was a striking difference between short and long tunnels for end positions of low eccentricity, with significantly larger absolute errors for short tunnels. For long tunnels, absolute error increased near monotonically with increasing eccentricity of end position, with the smallest errors for 5° and 15° eccentricities. Short tunnels displayed the reverse pattern, with end positions of 5° and 15° eccentricity exhibiting the largest absolute errors for both strategy groups. This confirms that with short tunnels, the large absolute errors for end positions of small eccentricity are a robust finding.

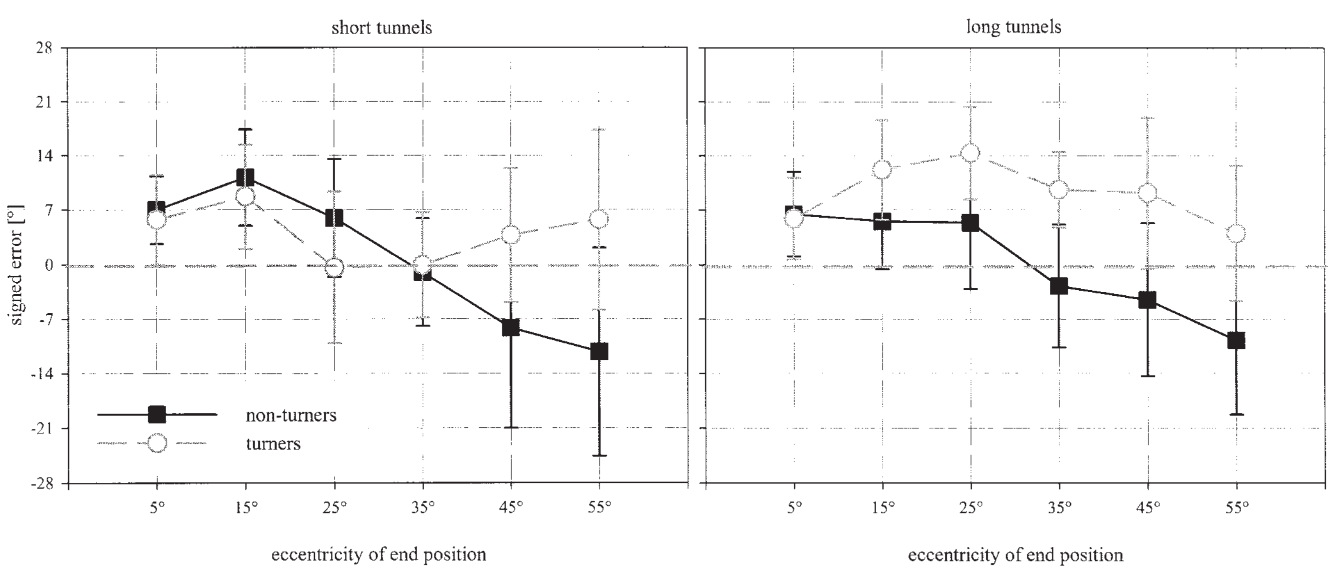

Figure 11. Mean signed error (± 1 *SD*, depicted by the error bars) of angular adjustment within the homing-arrow format dependent on the eccentricity of end position, separately for turners (dotted line) and nonturners (continuous line) in short and long tunnels.

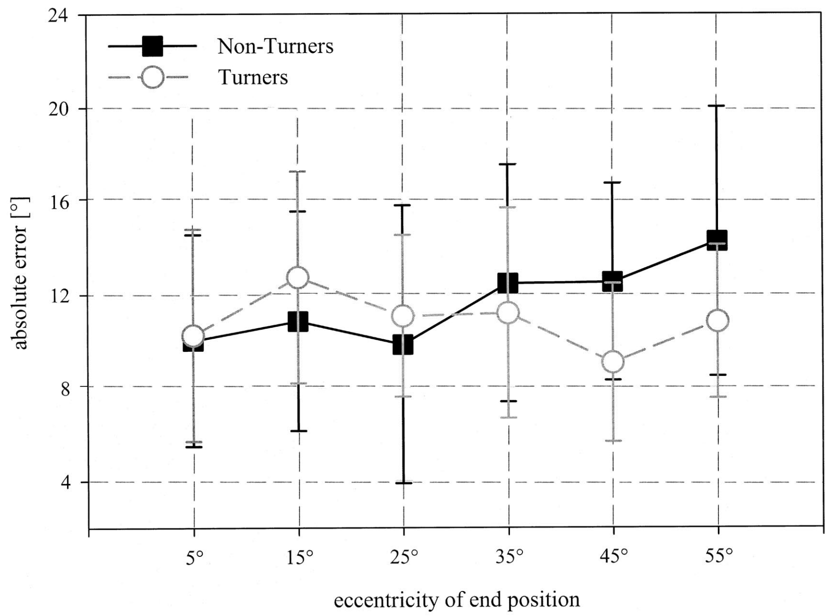

Figure 12. Mean absolute error (± 1 *SD*, depicted by the error bars) of angular adjustment with the maplike reaction format dependent on the eccentricity of end position, separately for turners (dotted line) and nonturners (continuous line).

Relative error. The signed-error scores were examined by an analogous mixed-design ANOVA, which revealed significant main effects of tunnel length, $F(1, 21) = 8.14$, $p < .010$, and eccentricity of end position $F(5, 105) = 25.89$, $p < .0001$, $\varepsilon = .628$, and a significant interaction between these two factors, $F(5, 105) = 25.89$, $p < .001$, $\varepsilon = .598$.

Figure 14 presents the signed error as a function of eccentricity of end position, separately for short and for long tunnels. As can be seen, the results mirror those for the absolute errors (see Figure 13). For both tunnel lengths, eccentricities were overestimated for end positions up to 35°, whereas relatively exact estimations, or slight underestimations, were evident for positions of eccentricities

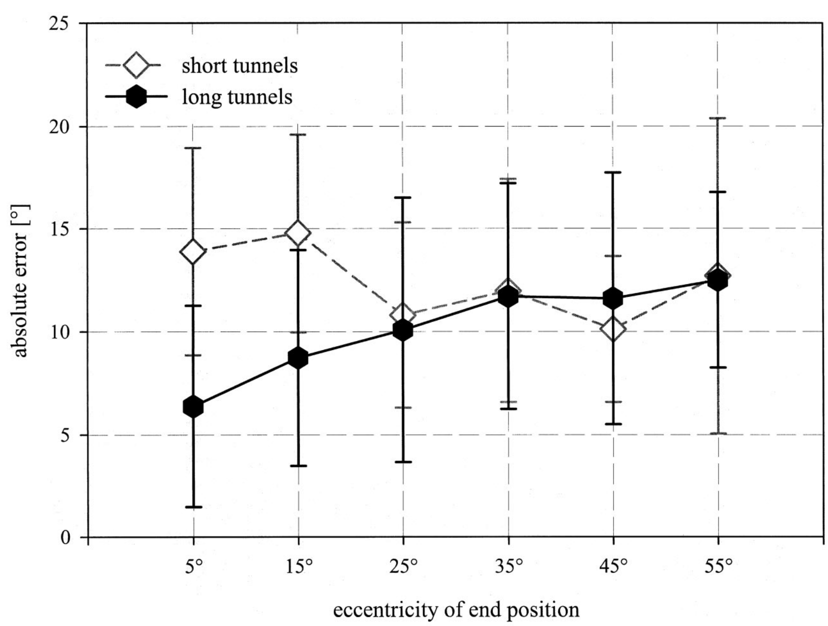

Figure 13. Mean absolute error (± 1 *SD*, depicted by the error bars) of angular adjustment within the maplike reaction format dependent on the eccentricity of end position, separately for tunnels with four segments (dotted line) and six segments (continuous line).

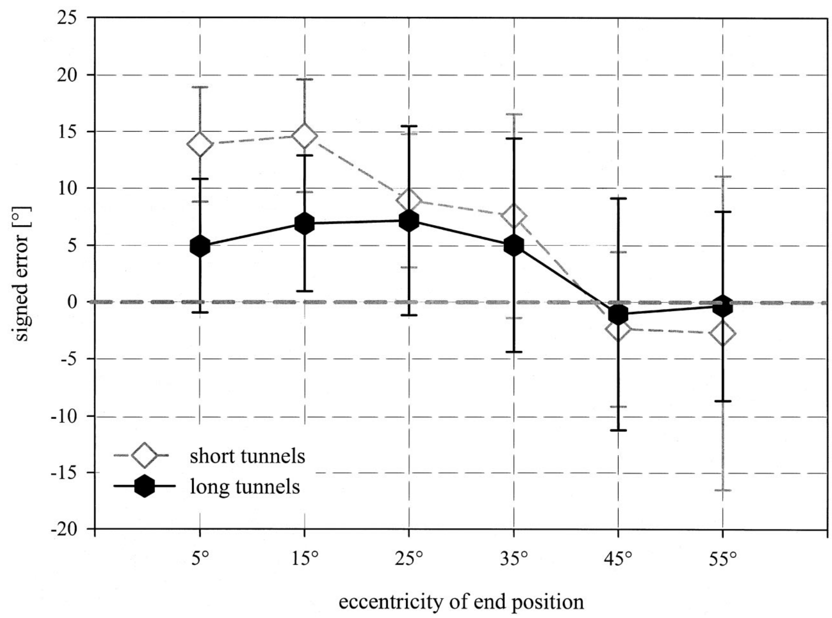

Figure 14. Mean signed error (± 1 *SD*, depicted by the error bars) of angular adjustment within the maplike reaction format dependent on the eccentricity of end position, separately for tunnels with four segments (dotted line) and six segments (continuous line).

greater than 35°. Furthermore, larger errors with short, relative to long, tunnels for end positions of 5° and 15° eccentricity were also manifest in the signed error scores, confirming this difference as a robust finding.

This raises the question as to the cause of this differential tunnel length effect. One possibility arises from the difference in the turning angle dependent on the length of a tunnel and the eccentricity of its end position. When the turn is placed within the same segment, short tunnels, compared with long tunnels, have to traverse a more acute-angled turn to reach an end position of identical eccentricity. Furthermore, for tunnels of the same length, turns have to be more acute angled when placed later, rather than earlier, in the tunnel passage to reach identical eccentricity. These three factors, (a) angle of the turn, (b) position of the turn within the tunnel passage (early vs. late), and (c) length of tunnel, are perceptually accessible parameters for the subjects. Each of the three factors is expected to have an influence on the reaction if all the relevant information is used.

To examine the relative influence of these three perceptible spatial factors (angle of turn, position of turn, and length of tunnel) on the angular adjustment, we carried out canonical correlation analyses separately for turners and nonturners. The first set of factors, representing the experimental variables, were angle of turn (continuous angles ranging from 90° to the left to 90° to the right side), length of tunnel (four vs. six segments), and position of turn (Segment 2 vs. Segment 3). The latter two dichotomous variables were coded as dummy variables. To examine the adjusted homing vectors of the two strategy groups, we entered the Cartesian *x*- and *y*-coordinates of their adjusted homing vectors as a second set of factors, representing the goodness of the spatial representation.

For nonturners, the analysis yielded an overall canonical correlation of .95, $\chi^2(8, N = 12) = 133.03$, $p = .0001$. Both functions were statistically significant ($p < .006$; see Table 1). The first and the second variate produced canonical correlations of .95, $\chi^2(8, N = 12) = 133.03$, $p < .0001$, and .45, $\chi^2(3, N = 12) = 12.19$, $p < .006$, respectively. The canonical loadings reflect the extent to which the original variables are represented by the canonical variate, and the canonical weights indicate the contribution of each variable to the variance of the respective within-set canonical variate. Canonical loadings and weights were highly similar, indicating that there was no influence of moderator or suppressor variables. This result suggests that Variate 1 is best described in terms of the association of angle of turn and angular adjustment. Additionally, tunnel length is involved in Variate 1 to a substantial degree. Variate 2 is best described in terms of the association of

Table 1
Canonical Correlation Analysis for Nonturners, With Canonical Loadings and Weights for Variates 1 and 2

Variable	Variate 1 Canonical loadings	Variate 1 Canonical weights	Variate 2 Canonical loadings	Variate 2 Canonical weights
Predictor set				
Segments	+.21	+.21	−.97	−.97
Position of turn	−.01	−.01	−.16	−.14
Angle	−.98	−.98	−.20	−.20
Variance explained	33.4%		33.6%	
Criterion set				
x adjustment	−.98	−.98	−.20	−.20
y adjustment	+.20	+.20	−.98	−.98
Variance explained	50.1%		49.9%	
Canonical correlation	.95		.45	
Redundancy R^2	0.36		0.55	

tunnel length and adjusted y value, reflecting responses of increasing distance with increasing tunnel length. Additionally, angle as well as position of turn is reflected in Variate 2 to a substantial degree. Some 36% of the variation in the angular response is accounted for by the variation of the (perceptible) factors length of tunnel, position of turn, and angle of turn in the first variate. In the second variate, 55% of the residual variance in the criterion set is accounted for by the experimental variations.

For turners, the analysis revealed comparable solutions, with an overall canonical correlation of .95, $\chi^2(8, N = 11) = 133.31$, $p = .0001$. Both functions were statistically significant ($p < .005$; see Table 2). The first and second variates produced canonical correlations of .94, $\chi^2(8, N = 11) = 133.03$, $p < .0001$, and .45, $\chi^2(3, N = 11) = 12.79$, $p < .005$, respectively.

As for nonturners (see above), the first variate is best described as the association of the acute angledness of the turn and the adjusted eccentricity of end position, with tunnel length reflected to a lesser, though substantial, degree in the first variate. The second variate, by contrast, is best described as the association of tunnel length and adjusted distance of end position, with angle of the turn reflected to a lesser degree in the second variate. Again, a large percentage of variance, 91%, in the angular adjustment is accounted for by the variation of the factors length of tunnel, position of turn, and angle of turn. For the first variate, 37% of the variation in the angular response is accounted for by variation of length of tunnel, position of turn, and angle of turn. For the second variate, 54% of the residual variance in the criterion set is accounted for by the experimental variations.

For both strategy groups, the different eccentricities and distances with respect to the origin of the path are reflected in the x- and y-coordinates of their angular adjustment. This indicates that for both strategy groups, the underlying spatial representations contain information about the different eccentricities and distances of end position. Because the canonical correlation analysis indicated a differentiated representation of distances as well as eccentricities, a multiple stepwise regression analysis was conducted involving the same factors. In addition, the interaction of the dummy-coded variables was calculated and added as a fourth variable. For both nonturners and turners, the angle of the turn significantly predicted the adjusted homing vector, nonturners: $\beta = .976$, $t(55) = 33.46$, $p < .0001$; turners: $\beta = .980$, $t(55) = 36.76$, $p < .0001$. Because the angular response is composed of the x- and y-coordinates, the regression approach replicates the findings of the canonical correlation analysis. For both groups, the angle of the turn accounted for more than 95% of the variance in adjusting the homing vector (R^2s = .953 and .961 for nonturners and turners, respectively).

The same stepwise regressions were calculated to examine which of the perceptible spatial factors influenced absolute error. For turners, the analysis revealed the length of tunnel ($\beta = -1.37$), $t(53) = -3.76$, $p < .0001$, the position of the turn ($\beta = 1.02$), $t(53) = 2.79$, $p < .007$, and the interaction of these factors ($\beta = -.938$), $t(53) = -2.57$, $p < .013$, to predict absolute error magnitude. These factors account for 36% of the variance in the absolute errors ($R^2 = .363$). For nonturners, by contrast, the analysis revealed none of the experimental factors to have a significant influence on absolute error magnitude.

Table 2
Canonical Correlation Analysis for Turners, With Canonical Loadings and Weights for Variates 1 and 2

Variable	Variate 1 Canonical loadings	Variate 1 Canonical weights	Variate 2 Canonical loadings	Variate 2 Canonical weights
Predictor set				
Segments	+.27	+.27	−.96	−.96
Position of turn	+.01	−.18	−.06	−.02
Angle	−.96	−.96	−.27	−.27
Variance explained	33.3%		33.4%	
Criterion set				
x adjustment	−.95	−.97	−.30	−.25
y adjustment	+.25	+.30	−.97	−.96
Variance explained	48.7%		51.3%	
Canonical correlation	.94		.45	
Redundancy R^2	0.37		0.54	

Discussion

Taken together, the results revealed turners and nonturners, using two different reaction formats within one experimental session, to achieve comparable performance.

Both strategy groups exhibited a negligible degree of orientation loss, as indicated by the small number of side errors (only 1% of all trials). Compared with the number of side errors in Experiments 1 and 2, this negligible number is likely due to the fact that tunnels in Experiment 3 had one turn only. This simplified the task, with side errors likely to reflect lapses of attention rather than true losses of orientation.

Moreover, both strategy groups built up a spatial representation that enabled them to highly accurately determine tunnel end positions of varying eccentricity relative to the starting point. This holds true for responses made within different reaction formats for subjects preferring an allocentric frame of reference (i.e., nonturners). The critical question was whether turners, who prefer to use an egocentric reference frame during the tunnel passage, would be able to determine their end position within a reaction format that displayed an allocentric coordinate system (i.e., the maplike format), with this (or the alternative) reaction format being unpredictable at the start of a trial. The results clearly showed that turners had no difficulties reacting accurately even with the maplike format (requiring responding within allocentric coordinates).

Furthermore, as in Experiments 1 and 2, when adjusting a homing vector using the arrow format, both strategy groups made response errors that depended on the eccentricity of the tunnels' end position, with the direction of the error deviation exhibiting a tendency toward the middle. Nonetheless, any direct comparison between turners' and nonturners' performance is subject to the caveat that the homing vectors of the two strategy groups are derived from different reference frames, with distinct underlying coordinate systems.

However, by forcing the use of an allocentric coordinate system (maplike reaction format), it was possible to compare turners' and nonturners' performance directly. Subjects made hardly any side errors, indicating that with tunnels with one turn only, they had no difficulty building up a spatial representation adequate for orientation. Increasing eccentricity of end position was associated with a corresponding increase in angular responses for both strategy groups. This provides evidence that within an allocentric coordinate system, turners' performance is comparable with that of nonturners. Convergent evidence is provided by the missing influence of preferred strategy on response accuracy (i.e., absolute errors), with both strategy groups showing similar accuracy with the maplike reaction format. That is, turners can use an allocentric coordinate system without loss of accuracy. Turners' comparable accuracy with both reaction formats provides indirect support for the idea that they might use two frames of reference in parallel. For nonturners, no such conclusion can be drawn, because they used an allocentric frame of reference with both reaction formats. However, despite the support for the assumption of coexisting frames of reference, this hypothesis remains tentative.

The results of the canonical correlation analysis demonstrate that subjects build up a spatial representation that contains information about the eccentricity and distance of positions in space. The analysis yielded near-equivalent results for turners and nonturners, which supports the assumption that both strategy groups solved the task by using the same spatial representations. This is reinforced by the results of the multiple regression analysis, which revealed, first, that the most important type of information for the representation of spatial position was the angle of the turn and the end position's distance from the origin for both turners and nonturners, and, second, that the variables that influenced absolute error differed between turners and nonturners. Turners seem to be affected mainly by the angle of the turn, with the other perceptible factors, the length of the tunnel and the position of the turn in the passage, having an additional influence on absolute error. For nonturners, by contrast, none of these factors was revealed to have an influence on absolute error. However, it should be kept in mind that tunnels with one turn only had to be traversed in Experiment 3. Therefore, the highest amount of variance in the eccentricity of end position is accounted for by the angle of the turn, and it seems plausible that subjects allocate greater weight to this kind of information.

General Discussion

The present study was designed to examine the accuracy of spatial representations built up during navigation through virtual tunnels that provided only visual flow but no vestibular or proprioceptive information; furthermore, it was examined whether a reduction of spatial information to sparse visual flow would have an influence on the preferred use of a particular reference frame. Three experiments examined whether subjects can develop an accurate spatial representation on the basis of visual-flow information only, whether they can learn to use different strategies for navigation, and whether more than one frame of reference is available to them at any one time. In the General Discussion, we first consider the performance of subjects presented with sparse visual information and the resulting spatial representations. Next, we consider the capability of subjects to use different strategies of spatial orientation, followed by a discussion of their possible use of multiple spatial representations in navigation tasks.

Information Inputs to Path Integration

One fundamental question addressed in the present study was whether sparse visual-flow information would be sufficient for subjects to develop an adequate spatial representation. The answer is clearly positive: Subjects displayed highly accurate orientation performance, indicating that they were indeed able to build up a differentiated spatial representation under such conditions. This is in line with other studies that have used computer-simulated environments to examine spatial cognition (Annoshian & Seibert, 1996; May et al., 1997; Wartenberg et al., 1998). The simulated tunnel environment conveys visually perceptible and nonperceptible spatial information. The latter, namely, distance and eccentricity of end (relative to the starting) position, was crucial for solving the task. But this information became available only by integrating perceptible information within a coherent spatial representation (semantic coding of spatial information was prevented, as far as possible, by the absence of visual landmarks and the poverty of the optical-flow information). Thus, it is safe to conclude that the simple desktop virtual environment provided by the tunnel task was sufficient for establishing an accurate spatial representation.

More important, when presented with the tunnel task, subjects were found to react characteristically in their adjustment of a homing vector from the end position of the traversed path back to the origin, spontaneously using either an egocentric or an allocentric frame of reference (even though the visual input was identical). We assume that this systematic difference between turners and nonturners in their homing-vector adjustments is dependent on the subject's imagined heading at the end of the path. Both strategy groups have to interpret information about translational (provided by the length and number of segments) and rotational changes (provided by the turns) to successfully solve the task. The critical difference between the groups is whether the navigator tracks the visual orientation changes by mentally adopting them or whether he or she tracks the changes relative to his or her initial orientation without adopting them. It seems that turners adopt the changes in orientation and, therefore, display an altered heading at the end of the passage. Nonturners, by contrast, seem to track information on rotational changes relative to their invariant sagittal axis during a turn and, therefore, overrespond by the amount of the turn. The latter strategy reveals an influence of the initial heading direction on spatial memory, reflecting a general significance of the subjects' initial orientation when being exposed to a new environment (McNamara, 2003; Shelton & McNamara, 1997, 2004). This effect is observed in real as well as virtual environments (Richardson, Montello, & Hegarty, 1999). The differential performance between the two strategy groups supports the conclusion that turners use an egocentric reference frame, representing updated changes in heading direction, and nonturners use an allocentric reference frame, centered on a representation of the original heading direction. However, the questions remain why subgroups of subjects prefer to use differential strategies and what the differences in the resulting representations are. Although the use of alternative (turner vs. nonturner) strategies may be inferred from the observed differences in reaction with the homing vector and verbal reports of our subjects, the representational differences between the two strategies have to be elaborated in future studies.

Several studies that have investigated the information required for egocentric spatial updating came to conclude that vision is not crucial when landmark-based orientation was learned before. However, when subjects have to imagine movements, performance is impaired, with greater impairment for imagined rotational, relative to translational, changes (Easton & Sholl, 1995; Presson & Montello, 1994; Rieser, 1989). It appears that idiothetic information supports automatic updating of spatial relations to objects in the environment (Berthoz, 1997; Easton & Sholl, 1995; Farrell & Robertson, 1998; Klatzky et al., 1998; Loomis et al., 1992, 1993; May & Klatzky, 2000; Rieser, 1999; Rieser et al., 1986; Sholl, 1989), whereas pure visual-flow information is not sufficient to permit egocentric spatial updating (Chance et al., 1998; Klatzky et al., 1998; Lathrop & Kaiser, 2002; Loomis, Beall, Klatzky, Golledge, & Philbeck, 1995). Taken together, these studies suggest that idiothetic information is needed to successfully update rotational changes and to integrate these, together with updated bearing from different landmarks, within an egocentric spatial representation. However, this view is challenged by the present study, which shows that pure visual information without idiothetic information can be sufficient for building up an egocentric spatial representation that represents changes in heading direction and bearing from the origin. However, even if sparse visual information is sufficient for developing an egocentric representation, one question remains, namely: why subjects do use an ego- or an allocentric frame of reference for navigation.

Strategies in Spatial Orientation

To provide an answer, one has to consider what information is provided and what information has to be represented to solve the task. The available perceptible spatial information comprises the reference direction defined by the orientation of the first segment, the length of the tunnel (and, thus, the distance between origin and end position), and the angle of the turn. The information that has to be represented to solve the task is the bearing (allo- or egocentric) of the end position from the origin (distance was queried only in the maplike reaction format and is, therefore, not further discussed here). As already stated, the representation of varying eccentricities of end position is a nonperceptible parameter that needs to be computed from the perceptible spatial information. This can be done using either an ego- or an allocentric reference frame. Within an egocentric frame, the egocentric bearing of a point—in the present case, the origin—is a representational primitive. The same holds true for an allocentric representation. Therefore, both types of reference frames are suitable to solve the task, and which one is actually used is left open. In fact, it turned out that both strategies led to similar performance when an angular reaction could be based on an ego- or an allocentric bearing from the origin. Both strategy groups, turners and nonturners, were able to build up spatial representations that enabled them to react relatively accurately to end positions of varying eccentricity. Furthermore, both groups exhibited a tendency toward the middle as a source of error in their representations. These findings support the conclusion that the use of egocentric or allocentric reference frames results in qualitatively equivalent spatial representations. Because both strategy groups received identical visual stimulation, the choice of one or the other frame of reference appears to depend on individual preferences. This means that the individual preference for one or the other frame is an important factor contributing to subjects' performance in navigation tasks.

Experiment 2 was designed to evaluate whether turners and nonturners, preferentially using an ego- or an allocentric frame of reference, are able to learn using their nonpreferred frame of reference in performing the tunnel task. Both strategy groups were able to do so, with neither group showing impaired accuracy when using their nonpreferred, compared with their preferred, reference frame. Quite plausibly, turners and nonturners build up spatial representations that differ with respect to the reference frame used. The resulting representations are unlikely to be identical in terms of the primitives. Imagine, for example, nonturners using their preferred spatial representation but reacting within an egocentric frame of reference. Because the egocentric bearing of the end position from the origin is not a primitive within the allocentric representation, it requires computation. This additional computational step should lead to larger errors or at least greater response variability, which was not observed. On the other hand, if turners use their preferred egocentric representation but have to react by using an allocentric frame of reference, the bearing of the end point from the origin has to be subtracted from their egocentric bearing. It seems unlikely that turners would be able to integrate the angle of three turns within an allocentric reference frame without showing a performance decrement compared with their preferred strategy.

In agreement with reports that individuals prefer different strategies in spatial tasks and that these strategies are influenced by the kind of information given (Bard, Fleury, & Paillard, 1992; Denis, Pazzaglia, Cornoldi, & Bertolo, 1999; Kyllonen, Lohman, & Woltz, 1984; Lawton, 1996; Pazzaglia & De Beni, 2001), the results of Experiment 2 imply that subjects in both strategy groups are able to establish and use more than one frame of reference and, thus, they can learn to build up qualitatively different spatial representations. Thus, the tunnel task provides a useful tool to explore different strategies in spatial orientation and allows for a comparison of orientation performance dependent on the difficulty of the spatial layout and the strategy used.

How Many Spatial Representations?

Because subjects in Experiment 2 learned to use their preferred and their nonpreferred strategy on consecutive days, the question remains whether more than one spatial representation is used at any one time. Experiment 3 was designed to answer this question by introducing a second allocentric reaction format for responding (on randomly chosen trials) within the same experimental session. Several theories assume that two or more spatial representations can coexist in parallel (e.g., Aguirre & D'Esposito, 1999; Bridgeman et al., 1997; Milner & Goodale, 1995; Mou et al., 2004; Paillard, 1991; Perrig & Hofer, 1989; Redish, 1999; Redish & Touretzky, 1997; Sholl, 2001; Sholl & Nolin, 1997; Wickens, 1992). Further support for this assumption is provided by Experiment 3, in which turners were forced to react within two distinct reference frames: the preferred egocentric frame of reference and a nonpreferred allocentric frame of reference. It is important to note that turners responded equally accurately either adjusting a homing vector or marking end positions within the maplike reaction format. This result argues in favor of the coexistence of multiple spatial representations.

Turners were found to show at least equivalent accuracy (Experiment 3), if not a slight improvement (Experiment 2), when using their nonpreferred, compared with their preferred, frame of reference—which raises the question as to potential advantages of using an allocentric frame of reference. The tunnel task presents a special case of spatial navigation without landmarks (which is rarely encountered under real-world conditions), and this task permits both strategies to be used. In this situation, the preference for the use of either one or the other strategy under real-world conditions might be the only decisive factor for its use in the tunnel task. Furthermore, when subjects prefer a particular strategy in spatial navigation, they are not necessarily aware of the fact that (a) they build up more than one spatial representation (nonawareness of this is supported by the postexperimental interviews) and that (b) the use of another frame of reference might be more advantageous in certain situations. In real-world navigation, there is hardly ever a complete absence of landmarks. Therefore, the use of an egocentric frame of reference might be just as effective or even more effective under certain circumstances, compared with the use of an allocentric frame of reference. It is the specific demands posed by the tunnel task that make it advantageous to switch from a spontaneous egocentric strategy to an allocentric strategy.

The present results support the notion of coexisting spatial representations on the basis of performance measures. Additional support stems from psychophysiological (electro-cortical) data that reveal distinct cortical networks to be active when an ego- and an allocentric reference frame is used during performance of the tunnel task (Gramann, Müller, Schönebeck, & Debus, 2005). Taken together, these results lend support to the idea of two or more coexisting spatial representations in humans. Individual preferences for the use of an allocentric or an egocentric reference frame, however, might obscure the fact that more than one spatial representation is accessible. Finally, the experiments reported here support a strong influence on the frame of reference used during a simulated tunnel passage without landmarks, not only by the kind of information provided but also by the individual preference for either one or the ego- or the allocentric frame of reference.

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Appendix

Instruction

Dear Ms./Mr. . . .,

Thank you for participating in our study. We hope that you will enjoy it. The experiment is concerned with how humans orient in space. If you are interested in the background of the experiment, please feel free to ask the investigator after the experiment.

Before and after each trial, a fixation cross will appear which you should focus on.

The task on each trial comprises a virtual journey through simulated tunnels with straight and curved segments. At the end of the journey, your task is to point back to the tunnel entrance, that is, the starting point of your journey. To solve this task, it is crucial that you keep up orientation during the journey.

A single trial will look like this: each tunnel starts with a straight segment and ends with a straight segment. After each curve, a straight segment follows. During this simulation, you are "moving" forward into the depth of the simulated space through straight and curved segments.

Imagine that the first segment points into the depth of the simulated space, straight to direction "north." At the end of the tunnel, you stand still while viewing outside of the last segment (the last segment will stay on screen for a little while).

Then, after a short time, two arrows will appear, pointing toward the starting point of the tunnel, the tunnel entrance. Your task is to decide which one of the two arrows represents the correct direction toward the tunnel entrance. If it is the right arrow, please press the right mouse button; if it is the left arrow, please press the left button. Take your time for the decision to avoid premature answers. If you lost orientation during the passage, choose the arrow that you feel most likely represents the correct answer.

If you have any questions concerning the task or the experiment, please contact your investigator now. Please let us know how you solved the task and any suggestions you might have at the end of the experiment. Thank you very much.

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