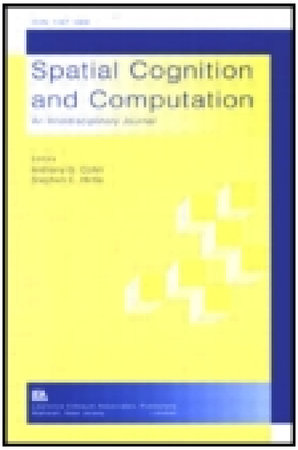

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Switching Spatial Reference Frames for Yaw and Pitch Navigation

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Switching Spatial Reference Frames for Yaw and Pitch Navigation

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Abstract: Humans demonstrate preferences to use egocentric or allocentric reference frames in navigation tasks that lack embodied (vestibular and/or proprioceptive) cues. Here, we investigated how reference frame proclivities affect spatial navigation in horizontal versus vertical planes. Point-to-origin performance after visually displayed vertical trajectories was surprisingly accurate and almost matched yaw performance for both egocentric and allocentric strategies. For vertical direction changes, 39% of participants unexpectedly switched to their non-preferred (allocentric) reference frame. This might be explained by vertical (25°–90° up/downward pitched) trajectories having lower ecological validity and creating more pronounced visuo-vestibular conflicts, emphasizing individual differences in processing idiothetic, embodied sensory information.

Keywords: spatial navigation, egocentric, allocentric, reference frames, individual differences, yaw pitch navigation, navigation strategies

1. INTRODUCTION

Spatial navigation is a complex task that requires the integration of multisensory information on the navigator's movement in space, the location of other agents and objects, and action plans. The different forms of spatial information can be processed using distinct reference frames as a means to represent entities in space (Klatzky, 1998). A general distinction between an egocentric reference frame and an allocentric reference frame can be made

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with respect to its origin: egocentric reference frames are "embodied" in the sense that they are centered on the navigator's body, anchored in receptor and effector systems (e.g., centered on the retina or the hand), as allocentric reference frames have their origin outside of the navigator's body, utilizing prior experience, salient objects or boundaries of the environment, or cardinal directions established by the self or the environment (McNamara, Sluzenski, & Rump, 2008; Mou, Fan, McNamara, & Owen, 2008).

However, both egocentric and allocentric reference frames are embodied in the sense that they are neuronally soft-wired (i.e., neural structures exist that compute spatial relations based on egocentric as well as allocentric coordinates) (Gramann, in press). Although perceiving spatial relations in the real world is primarily based on egocentric processing of information from our visual, auditory, vestibular, and proprioceptive systems, active orientation typically requires the navigator to integrate information from both egocentric and allocentric representations.

Even though different reference frames equally contribute to successful spatial orienting, several factors influence the use of one specific reference frame or a combination of different frames of reference. One factor is the perspective from which the space is experienced. Learning new environments from an aerial perspective is associated with the preferred use of an allocentric reference frame and accompanied by increased activity in the hippocampus and parahippocampal cortex (e.g., Maguire et al., 1998; Shelton & Gabrieli, 2002). In contrast, experiencing an environment from the first-person perspective is associated with the preferred use of an egocentric reference frame accompanied by activation in a distinct but partially overlapping neural network (Shelton & Gabrieli, 2002).

Another factor is the individual proclivity or ability to use one specific reference frame during spatial orientation. Participants in virtual orienting tasks with only sparse visual flow and no landmarks demonstrate a stable preference to use an egocentric or an allocentric reference frame (Gramann, Muller, Eick, & Schonebeck, 2005; Gramann, Muller, Schonebeck, & Debus, 2006; Gramann et al., 2010; Lin et al., 2009; Plank, Müller, Onton, Makeig, & Gramann, 2010; Seubert, Humphreys, Muller, & Gramann, 2008).

Moreover, some participants seem to be impaired in using the non-preferred reference frame when the environment requires them to do so (Bohbot, Lerch, Thorndycraft, Iaria, & Zijdenbos, 2007; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003). The preference to use one or the other reference frame for spatial navigation as well as the ability to select different reference frames dependent on the specifics of an environment seems to critically depend on individual abilities and experience with different environments.

Humans typically experience the specifics of an environment from a first-person perspective, integrating visual flow information from the visual system with sensory feedback from the vestibular and proprioceptive systems while walking, riding a bicycle, or driving a car. Heading changes during human self-motion are primarily defined by rotation about the vertical (yaw) axis. Even in the case of navigating buildings with several floors the navigator's head is usually kept upright relative to gravity (Pozzo, Berthoz, & Lefort, 1990).

The extensive experience with heading changes in yaw is associated with a seemingly effortless integration of multidimensional sensory input to compute and update changes in the resultant spatial representation. In contrast, operators confronted with navigation challenges in 3D space including direction changes in pitch (upward/downward) have to be trained extensively to achieve comparable orientation performance as during azimuth orienting (Cheung, 2004). One example of cognitively more effortful spatial orienting including pitch and yaw rotations in space is operating a helicopter or plane. Although pilots receive information on direction changes in all three dimensions through their vestibular system, remote controller of unmanned flying vehicles are forced to resort to cognitive strategies to integrate direction changes based on pure visual flow (Bles, 2004). Similarly, users of fixed-base virtual reality or gaming simulators have to learn to rely on visual cues only while ignoring conflicting (or missing) vestibular signals.

For 2-dimensional navigation, it has been demonstrated that visual flow information is sufficient for accurate spatial orienting (Bulthoff, Riecke, & van Veen, 2000; Riecke, Cunningham, & Bulthoff, 2007; Riecke, van Veen, & Bulthoff, 2002). In contrast, updating roll and pitch rotation (see Figure 1 for a description of the rotation axes) based on visual flow seems to be severely limited (Vidal, Amorim, & Berthoz, 2004). The evolution of the human orienting system based on an erect physical structure aligned with gravity was accompanied by the development of different sensitivity thresholds of the vestibular system for different axes of rotation. Vestibular sensitivity varies between the horizontal axis (sagittal) and the vertical axis (spinal) for the erect head in normal humans (Hixson, Niven, & Correia, 1966).

Further support for sensory differences in the vestibular system comes from vestibular-healthy subjects that are more likely to be confused about the direction of vertical motion as compared to the direction of horizontal motion (Malcolm & Jones, 1974). Thus, deviations from adequate visual stimulations of an orienting system that evolved based on the specifics of the human physical structure (upright position aligned with gravity, bipedal movement, etc.) and its surrounding environment are accompanied by significant impairments in orienting performance, and little is known about the underlying reference frames used when confronted with navigation tasks involving pitch or roll changes.

Only a few studies investigated orienting in three-dimensional (virtual or real) environments (Garling, Book, Lindberg, & Arce, 1990; Montello & Pick, 1993; Vidal et al., 2004) and none of these investigated the influence of individual preferences or abilities to use distinct reference frames during 3D orienting. The only study using 3D orientation dependent on distinct reference frames used a variant of the tunnel paradigm introduced by Schoenebeck and

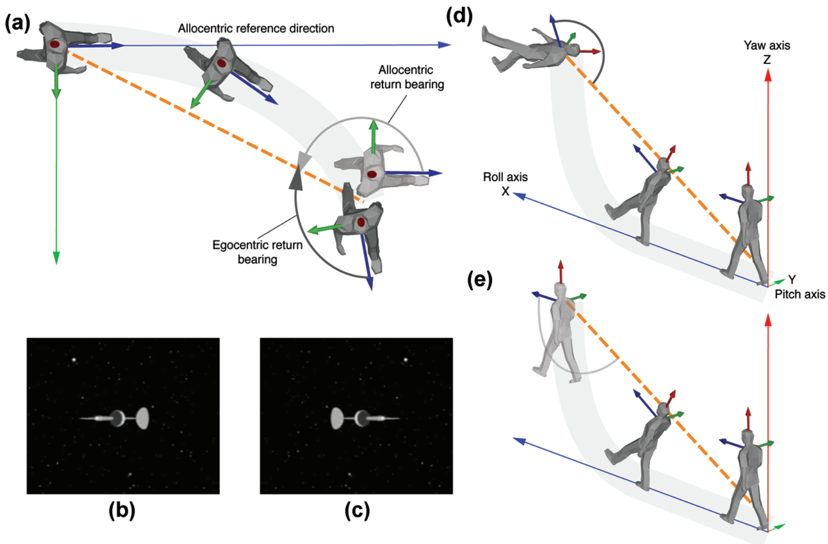

Figure 1. Schematic depiction of strategy differences in the path integration task. (A) Displays the aerial view of a participant traversing a virtual passage in the yaw plane with a turn to the right. (D) Displays the axes labels of the underlying coordinate system. The arrow pointing straight ahead of the participant in walking direction represents the cognitive heading. (A) At the end of the passage Non-Turners (light grey upper figure) react based on a cognitive heading that is not updated according to the turning angle and is aligned with the perceived (and cognitive) heading at the beginning of the passage. The according homing arrow adjustment is shown in (B). Turners (lower dark grey figure) will react based on a cognitive heading that is updated during a turn according to the perceived heading changes. The according homing arrow adjustment is shown in (C). Please note that the homing arrows do not reflect the geometrically correct angles for the depicted passage and are intended to clarify egocentric and allocentric return bearings only. (D) Shows a perspective view on a navigator traversing a virtual passage with an upward direction change and the expected egocentric (dark grey) orientation of the navigator with the respective return bearing. (E) Same perspective view with the orientation of a navigator without updated cognitive heading and the respective allocentric (light grey) return bearing (color figure available online).

colleagues (Schonebeck, Thanhauser, & Debus, 2001) and further developed by Gramann (Gramann et al., 2005).

In this task, participants traverse virtual tunnel passages with turns to the left or right and at the end of the trajectory have to adjust a homing vector to point back to the origin of the passage. This study by Vavrecka and colleagues investigated the neural correlates associated with egocentric and allocentric space processing but unfortunately did not report behavioral data (Vavrecka, 2009). To address this gap in the literature, the current study analyzed orienting performances of participants preferentially using an egocentric or an allocentric reference frame during passages through 3D space with visually simulated direction changes in yaw and pitch.

We specifically wanted to know whether a proclivity to use an allocentric or an egocentric reference frame for normal 2D navigation on a ground plane would be preserved for orienting in an ecologically less experienced pitch plane. To this end, this study used a 3D path integration task, based on a well-established point-to-origin paradigm (e.g., Gramann et al., 2005; Riecke, 2008) presenting visually simulated flights through star fields with direction changes in yaw or pitch, at the end of which participants had to point back to the origin of paths by adjusting a visually displayed pointer. In a first experiment, yaw and pitch trials were mixed and unpredictable.

In a second experiment a block of path integration trials with direction changes in the horizontal plane always preceded a block of trials with heading changes in the vertical plane. Thus, participants could use their preferred reference frame during the first block without experiencing direction changes in pitch that might influence their cognitive strategy to solve the task. Conversely, in the second block that included only pitch motions, we hypothesized that participants might develop a more consistent strategy due to the lack of potentially interfering yaw trials.

We expected faster, more consistent, and more accurate pointing performance for yaw trajectories as compared to pitch trajectories based on the higher familiarity of yaw motions during the categorization and subsequent training regiment. In addition, the difference in ecological validity for the two movement patterns as well as differences in vestibular sensitivity and distinct visuo-vestibular conflicts should further contribute to increased homing accuracy after yaw trials as compared to pitch trials.

Even though both yaw and pitch trajectories evoke a visuo-vestibular conflict between the visual cues indicating motion whereas the vestibular and proprioceptive cues indicate stationarity, the conflict associated with pitch trajectories is more pronounced: Whereas the perceived vertical defined by visual cues and gravity is aligned for horizontal (yaw) paths, there is a strong conflict between the visually defined and the gravity-defined vertical for pitch trials (i.e., movements in the vertical plane). This visuo-gravitational conflict for pitch but not yaw trials corroborates our expectation of a performance decrease for pitch trials.

In addition, as larger turns are more challenging to update, we expected increasing turning angles to yield larger pointing errors, pointing variability, and response times. This increase in errors and response times should be independent of the axis of rotation.

Finally, we expected participants to use their preferred reference frame consistently for yaw trials as previously reported (Chiua et al., in press; Gramann, El Sharkawy, & Deubel, 2009; Gramann et al., 2005; Gramann et al., 2006; Gramann et al., 2010; Lin et al., 2009; Plank et al., 2010) but not necessarily for pitch trials. The latter might be associated with changes in spatial strategies based on the above described differences in vestibular sensitivity and visuo-vestibular conflict, although we do not have sufficient prior data to make any clear predictions.

2. EXPERIMENT

2.1. Methods

2.1.1. Participants. In Experiment 1, eleven right-handed male participants were recruited from the participant pool of the University of California, San Diego (range 19–52 years; $x_{mean} = 24.1$). Participants were either paid ($12 per hour) or received course credits for participating. All participants had normal or corrected to normal vision and reported no history of neurological disorders. The local ethics committee approved the Experimental procedure in accordance with the declaration of Helsinki.

2.1.2. Task. Participants were seated in a dimly illuminated room in front of a 21-inch display monitor at a distance of approximately 50 cm, resulting in a physical field of view of about 47° × 35°. For each trial, participants were asked to keep up orientation while watching a visually simulated pathway through a star field consisting of randomly positioned white spheres in front of a black background (see Fig. 1). The simulated field of view that was used for rendering the virtual scene was set to 80° × 60°. Participants underwent a sequence of different tasks starting with a categorization of their preferred reference frame using the tunnel categorization task (Gramann et al., 2005), followed by a training phase with strategy-specific feedback using the 3D visual flow task, which was followed by the test phase. During categorization and training phases, participants experienced heading changes only in the yaw axis (horizontal plane). During the test phase, direction changes in the yaw axis (horizontal plane) or the pitch axis (vertical plane) were introduced (see supplementary videos and screenshots for illustrations: http://ispace.iat.sfu.ca/projects/pathIntYawPitch/).

2.1.3. Turner vs. Non-Turner Point-to-Origin Behavior. Previous visual path integration Experiments revealed two qualitatively distinct response patterns for point-to-origin tasks (e.g., Gramann et al., 2005; Riecke, 2008; Riecke & Wiener, 2006, 2007). On the one hand, one group of participants use the visual flow field to update their position and orientation during the simulated excursion, such that a curve to the right yields a point-to-origin response to the participants' back-right (e.g., 5 o'clock in the example of Figure 1a), thus matching the egocentric return bearing. This response matches the pointing response observed when participant actually walk the trajectory and thus have proprioceptive and vestibular cues about the direction changes (Klatzky, Loomis, Beall, Chance, & Golledge, 1998). Participants using this strategy have been coined as "Turner" by Gramann and colleagues (2005), because they respond as if they properly update their egocentric representation during the outbound journey.

Using the nomenclature of Klatzky and colleagues (Klatzky et al., 1998) these participants would react based on an updated cognitive heading. On the other hand, when only visual flow without salient landmarks or vestibular or proprioceptive cues about turns is available, a second group of participants exhibits point-to-origin responses where they point to the left-right reversed direction (coined "left-right-inverters" by Riecke, 2008 and "Non-Turner" by Gramann et al., 2005). That is, in the example of a rightwards trajectory as in Figure 1a, they would point back and to their left (e.g., 7 o'clock) instead of back and to their right (e.g., 5 o'clock) as Turner participants would do (Gramann et al., 2005; Klatzky et al., 1998; Riecke, 2008).

Using the nomenclature of Klatzky and colleagues (1998) these participants would respond based on the perceived heading that is aligned with the axis of their physical body. Note, however, that the terms perceived heading can be misleading in the case of visual VR, as cognitive heading is in fact defined by the visually simulated and perceived heading. Hence, we refrain from using Klatzky et al.'s terminology here, and replace the term perceived heading with the unambiguous term real-world or physical heading.

Although we can only speculate about the underlying strategies, many of these "Non-Turners" respond based on a spatial representation that does not include an updated cognitive (visually perceived) heading as if participants were still facing the original orientation (Gramann et al., 2005, Riecke, 2008). One possible explanation is that participants use an allocentric reference frame that properly includes the trajectory, but not the updated orientation. Alternatively, one might argue that these Non-Turners use an egocentric reference frame for the pointing task that does not incorporate the orientation changes. Note that the current Experiment was not designed to disambiguate between these possible explanations of Non-Turner behavior (see Riecke, 2008 for a discussion of possible underlying factors and representations).

Thus, we use the term "Turners" and "egocentric reference frame" here to refer to participants whose point-to-origin responses could be explained by an updated egocentric representation (cognitive or visually perceived heading), whereas "Non-Turners" using an "allocentric reference frame" refers to participants who point in the left-right reversed direction, which might be explained by the use of an allocentric reference frame that does not include orientation changes (physical or real-world heading; "perceived heading" in Klatzky's terms). Finally, participants who seem to switch between Turner and Non-Turner behavior are coined as "Switchers."

Please note that this differentiation of possible underlying processes does not imply that Turners or Non-Turners build up only an egocentric or only an allocentric spatial representation, respectively. In fact, we assume that both strategy groups build up both egocentric and allocentric spatial representations during a virtual outbound path as indicated by activation of overlapping cortical networks for both strategy groups (Chiua et al., in press; Gramann et al., 2006; Gramann et al., 2010). They do, however, seem to prefer to use only one spatial representation to respond to the homing challenge. To investigate the use of egocentric vs. allocentric strategies for horizontal homing responses, a strategy categorization task was used as described next.

2.1.4. Strategy Categorization Using Tunnel Task. Prior to the main Experiment, participants were categorized with respect to their preferred use of an egocentric reference frame (Turners, where orientation changes are updated) or an allocentric reference frame (Non-Turners, where orientation changes are not updated and participants respond as if still facing the initial orientation) (for more details see Gramann et al., 2005). To acquire equal group sizes for statistical analyses we categorized and selected participants from each strategy group until both groups reached a comparable number of participants. There was a slight shift in the distribution towards an allocentric strategy (approximately 60%) and thus a few participants using an allocentric strategy were excluded until the desired number of egocentric participants was reached.

This was the case in both experiments but the data pool was not sufficiently large for analyzing systematic shifts in strategy distributions in the current investigation. During categorization, participants saw 30 visually simulated tunnel passages with one turn to the left or the right. At the end of each passage, they selected one out of two homing arrows on the screen pointing back to the origin of the passage. The homing arrows indicated the correct pointing response with respect to an egocentric or an allocentric reference frame, i.e. the egocentric and the allocentric bearing from the origin, respectively. After a tunnel passage with a turn to the right the allocentric homing arrow pointed back to the left, yet the egocentric homing arrow pointed back to the right (see Figure 1 for further explanations). The correct homing arrow, i.e., the return bearing can be computed as the angle between a line representing the cognitive (or visually simulated) heading (the mental representation of the navigator's heading; blue coordinate axis in Figure 1) intersecting with a line connecting the navigator to the origin of the passage (dashed orange line in Figure 1).

To be categorized as Turner (using an updated egocentric reference frame) or Non-Turner (using an allocentric reference frame) participants had to consistently select reference frame-specific homing arrows on 75% or more of all trials. In Experiment 1, six participants were categorized as Turners and five as Non-Turners based on this forced choice homing vector selection task. Overall, participants consistently choose one reference frame during categorization ($x_{mean} = 92.1\%$; $sd = 10.8\%$). The selection of one strategy-specific homing arrow was highly consistent for both, Turners ($x_{mean} = 93.6\%$; $sd = 9.6\%$) and Non-Turners ($x_{mean} = 92.8\%$; $sd = 9.8\%$).

2.1.5. Training Phase. A training block of 25 trials followed the strategy categorization. Instead of the visual flow field simulating passages through virtual tunnels, a 3D star field simulation was used during the training and the subsequent test phases. Because the categorization of the preferred reference frame was based on heading changes only in the yaw axis, training trials included heading changes only in the horizontal plane to allow individual feedback on pointing accuracy. Participants experienced passages through visual flow fields with one heading change to the left or to the right. At the end of each passage a 3D arrow appeared in the center of the screen that initially faced towards the observer.

Participants were asked to use the cursor keys to rotate this arrow until it points back to the origin of the passage (this is illustrated in the videos available at http://ispace.iat.sfu.ca/projects/pathIntYawPitch and in Fig. 1B). On each training trial, participants received strategy-specific feedback about their performance by subsequently displaying the correct homing arrow (based on the categorized strategy preference) alongside with the participants' adjusted homing vector. Training trials incorporated turning angles between 15 and 90 degrees to the left or the right.

2.1.6. Test Phase. The test phase commenced after a short break following training. In Experiment 1, direction changes in yaw and pitch were presented unpredictably on a trial-by-trial basis. Each passage started with a first straight segment followed by a turning segment with turning angles ranging from 0 to 90 to the left/up or right/down. A final straight segment followed each turning segment with a deceleration phase at the very end of the passage. After the flow field stopped the image of a 3D homing arrow was shown on the display. Participants were asked to adjust the homing arrow to point back to the origin of the passage by using the cursor keys. There was no feedback about the accuracy of the adjustment during the test phase.

2.1.7. Trajectories. All passages were displayed as continuous visual flow fields consisting of an initial translation (segment 1), followed by a turning segment (segment 2) and a subsequent straight translation (segment 3). Apart from a smooth initial acceleration and final deceleration, simulated movement velocities were kept constant at 3 m/s. The angle of the turns varied unpredictably on a trial with angles of 0°, 25°, 50°, 75° and 90° to the left or right (up or down for pitch trials).

Duration of passages including a turning segment was 13 seconds and 8 seconds for passages without turn, as these paths were shorter. The Experiment thus comprised a fully crossed design with 2 turning planes (yaw vs. pitch, randomized) $\times$ 2 turning directions (clockwise vs. counterclockwise, randomized) $\times$ 4 turning angles (25°, 50°, 75° and 90°, randomized) $\times$ 5 repetitions per condition = 80 trials plus 10 trials without any direction changes. The trials were arranged in two blocks of 45 trials with durations of approximately 30 minutes for each block with a self-paced break between blocks.

2.1.8. Analyses. To test for possible asymmetries in the spatial representation of participants, i.e. effects of turning direction in the yaw (left vs. right) or the pitch plane (upward vs. downward), an ANOVA with repeated measures over the axis of the turn (yaw vs. pitch), the direction of the turn (left vs. right in the first ANOVA; upward vs. downward in a second ANOVA) and the angle of the turn (25°, 50°, 75° and 90°) with strategy of participants as a between subject factor was computed. In case of missing effects of the factor side the data was aggregated over left/right and up/down. Subsequent mixed-design Analyses of Variance (ANOVAs) were computed for the factors 2 turning plane (horizontal vs. vertical) $\times$ 4 turning angle (25°, 50°, 75° or 90°) as repeated measures, with the preferred strategy of participants (egocentric vs. allocentric reference frame) as between-subject variable. Participants who clearly switched strategies were excluded from the ANOVA analysis as described next. Whenever required, significant main effects and interactions were further examined using Tukey HSD post-hoc tests. Effect sizes were estimated using partial eta square.

3. RESULTS

For yaw trials, participants' demonstrated two qualitatively different modes of homing vector adjustments (Figure 2, left). Although one group of participants adjusted the homing vectors as pointing back to their left/right for heading changes to the left/right ("Turners," using an updated egocentric

Figure 2. (See figure on page 169.) Left: Schematic top-down view of different path layouts (gray solid lines) aggregated over left and right turns for trajectories in the horizontal plane. Right: Schematic side view for different trajectories in the vertical plane aggregated over trials with turns up and down Individual circular plots show the circular mean pointing vector for each turning angle and participant (different colors are used for different participants; Solid and dashed colors depict circular mean pointing directions for Turners and Non-Turners, respectively). The length of the mean pointing vectors indicate the consistency of that participant's individual pointings: Shorter mean pointing vectors indicate higher circular standard deviations of the individual pointing (e.g., participant 6 in purple), whereas longer mean pointing vectors extending to the surrounding black unity circle indicate higher consistency and thus low circular standard deviations of the individual pointings (e.g., participant 11 in green; (Batschelet, 1981)). Expected (i.e., correct) pointing directions for Turner and Non-Turner strategies are displayed as dashed dark grey and solid light grey arrows, respectively. Note how participants' pointing responses clearly categorize into two groups, which are roughly mirror-symmetric and aligned with the predicted Turner and Non-Turner responses. Whereas facing directions for Turners are always aligned with the trajectory (labeled "turner facing direction" for the 50° trials) and thus change for different turning angles, facing directions for Non-Turners are (by definition) not updated and thus always match the initial facing direction (horizontal dotted lines, labeled "Non-Turner facing direction" for the 50° trials) (color figure available online).

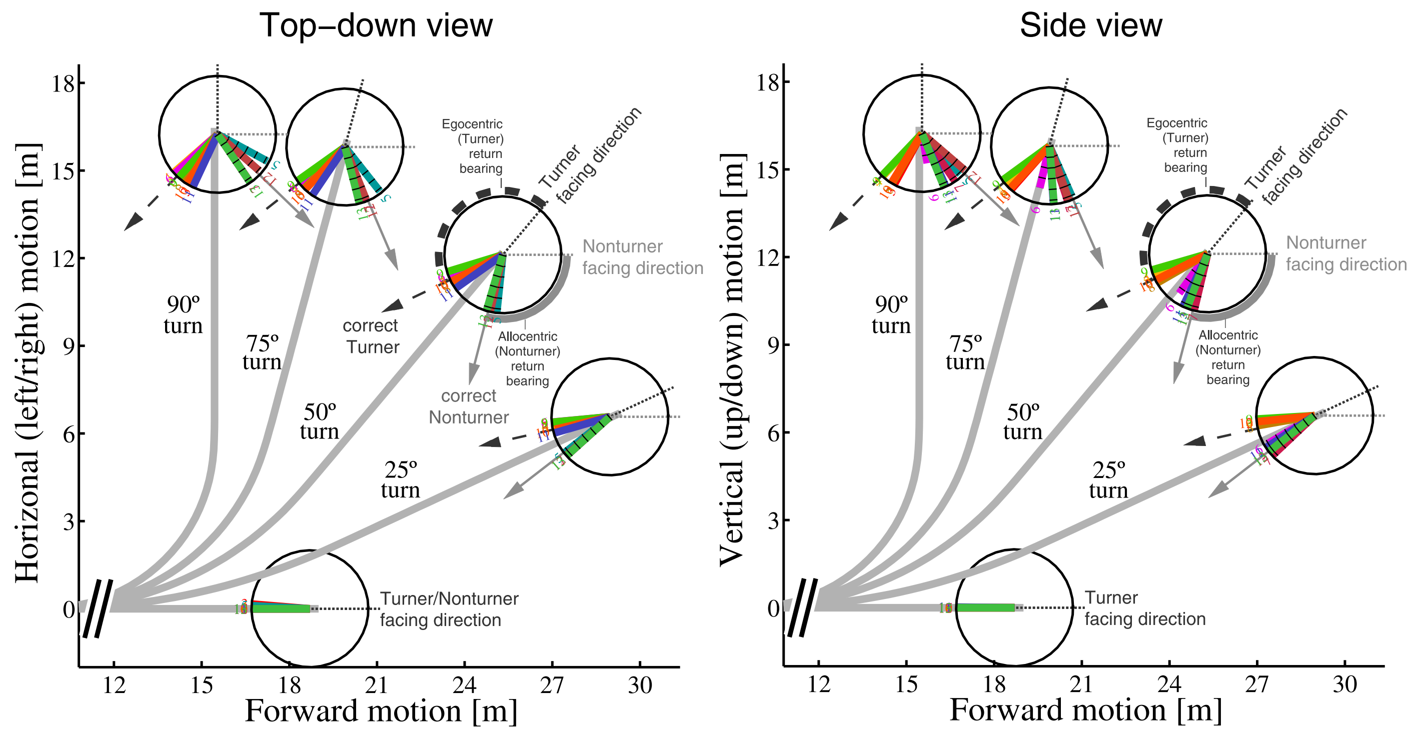

Figure 2. (See caption on page 168.)

reference frame; solid colored mean homing vectors), a second group adjusted the homing vectors as pointing back and to their left/right for right/left heading changes ("Non-Turners," as if using an allocentric reference frame that did not incorporate orientation changes; dashed colored vectors). These results replicate findings from previous studies (Gramann et al., 2005, 2006, 2009, 2010; Riecke, 2008). Pitch trials revealed similar bimodal response patterns, reflecting updated egocentric reference frames (Turner) as well as nonupdated (Non-Turner) allocentric reference frames (see Figure 2, right).

3.1. Correlation Between Expected and Observed Pointing Directions. As depicted in Figure 4(A), mean pointing directions were fairly close to the expected (correct) homing vectors for both Turners and Non-Turners. This was corroborated by a strong and highly significant correlation between the adjusted and expected homing vectors for Non-Turners [$r(90) = .876$; $p < 0.001$]. Correlation coefficients, computed separately for direction changes in yaw and pitch replicated a significant concordance for Non-Turners in both axes [$r_{yaw}(45) = .871$; $p < 0.001$; $r_{pitch}(45) = .882$; $p < 0.001$].

The correlation for Turners' adjusted homing vectors with correct egocentric homing vectors revealed significant covariation for all trials [$r(108) = .699$; $p < 0.001$]. Separate correlations for Turner participants, however, revealed stronger covariation of expected and adjusted homing vectors for heading changes in yaw [$r_{yaw}(54) = .904$; $p < 0.001$], and less agreement of expected and adjusted homing vectors for direction changes in pitch ($r_{pitch}(54) = .496$; $p < 0.001$).

To test for significant differences between expected and adjusted homing arrows in yaw and pitch, a mixed measures ANOVA was computed using Fisher-transformed correlation coefficients for yaw and pitch as repeated measures and the preferred strategy as a between subject factor. The results revealed no factor to have a significant effect. However, visual inspection confirmed comparable correlations for Non-Turners for the yaw and pitch axes (Fisher-transformed values of 2.02 and 2.03, respectively), yet in Turners, Fisher-transformed correlation coefficients decreased from yaw to pitch (4 to 1.9, respectively). The number of participants might not have been sufficient to secure enough statistical power to obtain significant effects.

3.2. Analysis of Strategy Switchers. Based on the pronounced decrease in covariation for Turners as compared to Non-Turners we further inspected the data of all participants to identify possible causes for the observed statistical effects. Even though the use of the preferred reference frame was stable for direction changes in yaw and pitch for most participants and matched the results of the prior tunnel categorization test, a minority of participants seemed to have used different reference frames for different trials. Such a behavior would explain the observed decrease in correlation coefficients for Turners.

Manual inspection of individual adjustments for all trials revealed two participants who were initially categorized as Turners but used an allocentric reference frame on a subset of trials. This resulted in a bimodal distribution of their pointing responses. The use of the alternative reference frame was not random but showed systematic switches to an allocentric reference frame for pitch trials only (Figure 3, dashed black lines). Although one participant consistently used an egocentric reference frame for direction changes in the horizontal plane and an allocentric reference frame for direction changes in the vertical plane, a second participant used an egocentric reference frame for all direction changes but downward turns. Participants showing this behavior, i.e., systematically using an alternative reference frame for a subset of trials, will be referred to as "Switchers" in the remainder of this document.

Visual inspection of the two Switchers revealed no obvious differences in homing adjustments based on an egocentric or an allocentric reference frame. Even though pointing performance was by no means perfect for yaw or for pitch trials, the Switchers were still able to indicate the correct (with respect to the updated or nonupdated heading) homing direction with highest accuracy for small direction changes and increasing deviation from

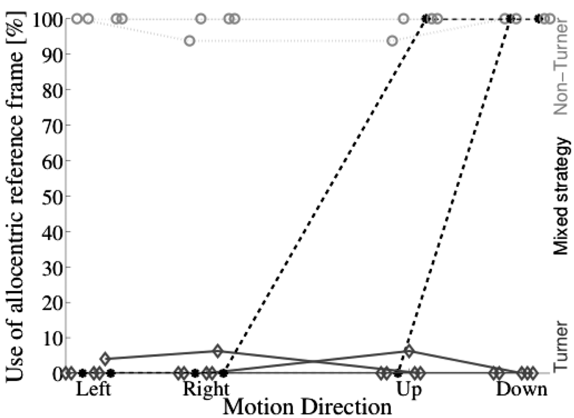

Figure 3. Participants' individual trials were categorized as Turner vs. Non-Turner responses separately for left, right, up, and down trajectories. The use of an allocentric reference frame in percent is displayed at the top of the scale (100% allocentric responses—0% egocentric responses), whereas the use of an egocentric reference frame is displayed at the bottom of the scale (100% egocentric responses—0% allocentric responses). Note that one participant (participant 11 displayed as dashed black line) switched from a consistent use of an egocentric (Turner) reference frame for yaw trials (left/right) to a consistent use of an allocentric reference frame (Non-Turner) for pitch (up/down) trials. A second participant (participant 6 displayed as dashed black line) consistently used an egocentric (Turner) reference frame for all yaw trials (left/right) and upwards pitch trials, while responding based on an allocentric (Non-Turner) reference frame on all downward pitch trials.

the correct homing adjustment with increasing turning angles (see Figures 4A and C). The absence of any obvious performance deterioration when switching between reference frames indicates that the Switchers were able to use both reference frames successfully to solve the task.

To statistically compare the pointing performance of participants consistently using an egocentric or an allocentric reference frame for both yaw and pitch trajectories we excluded the two Switchers (participants 6 and 11) from further statistical analyzes. To analyze how point-to-origin performance depended on participants' strategy, turning angle, and turning axis, we plotted the different dependent measures in Figures 4(B–E) with respect to these factors and provide statistical analysis using mixed-model ANOVAs here. The initial analyses indicated no influence of the turning direction in the yaw or pitch plane on any of the four dependent variables and thus, the data were aggregated over the factor turning direction for further analyses.

3.3. Absolute Pointing Error. The mixed measures ANOVA for absolute errors dependent on the participants' strategy, turning angle and turning axis revealed a significant main effect of the turning angle $[F(3, 21) = 11.85; p = .001; \eta^2 = .629]$. Absolute errors in participants' homing adjustments increased with increasing turning angles. This effect was quantified by the significant interaction of turning angle × strategy $[F(3, 21) = 3.69; p = .028; \eta^2 = .345]$. Both strategy groups showed significantly smaller pointing errors for smaller turns. In addition, Non-Turners demonstrated a more pronounced, monotonic increase in absolute pointing errors with increasing turning angles than Turners.

3.4. Signed Pointing Error (Over-/Underestimation of Turns). As Figure 4A and C show, direction changes in the horizontal plane were accompanied by over- and underestimations of the visually presented turn that revealed strong differences dependent on the preferred reference frame, the axis of direction changes, as well as the direction of direction changes. The main effects of axis $[F(1, 7) = 6.46; p = 0.039; \eta^2 = .480]$ and angle $[F(3, 21) = 8.08; p = 0.013; \eta^2 = .536]$ were quantified by the significant interaction of both factors $[F(3, 21) = 3.87; p = 0.024; \eta^2 = .356]$. Signed errors for yaw and pitch trials revealed an overestimation of small turns that decreased to underestimation of larger turns. Signed errors for pitch trials increased more strongly with increasing angle as compared to yaw trials. Although the mean signed error for yaw trials was negligible, there was a slight general underestimation of pitch turns, indicated by mean signed errors of −3° for pitch trials.

3.5. Pointing Variability (Circular Standard Deviation). As predicted, larger turns resulted in increased pointing variability, as indicated by Figure 4D and the main effect of turning angle $[F(3, 21) = 4.93; p < 0.023; \eta^2 = .413]$. This effect was quantified by an interaction of turning angle and strategy

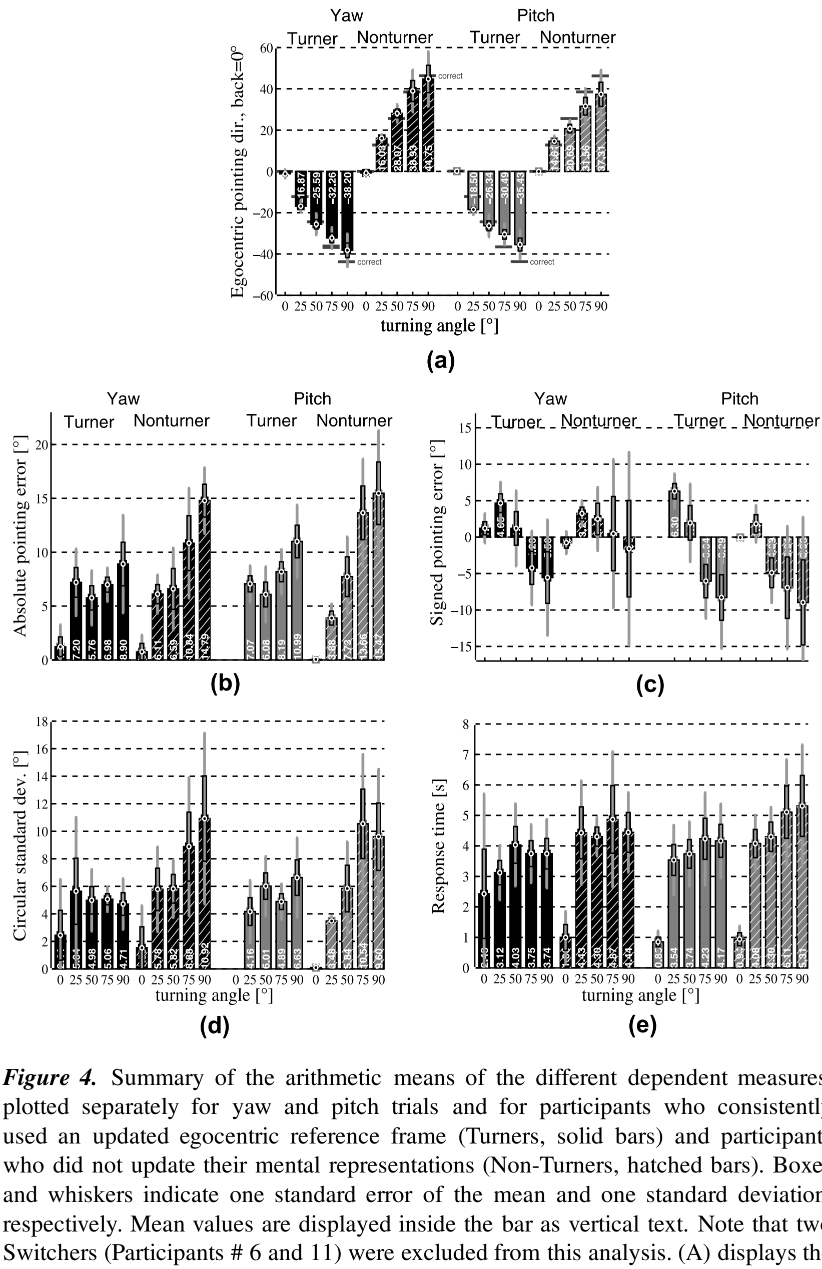

Figure 4. Summary of the arithmetic means of the different dependent measures, plotted separately for yaw and pitch trials and for participants who consistently used an updated egocentric reference frame (Turners, solid bars) and participants who did not update their mental representations (Non-Turners, hatched bars). Boxes and whiskers indicate one standard error of the mean and one standard deviation, respectively. Mean values are displayed inside the bar as vertical text. Note that two Switchers (Participants # 6 and 11) were excluded from this analysis. (A) displays the mean egocentric pointing direction. For comparison, the expected (correct) response is displayed as green bars labeled "correct." Note that participants tended to overestimate the smaller turning angles. (C) Pointing errors above zero indicate over-estimation of the visually presented turns, whereas negative pointing errors indicate under-estimation of turning angles. Note that straight trajectories (0°) were not included in the statistical analyses below because they could not be attributed to the yaw or the pitch plane.

of the participants $[F(3,21) = 4.08; p = 0.020; \eta^2 = .368]$, indicating an increase of pointing variability with increasing turning angles for Non-Turners but comparable pointing variability for Turners.

3.6. Response Time. Apart from one outlier, response times were around 3 seconds shorter for straights paths (0° trials) than for curved paths (see Figure 4E). For the ANOVA, however, straight trajectories were not included. The results revealed a significant main effect of turning axis $[F(1,7) = 6.74; p < 0.036; \eta^2 = .491]$ with increased response times for trajectories in the pitch (4.3 s) as compared to the yaw plane (4.1 s). Note that the absolute difference between Response times was very small, though (0.2 s). There were no further effects.

4. DISCUSSION

Results of the first Experiment demonstrate that the proclivity to use an egocentric or an allocentric reference frame is not restricted to a specific virtual environment, like the tunnel paradigm used in earlier studies. The majority of participants revealed a stable preference to use one spatial reference frame for heading changes in the yaw plane when an open-field 3D visual flow pattern without landmarks was used. The consistent use of distinct reference frames in the first Experiment, in addition to investigations revealing spatial orientation differences for groups of participants (Bohbot et al., 2007; Iaria et al., 2003; Klatzky et al., 1998; Riecke, 2008; Wraga, 2003), provides further evidence that individual differences in reference frame proclivity bear a significant influence on spatial orientation behavior. All but two participants consistently used the same strategy (egocentric or allocentric) in the main Experiment as in the tunnel categorization pre-Experiment, irrespective of yaw or pitch motions. However, this consistent strategy-specific behavior might have been enforced by strategy-specific feedback provided during the training session. Overall, participants performed well for both yaw and pitch motions and were able to adjust a homing vector with reasonable accuracy, irrespective of their preferred strategy.

We predicted faster and more accurate pointing performance for yaw trajectories as compared to pitch trajectories based on (a) the higher ecological validity of yaw changes, (b) the extended exposure to yaw trials in the categorization and training phase, (c) the increased visuo-vestibular cue conflict for pitch trials, and (d) the different vestibular sensitivities. Signed pointing errors and response times indeed showed a small but significant benefit of yaw over pitch paths, although neither absolute pointing error nor pointing variability showed any such benefit for yaw motions.

This only slight advantage of yaw over pitch trajectories is quite surprising, as (a)–(d) all predict a performance advantage of yaw over pitch trials. First, yaw motions frequently occur in everyday life and are ecologically more valid. In our natural environments we walk upright and perceive direction changes through visual, auditory, vestibular, and proprioceptive senses. The structures underlying sensory processing developed based on translations as well as rotation along an upright physical skeleton with heading direction defined by the sagittal axis and aligned with earth gravitational force. Thus, the human sensory system is tuned to process idiothetic as well as allothetic information on heading changes in the horizontal plane (Graf, 1988; Soechting & Flanders, 1992). Orientation changes in the vertical plane can be detected very reliably when vestibular information is given (e.g., Soechting & Flanders, 1992) but are rarely experienced in our natural environments and should thus be more difficult to represent.

Second, because the perceived vertical remains upright for the visually simulated yaw trajectories, the upward and downward pitch trajectories induced a more pronounced visuo-vestibular cue conflict between the visually defined vertical and the gravity-defined and proprioceptively-defined body vertical which remains unchanged. In addition, the upright position of participants should be accompanied by improved sensitivity for yaw trajectories as compared to pitch trajectories because of differential vestibular sensitivity for the different axes of rotation. Third, and finally, participants received training with feedback only in the horizontal plane and might thus show an advantage for yaw as compared to pitch trajectories. Considering these factors, the relatively accurate and fast pointing responses for pitch trials in this Experiment are surprising and deserve further investigation. A conclusion from these first results can only be tentative. Even though several factors should have resulted in higher accuracy for yaw as compared to pitch motion only marginal differences between homing after yaw and pitch were observed. This might show that neither training, increased vestibular sensitivity, or less pronounced (but still present) visuo-vestibular conflict for yaw motion leads to a superior point-to-origin behavior in virtual 3D path integration. One possible explanation for the absence of larger effect between the different rotation axis might be the relatively easy path architecture with only one turn. However, this will have to be tested in future experiments.

As larger turns involve arguably a more challenging updating task, we further predicted a performance decrease for increasing turning angles. This was confirmed for pointing errors and pointing variability, which increased significantly for larger turns. Although response times were significantly lower for straight paths as compared to curved paths, the degree of path curvature (turning angle) did not systematically affect response times. In part, this might be related to insufficient statistical power and the large within- and between-subject variability in response times, which might have obscured potential differences.

As further predicted, participants consistently used their preferred reference frame for yaw trials. Most participants continued to use their preferred reference frame for pointing home after direction changes in the vertical plane. This demonstrates a strong influence of reference frame proclivities on the choice of a spatial reference frame in new environments and likely reflects a cognitive strategy that was learned over time and became highly automatized (Gramann, in press). However, two of 11 participants (18%) switched from an egocentric to an allocentric reference frame to respond to the increasing pointing challenge for pitch trajectories. Although one participant consistently used an egocentric reference frame for direction changes in the horizontal plane but an allocentric reference frame for direction changes in the vertical plane, a second participant used an allocentric reference frame only for downward direction changes. Both participants were categorized as Turners in the initial tunnel categorization task and showed a stable proclivity to use their preferred reference frame (100% consistent choice of an egocentric reference frame for both participants in both categorization and yaw trials).

Although different spatial behaviors for vertical direction changes as compared to horizontal direction changes might reflect increasing difficulty in spatial updating, the switch from one reference frame to another is unlikely to reflect a complete loss of orientation because of two reasons: first, it is unlikely that a loss of orientation would be restricted to direction changes in the vertical plane only (participant 11) or only to downward but not upward direction changes (participant 6), but never for direction changes in the horizontal plane. Second, and more importantly, both participants demonstrated consistent and accurate allocentric homing adjustments when switching to an allocentric reference frame and not just random pointing responses. This demonstrates successful orientation based on a distinct reference frame that is different than the individually preferred one.

Noticeably, the two Switchers were both initially classified as Turners and thus preferentially using an egocentric reference frame. None of the participants with a proclivity to use an allocentric reference frame demonstrated a switch to an egocentric reference frame, though. Although this asymmetry is interesting, more participants would be needed to reliably test for the influence of individual proclivities on the choice of reference frames during direction changes in yaw and pitch. Further, in Experiment 1, participants were confronted with yaw and pitch direction changes unpredictable on a trial. This might have been associated with a certain degree of surprise or confusion in some participants that in turn might have led to a switch of reference frames. To further investigate these questions, Experiment 2 recorded thirty participants traversing the same passages through virtual space as Experiment 1 but participants experienced direction changes in the horizontal plane in a first block followed by direction changes in the vertical plane.

As in Experiment 1, we expected better performance for yaw, as compared to pitch trials (Hypothesis 1) even though the difference might not be very pronounced because of the simple outbound paths containing only one turn. In addition, we expected decreasing pointing accuracy associated with increasing pointing variability and response times for increasing turning angles (Hypothesis 2). Finally, for reasons detailed here, we expected a subgroup of Turner participants to use their preferred reference frame for yaw trials but not for pitch trials: (a) In Experiment 1, two participant had switched from their preferred (Turner) strategy to their non-preferred (Non-Turner) strategy for pitch trials; (b) The sensitivity of the vestibular system is lower for vertical as compared to horizontal motions; (c) Although both yaw and pitch trials involve a visuo-vestibular cue conflict, in that there are no vestibular (acceleration) cues matching the visually displayed rotations and translations, the pitch trajectories in addition involve a visuo-gravitational conflict: whereas the perceived vertical defined by visual cues and gravity is aligned for horizontal paths, there is a strong conflict between the visually-defined and the gravity-defined vertical for pitch trials (i.e., movements in the vertical plane).

This might lead some participants to switch from their preferred egocentric strategy (for yaw trials) to an allocentric strategy for pitch trials to avoid this additional visuo-vestibular conflict. For participants preferentially using an allocentric reference frame, in contrast, no such switch was expected because the use of an allocentric reference frame would not be associated with an increase in visuo-vestibular conflict during pitch trials.

5. EXPERIMENT 2

5.1. Methods

5.1.1. Participants. Thirty-one (31) right-handed male participants from the UCSD participant pool were selected for Experiment 2 (range 18–40 years; $x_{mean} = 26.6$ years). Three of these participants (2 Non-Turners and 1 Turner as indicated by the tunnel categorization task; see below) had to be excluded from the data analyses as they clearly did not properly understand or follow the instructions, as indicated by not pointing backwards for the straight (0°) paths but instead (seemingly randomly) pointing left and rightwards. Participants were paid ($12 per hour) or received course credits for participating. None of the participants in Experiment 2 took part in Experiment 1 and all had normal or corrected to normal vision and reported no history of neurological disorders. The local ethics committee approved the Experimental procedure in accordance with the declaration of Helsinki.

5.1.2. Categorization Task and Trainings Phase. Categorization and training were the same as described for Experiment 1 with 14 of the 28 participants being categorized as Turners and 14 participants being categorized as Non-Turners in Experiment 2. Over all, strategy-specific choices were highly consistent during the categorization task ($x_{mean} = 90.4\%, sd = 8.8\%$) and both strategy groups demonstrated clear reference frame proclivities (Non-Turner: $x_{mean} = 88.5\%, sd = 8.6\%$; Turner $x_{mean} = 91.9\%, sd = 8.6\%$). After categorization of participants' reference frame proclivity and 24 yaw trials of training with strategy-specific feedback, the main test phase commenced with the first block presenting only direction changes in the horizontal plane followed by a second Experimental block with direction changes only in the vertical plane.

5.1.3. Test Phase. Trajectories in the second Experiment were the same as in Experiment 1. Duration of passages including a turning segment was 13 seconds (with minor variations based on the turning angle) and 8 seconds for passages without turn. The Experimental design was a fully crossed design comprised of 2 turning planes (yaw vs. pitch, blocked) × 2 turning directions (clockwise vs. counterclockwise, randomized) × 4 turning angles (25°, 50°, 75° and 90°, randomized) × 7 repetitions per condition = 112 trials plus 18 trials without any direction changes yielding a total of 130 trials. The trials were arranged in two blocks of 65 trials with a duration for each block of approximately 30 minutes with a self-paced break between blocks.

5.1.4. Analyses. To test for possible differences in the spatial representation of left as compared to right turns or upward as compared to downward turns, two separate ANOVAs with repeated measures over the direction of the turn (left vs. right in the first ANOVA; upward vs. downward in a second ANOVA) and the angle of the turn (25°, 50°, 75° and 90°) with strategy of participants as between-subject factor were computed. Because direction revealed no significant influence on pointing performance the data was aggregated over this factor. Subsequent mixed-design Analyses of Variance (ANOVAs) were therefore computed for the four dependent measures (absolute pointing error, signed pointing error, pointing variability, and response time) using the following factors: turning plane (horizontal vs. vertical), and turning angle (0°, 25°, 50°, 75° or 90°) as repeated measures, and strategy of the participants (egocentric vs. allocentric reference frame) as between-subject variable.

Please note that, in contrast to Experiment 1, straight trajectories could be included because of the block-wise design. Participants who did not consistently use a Turner or Non-Turner strategy ("Switchers") were excluded from the ANOVA analyses, as it cannot be with certainty determined which reference frame they used on a trial-to-trial basis (see below). Whenever required, significant main effects and interactions were further examined using Tukey HSD post-hoc tests. Effect sizes were estimated using partial eta square.

6. RESULTS

Inspection of participants' pointing directions for the different yaw trajectories replicated the two basic strategies found in Experiment 1 (Figure 5). Although one group of participants adjusted the homing vectors based on an updated

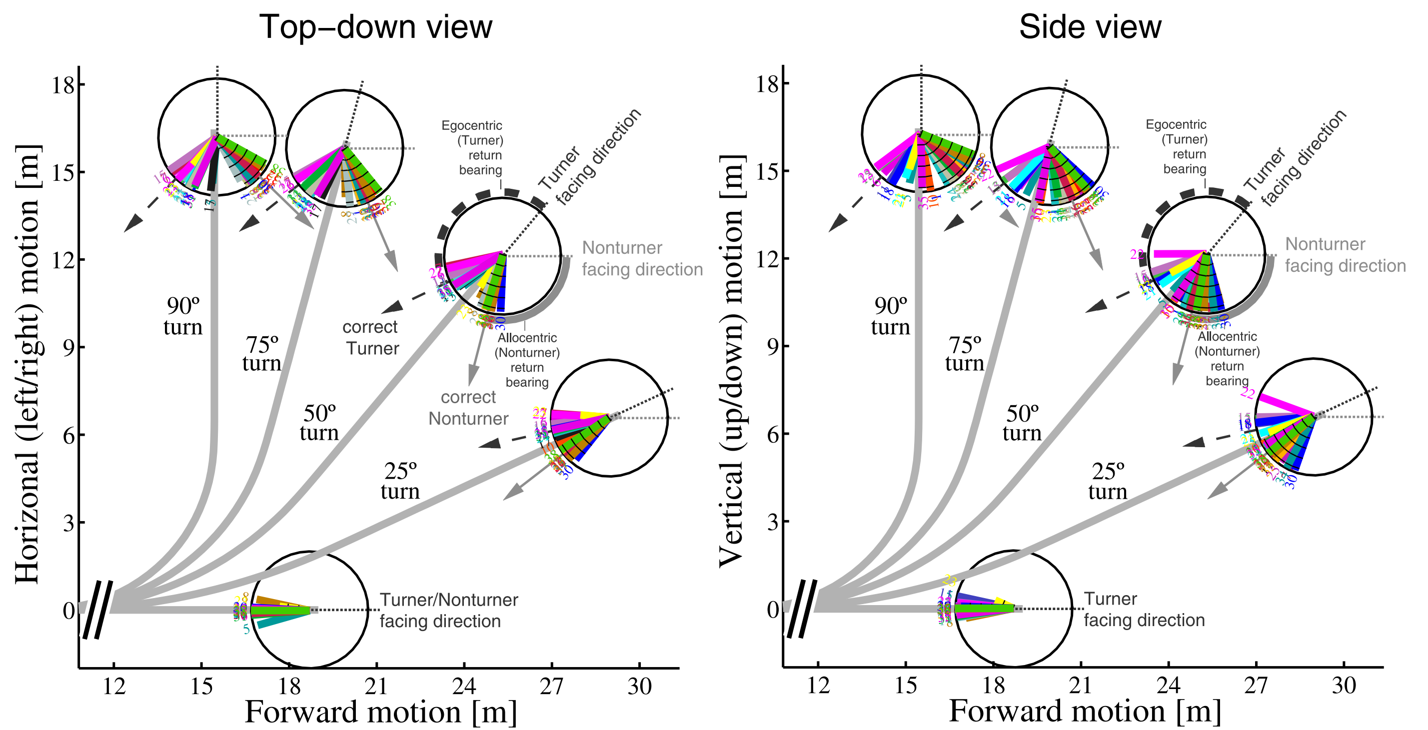

Figure 5. Schematic top-down (left) and side view (right) of the different path layouts and participants' responses in Experiment 2, plotted as in Figure 2 (color figure available online).

egocentric reference frame, a second group failed to update the visually displayed turns and adjusted the homing vector using an allocentric reference frame and thus responded as if facing the original (and not the updated) orientation. There was, however, a surprisingly large group of switchers who seemed to flexibly switch between egocentric and allocentric strategies for different trials, as elaborated upon next.

6.1. Data-driven Categorization of Turners, Non-Turners, and Switchers. To reliable categorize participants into Turners, Non-Turners, and strategy Switchers, the following criterion was used: Participants were categorized as Turners if they consistently pointed as if they updated the visually displayed rotations, i.e., if they pointed left-/rightwards for left/right turns and up-/downwards for up/down turns. Conversely, participants were categorized as Non-Turners if they consistently pointed as if they had not updated the rotation and thus were still facing the original orientation. These participants would point right-/leftwards for left/right turns and down-/upwards for up/down turns. There were, however, several participants who did not use a Turner or Non-Turner strategy consistently but instead switched between these two strategies.

Due to inherent noise in the data it is problematic to determine which strategy was used on any given trial. Instead of switching the reference frames participants might have mixed up left/right or up/down responses, might have lost orientation, encountered memory interference, or simply might not have paid attention. To account for these and other alternative explanations we defined a three-fold criterion to identify Switchers. First, the overall distribution of individual pointing responses had to follow a bimodal distribution to indicate responses into opposite directions associated with the distinct reference frames. Second, the bimodal pointing distribution had to be roughly left/right-symmetric for yaw trials and up/down-symmetric for pitch trials, assuming that the use of an alternative reference frame would be associated with comparable pointing accuracies based on that reference frame (Gramann et al., 2005). Finally, each of the two modes of the distribution had to contain at least 10% of the pitch or the yaw trials. The categorization data are summarized in Figure 6 and detailed here.

Based on this definition and compared to Experiment 1, a higher percentage of participants switched between Turner and Non-Turner strategies in Experiment 2 (11 out of 28 participants were switchers in Experiment 2 (39.2%) as compared to only 2/11 (18.1%) in Experiment 1). From the 14 participants that were categorized as Turners in the tunnel categorization task, only five (35.7%) continued to consistently used the same egocentric reference frame for the main Experiment for both yaw and pitch motions. The remaining nine original Turners were categorized as Switchers in the main Experiment.

As indicated in Figure 6, five of these switched from a consistent use of an egocentric reference frame for yaw trials to a consistent use of an

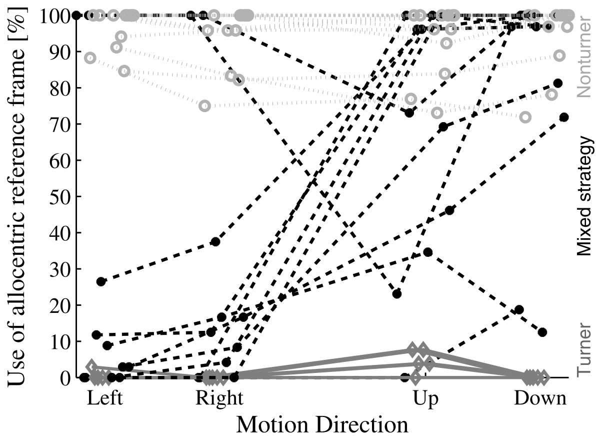

Figure 6. Participants' individual trials were categorized as Turner vs. Non-Turner responses separately for left, right, up, and down trajectories. Displayed is the average percentage of trials per participant that were categorized as Non-Turner trials (i.e., where for a left turn, the participant pointed to the right side and vice versa). Note that each individual pointing is subject to random error, such that even a consistent Turner sometimes exhibits trials that were categorized as Non-Turner trials and vice versa. Then, 12 of the 14 participants who were categorized as Non-Turners in the initial tunnel categorization phase continued to consistently use an allocentric strategy and did not update the visually displayed turns (each participant is displayed here separately as a light gray dotted line), yet the remaining two original Non-Turners switched between allocentric and egocentric strategies, as indicated by a bimodal distribution in their pointing behavior ("Switchers," displayed as black dashed lines). From the original 14 Turner participants, only five continued to consistently use an egocentric strategy for both yaw and pitch motions (displayed as solid gray lines). The remaining nine were categorized as Switchers.

allocentric reference frame for the pitch trials. The remaining four participants exhibited inconsistent data and seemingly switched between egocentric and allocentric strategies during the second block. In addition, two of the original 14 Non-Turners (14.3%, participants 1 and 9) alternated between egocentric and allocentric strategies for the pitch down but not pitch up trials. The remaining 12 Non-Turners continued to use allocentric strategies for both yaw and pitch motions.

6.2. Correlation between Expected and Observed Pointing Directions. After removing Switcher from further analyses, correlation coefficients and Fisher-transformed correlations were computed. As depicted in Figure 5 and Figure 7A, overall participants' pointing directions were close to the correct homing vectors. This was corroborated by a strong and highly significant correlation between adjusted and expected homing vectors for Non-

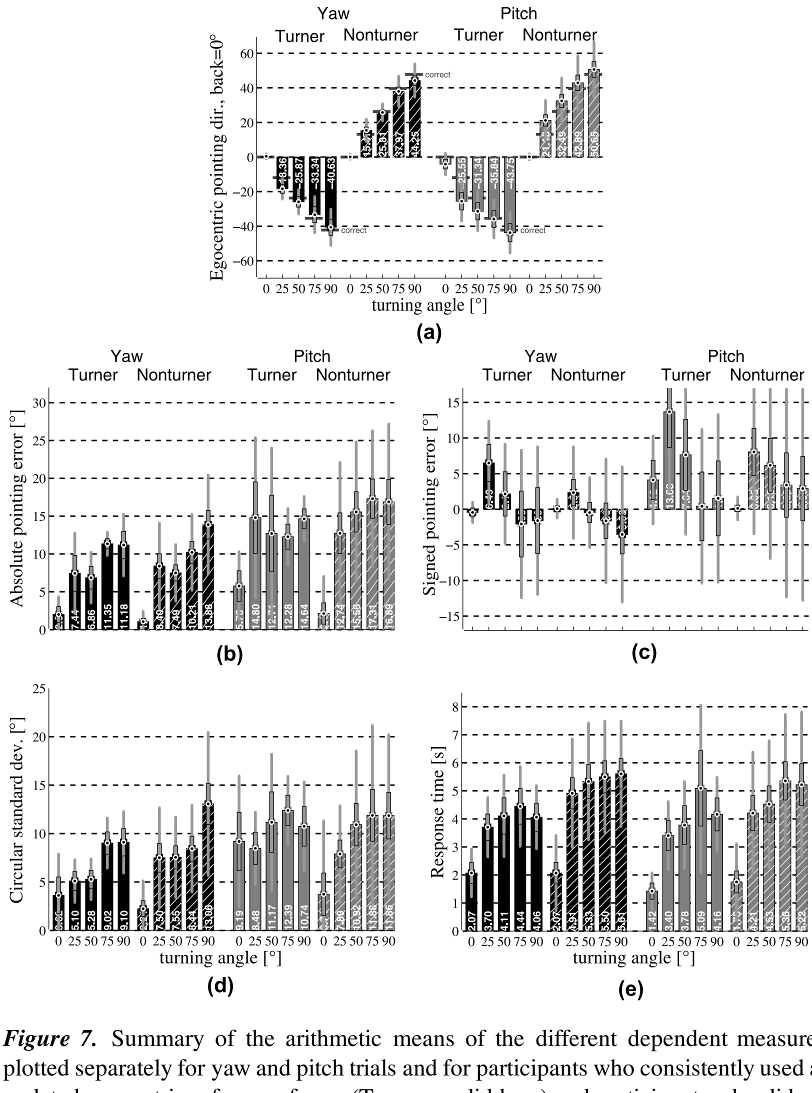

Figure 7. Summary of the arithmetic means of the different dependent measures, plotted separately for yaw and pitch trials and for participants who consistently used an updated egocentric reference frame (Turners, solid bars) and participants who did not update their mental representations (Non-Turners, hatched bars). Note that Switchers were excluded from this analysis. (A) displays the mean egocentric pointing direction. For comparison, the expected (correct) response is displayed as green bars labeled “correct.” Note that participants responded as if overestimating the smaller turning angles.

Turner participants [$r(216) = .849; p < 0.001$]. Separate correlations for expected and adjusted vectors for direction changes in yaw and pitch replicated the significant covariation for Non-Turners [$r_{yaw}(108) = .840; p < 0.001; r_{pitch}(108) = .858; p < 0.001$].

The same analyses for Turners revealed a significant covariation for all trials [$r(90) = .884; p < 0.001$], but separate correlations for yaw and pitch trajectories revealed higher correlation coefficients for yaw trials [$r_{yaw}(45) = .939; p < 0.001$], as compared to pitch trials ($r_{pitch}(45) = .831; p < 0.001$). A mixed measures ANOVA on Fisher-transformed correlation coefficients with the factors strategy (Turner vs. Non-Turner) and turning axis (horizontal vs. vertical direction changes) revealed a significant main effect of strategy [$F(1, 15) = 19.824; p = 0.001; \eta^2 = .569$] indicating higher Fisher-transformed correlation coefficients for Turner as compared to Non-Turner participants. There were no further effects. Figure 7 gives an overview of pointing accuracy and consistency and of the reaction times in Experiment 2 for Turner and Non-Turner who consistently using one reference frame for yaw and pitch. These data were further analyzed by mixed-measures ANOVAs for the different measures as described here.

6.3. Absolute Pointing Error. The initial ANOVA to test for possible influences of turning direction revealed significant interactions of the factor direction with participants' strategy [$F(1, 15) = 16.46; p = 0.001; \eta^2 = .523$], and with the axis of direction changes [$F(1, 15) = 12.25; p = 0.003; \eta^2 = .449$]. These were qualified by a significant interaction of direction × axis × strategy [$F(1, 15) = 19.46; p = 0.001; \eta^2 = .565$]. Non-Turner and Turner demonstrated comparable pointing errors for yaw trajectories (all p's > .97) and both strategy groups demonstrated an increase in pointing error for pitch trials. However, although Non-Turner revealed an increase of error for upward and downward motion, Turner participants' pointing errors increased only for down but not up trials (all p's < .002). Non-Turner demonstrated elevated absolute errors for pitch trials (confirming Hypothesis 1) but no differences between up or down direction changes.

The mixed measures ANOVA with repeated measures over the axis of the turn (yaw vs. pitch) and the angle of the turn (0°, 25°, 50°, 75° or 90°) with the participants' strategy as between-subject factor revealed a significant main effect of the turning axis [$F(1, 15) = 12.68; p = 0.003; \eta^2 = .458$]. Direction changes in yaw were associated with lower absolute pointing errors compared to direction changes on pitch trials, confirming Hypothesis 1. In addition, the main effect of turning angle reached significance [$F(4, 60) = 14.22; p < 0.001; \eta^2 = .487$]. This effect, however was explained by significantly lower errors for straight as compared to turning passages (all p's < .001), yet all trajectories with a direction change were accompanied by comparable pointing errors (all p's > .09), thus providing no support for Hypothesis 2.

6.4. Signed Pointing Error. The initial ANOVA to test for influences of the turning direction on the signed error revealed a marginally interaction of the factors axis × direction × strategy [$F(1, 15) = 4.35$; $p = 0.054$; $\eta^2 = .225$]. Separate ANOVAs computed for yaw and for pitch trials revealed no influence of the factor direction and thus the data was aggregated over left/right for yaw and up/down for pitch trials.

The mixed measures ANOVA with repeated measures over the axis of the turn (yaw vs. pitch) and the angle of the turn (0°, 25°, 50°, 75° or 90°) with the participants' strategy as between-subject factor revealed a strong tendency towards a significant main effect of the turning axis [$F(1, 15) = 4.06$; $p = 0.062$; $\eta^2 = .213$]. Although direction changes in yaw were associated with an average pointing error of 0°, pitch changes were associated with an average overestimation of 5°. Further, the main effect of turning angle reached significance level [$F(4, 60) = 4.73$; $p = 0.015$; $\eta^2 = .240$]. Straight passages were accompanied by very minor signed pointing errors that were comparable to passages with 75° and 90° turns. Passages with 25° and 50° direction changes, however, led to an overestimation of the turning angle. There were no further effects.

6.5. Pointing Variability (Circular Standard Deviation). The circular standard deviation was significantly influenced by the turning axis [$F(1, 15) = 6.56$; $p = 0.022$; $\eta^2 = .304$] and the turning angle [$F(4, 60) = 7.02$; $p = 0.003$; $\eta^2 = .319$]. As for absolute and signed pointing errors, pitch trials were accompanied by an increase in pointing variability (supporting Hypothesis 1) and increasing turning angles were associated with monotonically increasing pointing variability (supporting Hypothesis 2).

6.6. Response Time. Response times were on average 2 seconds shorter for straights paths (0° trials) than for curved paths (see Figure 7E). The ANOVA revealed significant increases of response times for increasing turning angles, thus supporting Hypothesis 2 [$F(4, 60) = 26.43$; $p < 0.001$; $\eta^2 = .638$]. This effect was mainly due to faster responses after straight trials (all p's $< .001$) but also due to a significant difference of reaction times after trials with 25° as compared to 75° turns. No other factors revealed a significant influence on response times.

7. DISCUSSION

In Experiment 2 horizontal and vertical motions were blocked such that participants in the first block could use their preferred reference frame for yaw trials without possible interference from pitch trajectories (as might have happened in Experiment 1). Statistical analyses on pointing performance of non-switchers revealed increased pointing errors and pointing variability for pitch as compared to yaw trajectories. This suggests that it might be more difficult for participants to path integrate in the vertical as compared to the horizontal plane.

However, because participants received training with feedback on their preferred strategy using only yaw trajectories, it cannot be concluded that homing accuracy after yaw is generally associated with better performance. Improved accuracy might also be attributable to additional experience of yaw trials during the categorization phase and the subsequent training regiment before the experiment. Thus, there is no clear answer with regards to hypothesis 1 and further experiments will have to investigate performance differences between yaw and pitch without a priori categorization and training of specific strategies. However, the absence of RT differences between yaw and pitch trajectories indicates that participants might not perceive motion in the vertical plane to be more difficult than in the horizontal plane. Increasing pointing errors might reflect the fact that movement in the vertical plane is less often encountered and evolutionary less relevant compared to movement that mirrors human bipedal transportation with an upright body in the real world.

Moreover, pitch trials induced a more pronounced visuo-vestibual cue conflict as compared to yaw trials. This is because of the conflict between visual cues indicating a change in the particiants' vertical when tilting upward or downwards and vestibular cues that did not indicate orientation changes with respect to gravity. In addition, increased vestibular sensitivity for yaw motion might have contributed to decreased performance for pitch trials.

Even though training of participants for yaw motion prohibits any definite conclusion, it seems that the cognitive processes during path integration are embodied in the sense that they rely on the processing of sensory information based on the upright orientation of our physical structure. Deviations from this upright locomotion behavior (for pitch trials) are less often, if at all, encountered during an individuals' development and learning of the spatial environments. Thus, participants' spatial orientation accuracy was impaired when confronted with direction changes in the vertical axis. Importantly, however, pointing performance after pitch trajectories was not random and participants demonstrated a general ability to navigate virtual passages with turns in the vertical plane, albeit with somewhat reduced accuracy and consistency. This relatively accurate path integration performance for pitch trials in the second Experiment again demonstrates the flexibility of the spatial representational system and the ability to adapt to new environments and tasks.

The absence of greater effects in pointing accuracy between yaw and pitch motion indicates that participants are readily able to adapt to unfamiliar environments and to achieve reasonable homing accuracy. Whether this is primarily a consequence of the low complexity of the outbound paths used in the present investigation has to be explored in future studies.

In addition, for both strategy groups larger turns were associated with increased pointing errors and increased response times, as predicted by Hypothesis 2. The drastic difference in response time and pointing accuracy for straight and curved passages reflects increasingly difficult computations for rotational changes as compared to pure translations.

As in Experiment 1, a subset of participants switched reference frames when moving from yaw to pitch trials (Hypothesis 3). The percentage of Switchers was much higher in Experiment 2 (39.2%) as compared to Experiment 1 (18.1%) but confirmed the trend that Turners, which preferentially use an egocentric reference frame for yaw trajectories, are more likely to switch reference frames when confronted with vertical trajectories than Non-Turners. The higher percentage of Switchers in Experiment 2 might be explained by the absence of any interference from different reference frames during blocks of only yaw or pitch trajectories. Although in Experiment 1 the use of an egocentric reference frame on a given yaw trial might prime the use of the same reference frame in the next, possibly pitch trajectory, no such priming of reference frames was possible in Experiment 2.

8. GENERAL DISCUSSION

8.1. Generalization of Bimodal Strategies from Tunnel and Ground Plane to Starfield

Previous point-to-origin studies using visual path integration based on optic flow devoid of any landmarks revealed two distinct and qualitatively different response patterns: On the one hand, "Turners" responded as if they updated the visually simulated turns, such that when presented with a left turn they pointed to the back-left, just as one would when actually walking this path and properly updating one's egocentric representation of the environment (Gramann et al., 2005, 2006, 2009, 2010; Klatzky, et al., 1998; Riecke, 2008; Riecke & Wiener, 2006, 2007). On the other hand, "Non-Turners" showed point-to-origin responses that appeared left-right mirrored as compared to Turner responses. That is, for left turns they point back-right instead of back-left as Turners would do.

Although one might argue that this is an incorrect reaction, these responses are far from random, and show a clear sensitivity to turning angles. In fact, Non-Turners consistently responded as if they did not update the change in orientation (although they tended to properly update all translations and rotations), and thus responded as if still facing the original direction. Hence, one might argue that Non-Turners use an allocentric representation that does not incorporate observers' heading changes instead of using an updated egocentric reference frame.

An alternative explanation for the observed differences in the experiments reported here comes from the reference-frame-conflict hypothesis that developed from the proposition of first-order and second-order embodiment of spatial cognitive processes by (de Vega & Rodrigo, 2001). The reference-frame conflict hypothesis put forward by Wraga and colleagues (Wraga, 2003) as well as Aavramides and colleagues (Avraamides, Klatzky, Loomis, & Golledge, 2004) states that heading changes during a path are associated with an updating of cognitive heading. However, when participants are required to give a homing response based on pointing, i.e., a response that requires the navigator to physically rotate his/her body or some other embodied response like pointing with a hand or device, such a response conflicts with the physical heading of the navigator during the response phase which is aligned with the first leg of the trajectory and thus does not incorporate heading changes experienced during the path.

Although this hypothesis explains different behaviors in specific experimental settings such as described here, it unlikely explains the observed differences in the present investigation or earlier studies on the distinction between Turners and Non-Turners for the following reasons: First, the reference-frame conflict hypothesis, in its strong formulation, predicts differences in spatial updating processes only during the response phase but not during the encoding phase of spatial updating. Even though we do not provide direct evidence in form of electrophysiological data in the present investigation, we recently demonstrated pronounced differences in brain dynamic activity *during* the encoding phase of different paths in a number of publications (Chiua et al., in press; Gramann et al., 2006; Lin et al., 2009; Gramann et al., 2010; Plank et al., 2010). These results clearly indicate differences between Turners and Non-Turners *during* encoding of tunnel passage with respect to modulation of distinct frequency bands and with respect to different cortical networks underlying the computation of egocentric and allocentric reference frames. These results clearly contradict the reference-frame conflict hypotheses.

Second, the reference-frame conflict hypothesis is based on a conflict between the response format being anchored to the physical body of the navigator and the cognitive heading that changed over the trajectory of an outbound path. The present investigation did not use a response format that required navigators to physically rotate to point to the origin of the path. The homing arrow was displayed on the screen and as such could be interpreted as the prolongation of the assumed individual heading at the end of the trajectory. This cognitive heading might have been an updated heading or the physical heading of the participant. Both representations could interpret the homing arrow to be an extension of the represented heading. In this sense, there is no evidence that the homing vector used in the present investigation would necessarily impose a conflict of reference frames. Even if we assume a reference frame conflict at the response stage, as argued above this cannot alone explain the experimental data indicating clear physiological differences between Turners and Non-Turners already during the motion phase.

Note, however, that there are other feasible explanations and underlying strategies that might explain the observed Non-Turner behavior, as discussed in more detail in Riecke (2008). In particular, for simple one-turn paths where the straight segments before and after the turn have equal length, failure to incorporate direction changes would lead to identical responses as simply left-right mirrored pointing responses. That is, for such isosceles paths Turner and Non-Turner responses are exact mirror-twins. Careful further investigation is needed to disambiguate between alternative explanations of underlying processes, and we are currently panning to use brain imaging combined with different path geometries to tackle this challenge. Given the pronounced visuo-vestibular cue conflict for pitch motions, not updating one's egocentric representation and instead using a stationary (allocentric) representation certainly seems a likely strategy.

This replication of individual difference in spatial strategies using a visual flow field with direction changes in yaw and pitch provides additional support to the notion that individual proclivities in using distinct reference frames for spatial orientation plays an important role and should be considered in future research to avoid averaging over distinct behavioral and brain dynamic patterns. The consistent use of the preferred reference frame for pitch trajectories in a large group of Turner and Non-Turner participants indicates that this proclivity might play an important role for more general spatial cognitive processes that involve the use of distinct reference frames.

8.2. More Than One Spatial Strategy—Turner, Non-Turner, and Switcher

Most of the participants in Experiments 1 and 2 consistently used their preferred reference frame irrespective of the axis of direction changes. One possible explanation for such a behavior is that participants less likely encounter changes in their upright body orientation during everyday navigation tasks and thus continued to use their preferred reference frame in new environments to solve the navigation challenge. The relatively accurate pointing behaviors even for pitch trials indicate that this strategy can be successful. This was the case for participants using an egocentric as well as for participants using an allocentric reference frame. One group of participants, however, switched from their preferred reference frame during yaw trials to an alternative reference frame for pitch trajectories. Why would such a behavior be observed for some but not all participants?

One possible explanation for the switching behavior might be the higher familiarity of yaw motion due to the a priori categorization and training regiment that used only horizontal trajectories. Because switching behaviors were more common in Turners, using an egocentric reference frame with a response based on an updated cognitive heading, switching to an allocentric reference frame during pitch trials might be simply due to increased difficulty of vertical motion associated with a failure to update cognitive heading during the trajectory. An alternative explanation for this strategy switching behavior is an interaction of differential vestibular sensitivity for yaw as compared to pitch motion with visuo-vestibular cue conflicts that arises for pitch trajectories with the individual ability to flexibly use distinct reference frames.

The distinction of two strategy groups (but no Switchers) in earlier investigations might have been a result of the restriction of trajectories to the horizontal plane, where path integration tasks were similar and easy enough that there was little need to change to a different strategy. Being confronted with uncommon direction changes in pitch and the associated increase in visuo-vestibular conflict (as compared to a less pronounced visuo-vestibular conflict for yaw motion), however, might have revealed a third strategy group that switched to using an allocentric reference frame for pitch motions and thus failed to update the visually displayed pitch rotations.

Finally, differences in the perceived salience of the allocentric reference frame might also explain why participants were more likely to use an allocentric reference frame for pitch as compared to yaw motions: One might argue that for pitch trial, while the visually displayed pitch changes, the gravity vector and proprioceptive cues do not change accordingly and thus serve as a constant reminder about the unchanged orientation of the allocentric reference frame. This might have increased the salience of the allocentric reference frame specifically for pitch motions, which in turn might have caused more participants to use this allocentric reference frame during pitch as compared to yaw motions. Although there is also a visuo-vestibular cue conflict for yaw trials, these perceptual reminders about the stationary allocentric reference frames are less pronounced for yaw trials, such that participants are more likely to properly update the visually displayed turns.

Note that data from Experiment 2 suggests two distinct groups of Switchers: Although five of the Switchers in Experiment 2 consistently switched from an egocentric strategy for horizontal trajectories to an allocentric strategy for vertical trajectories as predicted by Hypothesis 3, the remaining six Switcher showed both Turner and Non-Turner behavior for pitch trials, and the current data is insufficient to determine systematic patterns underlying their apparent strategy switch. Additional, carefully controlled Experiments are needed to further investigate why and under what conditions participants tend to change their behavior and (potentially) their underlying strategy.

8.3. Relation Between Strategy Preference and Underlying Neural Substrate

Recent neuroimaging studies have demonstrated individual differences in spatial tasks with a distinction of participants preferentially using an egocentric or an allocentric reference frame (defined as 'response strategy' or 'spatial strategy,' respectively; Iaria et al., 2003; Bohbot et al., 2007). Importantly, when investigating participants' performance in tasks that required distinct reference frames for optimal responses, a third strategy group was identified, switching from a 'response' (egocentric) to a 'spatial' (allocentric) strategy

(Etchamendy & Bohbot, 2007). Participants who relied on an egocentric reference frame showed higher grey matter in the caudate nucleus, whereas participants preferentially using an allocentric reference frame showed higher grey matter in the hippocampus (Bohbot et al., 2007).

Participants who flexibly switched navigation strategies, however, demonstrated average levels of grey matter in both cortical structures (Etchamendy & Bohbot, 2007). In contrast to the studies of Bohbot and colleagues we used only visual flow without significant landmarks or changes in the environment other than direction changes. However, the deviation from a standard horizontal trajectory to a naturally less frequent vertical direction change might have fostered a switch in reference frames for participants that are able to flexibly use different spatial strategies in their daily environments.

8.4. Accuracy of Yaw and Pitch Representations

Pointing after yaw motions was more accurate than pointing after pitch motions, but only when the two different trajectories were blocked (Experiment 2). Although this might reflect ecological validity and the embodied aspect of spatial information processing, it could also be related to the extended experience of yaw trajectories during the categorization and training phases. Nevertheless, participants were able to solve the pointing task for pitch trials reasonably well, yielding comparable pointing accuracy for yaw and pitch trials in Experiment 1 and relatively accurate pointing responses in Experiment 2. In addition, the participant pool for Experiment 1 was comparatively small and we initially did not use such a stringent criterion to identify Switcher.

Retroactively, using the same stringent Switcher categorization criterion from Experiment 2 in Experiment 1 yielded the same results as before, though. Note that training and strategy-specific feedback occurred only for horizontal motions, and participants never received any feedback about their performance or strategy use for the vertical motions. Future Experiments will have to investigate the influence on mixed yaw and pitch trials on pointing accuracy using a larger population of participants. Moreover, the potential influence of providing strategy-specific feedback awaits further investigation.

8.5. Conclusions and Outlook

The results of the present study corroborate the importance of individual reference frame proclivities for spatial tasks and the influence of embodied spatial sensory processing. The distinct pointing behaviors of Turner and Non-Turner are associated with differences in the activated cortical structures and the accompanying brain dynamics (Gramann et al., 2006, 2010; Lin et al., 2009; Plank et al., 2010). As a consequence, individual reference frame proclivities should be considered in research trying to investigate the cognitive and brain dynamic correlates of spatial processing. Addressing individual differences in the way idiothetic information is used for successful spatial orientation and the analyzes of the accompanying brain dynamics will require the comparison of traditionally restricted behavioral Experiments with mobile participants (Gramann, Gwin, Bigdely-Shamlo, Ferris, & Makeig, 2010; Makeig, Gramann, Jung, Sejnowski, & Poizner, 2009).

The fact that the present investigation identified Turners to be more prone to switch from an egocentric reference frame to an allocentric reference frame needs further investigations. Irrespective of the exact explanation for this switching behavior—whether subjective difficulty increased for pitch orientation or vestibular sensitivity interacted with increasingly prominent visuo-vestibular conflict—these results indicate that special attention needs to be directed to improve tasks that require embodied responses during 3D spatial orientation like remote control of unmanned aerial vehicles or robotic surgery.

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