Spatial Memory for Vertical Locations

Thomas Hinterecker[1,2] (thomas.hinterecker@tuebingen.mpg.de)

Caroline Leroy[1,3] (c.leroy@iwm-tuebingen.de)

Maximilian E. Kirschhock[2] (maximilian-eugen.kirschhock@student.uni-tuebingen.de)

Mintao Zhao[1,4] (mintao.zhao@uea.ac.uk)

Martin V. Butz[5] (martin.butz@uni-tuebingen.de)

Heinrich H. Bülthoff[1] (heinrich.buelthoff@tuebingen.mpg.de)

Tobias Meilinger[1] (tobias.meilinger@tuebingen.mpg.de)

[1]Department of Human Perception, Cognition and Action, Max Planck Institute for Biological Cybernetics, Max-Planck-Ring 8, 72076 Tübingen, Germany

[2]Graduate Training Centre of Neuroscience, Tübingen University, Österbergstraße 3, 72074 Tübingen

[3]Leibniz-Institut für Wissensmedien, Schleichstraße 6, 72076 Tübingen,

[4]School of Psychology, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, United Kingdom

[5]Department of Computer Science, Tübingen University, Sand 13, 72076 Tübingen

Author Note

Correspondence concerning this article should be addressed to Thomas Hinterecker

Abstract

Most studies on spatial memory refer to the horizontal plane, leaving an open question as to whether findings generalize to vertical spaces where gravity and the visual upright of our surrounding space are salient orientation cues. In three experiments, we examined which reference frame is used to organize memory for vertical locations: the one based on the body vertical, the visual room vertical, or the direction of gravity. Participants judged inter-object spatial relationships learned from a vertical layout in a virtual room. During learning and testing, we varied the orientation of the participants' body (upright vs. lying sideways) and the visually presented room relative to gravity (e.g., rotated by 90º along the frontal plane). Across all experiments, participants made quicker or more accurate judgments when the room was oriented in the same way as during learning with respect to their body, irrespective of their orientations relative to gravity. This suggests that participants employed an egocentric body-based reference frame for representing vertical object locations. Our study also revealed an effect of body-gravity alignment during testing. Participants recalled spatial relations more accurately when upright, regardless of the body and visual room orientation during learning. This finding is consistent with a hypothesis of selection conflict between different reference frames. Overall, our results suggest that a body-based reference frame is preferred over salient allocentric reference frames in memory for vertical locations perceived from a single view. Further, memory of vertical space seems to be tuned to work best in the default upright body orientation.

Keywords: spatial memory, vertical dimension, reference frames, object locations

Spatial Memory for Vertical Locations

Humans live in and interact with a three-dimensional world. We navigate to distant places and interact with surrounding objects. For this purpose, a mental representation is formed, which specifies locations of places or objects and their interrelations. Most of this memorized spatial information is distributed in the horizontal plane, as this is the plane we usually navigate. Nevertheless, we also interact within vertical space and thus need to represent vertically distributed spatial locations. For instance, when we put objects on a shelf for later use, we need to represent the object locations within the shelf mentally. While most spatial cognition research has focused on horizontal space, human encoding and retrieval of vertical object locations and their spatial relations are not thoroughly examined.

Locations in space are always defined within a frame of reference, specified by an origin and at least one direction of reference. The major distinction drawn in the literature is between egocentric and allocentric reference frames (Klatzky, 1998; Meilinger & Vosgerau, 2010). The egocentric reference frames relate locations in space to the observer, for instance, the printout of this article is in front of me. In contrast, the allocentric reference frames use locations and structures in the environment as the origin and orientation of reference. Here, the reference axes are usually intrinsic to an object, an object configuration, or to the environment itself (McNamara, Sluzenski, & Rump, 2008; Mou, Zhao, & McNamara, 2007; Waller & Greenauer, 2013). For example, the printout is on the tableside next to the wall.

Numerous studies endeavored to unravel the reference frames used in human spatial memory. A common approach used to investigate this question is the perspective change paradigm or judgments of relative direction tasks (McNamara et al., 2008). The underlying rationale is that egocentric views lying along the reference direction of the memory representation can be retrieved directly, while other views need to be inferred by costly transformations, causing greater error rate and longer latency. Thus, we can infer which reference frame is employed in spatial memory based on how spatial information is retrieved from different viewpoints. If performance is better for headings aligned with the egocentric viewpoint during learning, an underlying egocentric reference frame is generally inferred (Diwadkar & McNamara, 1997; Meilinger, Franz, & Bülthoff, 2012; Shelton & McNamara, 2001). In contrast, if performance is better for headings misaligned with the egocentric learning view, an underlying allocentric reference frame may be concluded (Greenauer & Waller, 2008; Mou & McNamara, 2002; Street & Wang, 2014).

Most studies were carried out in the horizontal dimension, that is, participants studied the layout of objects distributed on the ground or a table. Little has been investigated when it comes to memory of object locations or spatial relations in the vertical dimension (see Jeffery, Jovalekic, Verriotis, & Hayman, 2013, for a review). Most of the previous studies on this topic focused on memory for spaces in multi-floor buildings. For instance, they showed that memory for the vertical space is biased towards the horizontal plane (Tlauka, Wilson, Adams, Souter, & Young, 2007; Wilson, Foreman, Stanton, & Duffy, 2004), shows greater vertical than horizontal distortion of familiar buildings (Brandt et al., 2015), and leads to superior performance for pointing within a building floor compared to pointing between floors (Montello & Pick, 1993). While these studies can shed some light on the quality of memory for vertical space, studies investigating the selection of reference frames in memory for the vertical dimension are rare.

As an example for reference frames in not exclusively horizontal spaces, Kelly (2011) let participants learn an array of objects spread on a slanted table-like surface and showed that participants employed a reference frame that is aligned to the axis of the slope. However, if spatial learning occurred in a large-scale environment (e.g., locations of buildings), people do not appear to use slope as a reference, but simply as an additional cue for memory (Weisberg & Newcombe, 2013). Others let participants learn a vertically presented object configuration and tested them from multiple headings while imagining standing in the center of the configuration (Hintzman, O'Dell, & Arndt, 1981, Experiment 5; Tlauka & Nairn, 2004). Results indicate that participants selected a reference direction that was aligned to the up-down axis of the layout configuration. Participants' recall was best when their imagined headings were aligned with this reference direction. However, these findings cannot address the nature of the selected reference frame in memory because they did not manipulate the orientation and relationship of potential ego- and allocentric reference directions during learning. Participants could have used their own egocentric body vertical or an allocentric vertical axis as a reference.

Studies using vertical displays while manipulating reference frame orientations exist for research on short-term spatial memory span (Avons, 2007; Bernardis & Shallice, 2011). Bernardis et al. (2011) distinguished ego- and allocentric reference frames by introducing different head orientations relative to gravity and showed an important role of an allocentric frame of reference based on the gravitational axis. This finding fits considerations of Barnett-Cowan and Bülthoff (2013) that the gravitational force represents an ideal reference direction. Humans sense the force of gravity through their vestibular system in the inner ear (Angelaki & Cullen, 2008) and through somatic reception in the body (Mittelstaedt, 1998). They utilize gravity as a reference for spatial orientation and passage of time estimations (see Lacquaniti et al., 2015, for a review). The absence of the force of gravity (e.g., in outer space) seems to lead to impaired spatial memory processes (Oman, 2003). Based on these previous findings, humans might select the gravitational axis not only as a reference direction of a vertically presented spatial sequence in short-term memory (Bernardis & Shallice, 2011) but also for encoding vertical locations in long-term spatial memory.

Besides a gravity-based allocentric reference frame, humans might use an allocentric frame of reference based on the surrounding visual environment. For instance, humans might use the vertical axis of a surrounding room (as defined by the floor and ceiling) to encode vertical locations in memory. This vertical axis is often geometrically salient, as the floor and ceiling are clearly distinguishable from each other and from other sides of the room (e.g., by furniture standing on the floor, doors, windows, etc.). Such salient room geometry was previously shown to influence reference frame selection in the horizontal plane (Kelly & McNamara, 2008; Kelly, Sjolund, & Sturz, 2013; Shelton & McNamara, 2001; Valiquette & McNamara, 2007; Valiquette, McNamara, & Labrecque, 2007), which might apply to vertical space as well.

Thus, humans may select various kinds of reference frames in long-term spatial memory of vertical locations. Based on previous studies, we hypothesize three different reference frames that vary in terms of reference direction: an egocentric frame of reference using the body vertical as the reference direction, an allocentric reference frame defined by the visual room vertical, and an allocentric gravity-based reference frame.

In addition to the selection of reference frame in vertical spatial memory, we are interested in the *alignment effects* between the body, room, and gravity axes during learning and retrieval of vertical spatial locations. When we speak of alignment, we refer to two axes being in their canonical relationship at a given point in time. For instance, if the body is upright, the body vertical is aligned with the gravity axis. Previous studies have shown an alignment effect in both memory and non-memory tasks. For instance, Vidal & Berthoz (2005) found that path reconstruction was better when participants learned the path in an upright body position compared to lying sideways, indicating an advantage of aligned body and gravity axes for spatial memory. For non-memory tasks, vestibular and sometimes visual heading discriminations were more accurate when participants sat upright compared to when in a supine position (Hummel, Cuturi, MacNeilage, & Flanagin, 2016; MacNeilage, Banks, DeAngelis, & Angelaki, 2010). A similar effect has also been shown in a visual distance estimation task while being upright than when supine (Harris & Mander, 2014). It has been argued that aligned body and gravity axes facilitate spatial processing (Barnett-Cowan & Bülthoff, 2013; Vidal & Berthoz, 2005). In contrast, mental rotation speed was increased when participants were in a 60° tilted body position compared to an upright position (Bock & Dalecki, 2015), but not when they were supine (Francuz, 2010; Mast, Ganis, Christie, & Kosslyn, 2003). Mast et al. (2003) also showed that performance in an image inspection and composition task varies with body position, with superior performance when participants were in a supine or horizontal position.

Thus, although some studies suggest an advantage of aligned body and gravity axes, the findings on the alignment effects are not conclusive. Further, in spatial memory, the advantage for aligned body and gravity axes was only examined during encoding (Vidal & Berthoz, 2005). To our knowledge, none of the previous studies has systematically investigated the alignment effects of the body vertical, the visual room vertical, and the gravitational axes on spatial memory. We aim to address this question by manipulating their alignment both during learning and at memory retrieval.

Our third aim was to test the *consistency effects* of relative axes orientations across learning and testing. We regard two axes to be consistent if they are in the same relationship during learning and testing. According to the encoding specificity theory, retrieval performance is a function of the similarity between the encoding and retrieval condition (Tulving & Thomson, 1973). We aim to examine whether a consistent orientation of gravity and body axes or of gravity and visual room axes during learning *and* testing yield a memory advantage being in line with predictions of encoding specificity. For example, will participants who learned spatial information while lying sideways recall the information best when they are also lying sideways during retrieval? Alternatively, are the locations learned in an upside-down room recalled best when the room is upside down during retrieval (independent of one's body orientation)?

In sum, the purpose of the present study was threefold. Firstly, we asked whether participants dominantly use egocentric or allocentric frames of reference for representation of vertical object locations in long-term spatial memory. The reference frames at question differed in terms of reference direction. To address this, we performed three experiments. Participants made spatial judgments on inter-object relationships on a visually presented vertical object layout in virtual reality (VR). For each reference direction that participants potentially select to represent these inter-object relations, we predicted test situations that should yield best performances. To dissociate body-, visual room-, or gravity-based axes (i.e., whether and which axes were aligned) we introduced different body and visual room orientations with respect to gravity during learning and testing. Secondly, we addressed potential advantages of alignment of these vertical axes at learning and retrieval. Thirdly, we investigated effects of axes' orientation consistency between learning and testing in the sense of encoding specificity.

Experiment 1

Experiment 1 was a starting point for addressing the reference frames used to encode vertical object locations as well as effects of axes alignment and consistency during learning and testing. Participants memorized object locations on a vertical board in VR either physically upright or lying on their side, whereas the visually presented room vertical was always aligned with the body vertical during learning. Afterward, they retrieved their spatial memory in both body orientations, respectively.

Methods

Participants. Twenty naïve subjects (10 male) 19 to 33 years old (*M* = 25.55, *SD* = 4.25) were recruited through an online database of the Max-Planck-Institute for Biological Cybernetics in exchange for monetary compensation. They gave written consent after oral and written instruction. The study was approved by the Ethics Committee of the University Clinic of Tübingen (251/2008BO2).

Materials. During the experiment, participants found themselves in a cubic 2.2 x 2.2 x 2.2 m virtual room, visualized in Figure 1. We furnished the room with a hall clock to the right-hand, a bookshelf to the left-hand side, two distinct plants in the far bottom right and left corners, and a lamp on the ceiling. This rendered all walls and thereby orientations of, or positions within the room easily distinguishable for participants. A 0.75 m circular board was standing vertically on a wooden table leg in the middle of the room. Attached to the board were nine cylindrical objects arranged in a 3 x 3 grid, interspaced by 19.51 cm. All objects had the same size (radius: 4 cm, height: 2 cm), except the center object (radius: 2.7 cm, height: 3 cm), and all objects had one out of nine distinguishable colors assigned to them (Figure 1, left panel). We permuted the color assignment for every participant. Participants' point of view was situated 55 cm in front of the board, with the center stimulus appearing at eye height and therefore assuring that all the other stimuli were visible within the visual field.

Insert Figure 1 about here

Participants learned the layout of the differently colored stimuli on the vertical board in a learning phase either while sitting upright or while lying on their side on a daybed. During learning in Experiment 1, the visual room was always aligned with the participants' body vertical meaning that when participants were lying sideways, the room and its contents were rotated with respect to gravity accordingly. After learning, participants' location memory was tested by requiring them to reposition a target object onto the memorized location in two following testing phases (Figure 1, right panel), one with participants lying on their side, the other while participants were sitting upright. In every trial of the testing phases, only two reference stimuli, one out of which was always the center object, were shown on the board. The target stimulus appeared 0.5 seconds later also in the center of the board. Because of the different shapes of the target and center stimulus, participants could recognize the target object. Participants used a gamepad controller (Logitech Rumble Gamepad F510) for the task. They used the gamepads' left joystick to move the target object across the board and one of its buttons to confirm the position. In the test conditions participants spent lying sideways, they held the gamepad in parallel to the body. We rotated the gamepad controller output in these sideways conditions so that up/down controlling on the VR board corresponded to the gravitational up/down axis on the gamepad. Participants did not report any problems with controlling the target object in either body position. In every trial of the testing phase, the board and the room were rotated by one out of eight orientations (0°, ± 45°, ± 90°, ± 135°, or 180°) relative to the learning orientation. Each object—except for the center object—was used eight times as reference object and with each room orientation once, therefore yielding overall 64 trials for a complete testing phase. We chose the target object for a specific trial randomly and randomized the order of trials. Solving the task was possible by using the surrounding room orientation or the board orientation as given by the two reference stimuli.

We assigned the study condition to participants randomly and evenly. As we tested participants twice, first in the sitting upright or lying sideways body position and second in the respective other, we counterbalanced the order of these testing phases across participants within each learning condition.

Unity 3D (licensed version 4, Unity Technologies©, San Francisco) was used for the creation of the VR, running on a DELL laptop under Windows 7. Participants wore an Oculus Rift (Developmental Kit 1, Oculus VR, LCC) Head Mounted Display (HMD) showing the VR in 1268 × 800 pixels resolution for each eye, with a framerate of 60 frames per second. The interpupillary distance was set to 6.4 cm, with a 100 % visual image overlap between the eyes of all participants. Motion sensors within the HMD allowed participants to look around the VR without perceivable delay. Participants were sitting either upright or lying sideways on a daybed so that their head position was corresponding to the point of view in the VR. We controlled that participants were lying as horizontal as possible so that the HMD was sitting vertically on the participants face throughout the learning and testing phases while lying sideways.

We recorded latency as the time between the appearance of the reference stimulus and confirmation of the target position by button press. We also calculated absolute angular error, which was defined as the angle between the direction from the center object to the correct position of the target object and the direction to the location chosen by participants.

Procedure. After oral and written instruction about the procedure of the study, we obtained written consent from participants. Following instructions, the HMD was adjusted individually, and participants could familiarize themselves with the VR. For the learning phase, participants were brought into their respective body orientation, and after assuring they were comfortable and they could see the whole board, the stimuli were presented. We instructed them to memorize the position of the differently colored objects for at least three minutes and allowed to end the learning phase whenever they felt ready. Afterward, participants were asked to reproduce the layout via naming the color of the objects on a sheet of paper, with empty circles arranged in a 3 x 3 grid printed on it. They had to name the colors in the same body orientation in which the participants spent learning the layout. Upon successful reproduction, the first testing phase began in one of the two body orientations. If, however, participants could not reproduce the stimuli positions correctly, they were required to perform another learning phase on the same pattern. In the following testing phases, participants were instructed to reposition the target object as fast and as accurate as possible. After completion of the first testing phase, participants could take a short rest. They were then brought into the respective other body position for the second testing phase. Upon completion of both testing phases, we required participants to fill out a questionnaire asking about potential problems and strategies used in the experiment and debriefed them about the goals of this study.

To assure an equal level of expertise about the procedure of the task, all participants performed a practice run through the experiment beforehand, consisting of a learning phase (in the same body orientation as during the actual learning phase) and a short testing phase of 10 randomly chosen trials. The color layout of the practice stimuli was different from the layout used in the actual experiment. Participants performed the testing phase in the body orientation that they were required to occupy in the first testing phase of the experiment proper. However, they were told that they will have to perform the same task in the respective other body orientation. During the practice run, we could address potential problems with color naming or control of the target object.

Predictions. We split the predictions for the tested hypotheses into three sections. These are (1) predictions for the reference frames in memory, which differed in terms of reference direction, (2) predictions for the effects of axes alignment during testing, and (3) predictions for the effects of consistent axes orientation across learning and testing. These predictions are based on test situations that should lead to a better test performance than other test situations. To this end, for a given prediction, all test situations were divided into two categories (better versus worse) and then compared for performance differences. For example, when testing for an effect of aligned body and gravity axis during testing, trials in which body and gravity were aligned were compared in terms of performance with trials where they were misaligned during testing. The predictions are explained in more detail in the following.

Insert Figure 2 about here

Reference directions in memory. The corresponding predictions are summarized in Figure 2A. This figure shows test trials (as a combination of body and visual room orientations relative to gravity) for each of the proposed reference directions used in memory during learning in which performance should be better compared to the remaining test trials. These predictions are based on assumptions commonly shared within the community (e.g., McNamara et al., 2008).

The first general assumption is that participants encode the spatial locations in long-term memory relative to a certain reference direction during learning, namely the body vertical, the visual room vertical, or the direction of gravity. The second general assumption is that the memory representation is retrieved from memory and transformed into the orientation required for a test trial. For instance, if required to act based on an upside-down orientation with respect to the orientation during learning, the memorized representation must be rotated by 180° to be used. The third and crucial general assumption is that recall performance is best for those test trials in which the participants' body (or egocentric viewpoint) is aligned with the reference direction of the memory representation. In this case, the memory is simply accessed, and no further transformation is required. Depending on whether participants use a body, visual room, or gravity-based reference frame, this best performance orientation will differ (Figure 3 shows a visual illustration of this principle). The respective test trials that we hypothesize to yield best performance for each of the proposed reference direction in memory are explained in more detail in the following.

Firstly, using a body-based reference frame can be imagined like taking a snapshot of the objects' layout with a "mental camera." This snapshot is oriented relative to the body vertical at learning. Consequently, if the snapshot must be retrieved in the same orientation relative to gravity as during learning, better performance is expected when participants are tested in the same body orientation as occupied during learning, since then the snapshot can simply be retrieved as opposed to transformed. This mere retrieval and therefore better performance should also be true for the case when participants are tested in the respective other body orientation (lying sideways) with the visible test room rotated by 90° along the change of body orientation between learning and testing (see predictions for body vertical in Figure 2A and Figure 3A for a visual illustration).

Secondly, if participants used the visual room vertical as a reference direction, they should perform better when the memory representation is retrieved in a way in which the participants' body is aligned with the encoded visual room vertical. Again, memory can then simply be retrieved as opposed to transformed. Since the participants occupied an upright and a reclined body orientation during testing, two different body-room aligned test trials should lead to better performance compared to the body-room non-aligned respective other trials. If they are tested in an upright body orientation, the alignment between the body and the encoded visual room vertical axes is given for test trials in which the presented room is upright (i.e., not rotated) as well. If they are tested while lying on their side, better performance is expected when the presented room is tilted by 90° from the direction of gravity. These predictions for the room-based frame of reference are identical throughout the whole study (see predictions for visual room vertical in Figure 2A and Figure 3B for a visual illustration).

Thirdly, if participants encode spatial relations relative to the direction of gravity during learning, they should perform better during testing when their body is aligned with the represented direction of gravity. Here this means that if tested in a body upright position, the visual room orientation relative to gravity should be the same as during encoding. However, if the body is lying sideways, the visual room orientation during testing should be rotated 90° counter-clockwise with respect to the orientation seen at learning to meet this criterion. Importantly, at recall, the orientation of the represented gravity-based reference direction with respect to the actual direction of gravity is irrelevant (see predictions for the direction of gravity in Figure 2A and Figure 3C for a visual illustration).

Insert Figure 3 about here

Effects of reference axes alignment during testing. The corresponding predictions are summarized in Figure 2B. These predictions are independent of the constellation of the axes during learning. We tested for effects of gravity and visual room axes alignment during testing (hereafter called gravity-room alignment effect). Accordingly, we predicted better performance for test trials in which the visual room was in its canonical orientation (upright) and therefore aligned with gravity.

In addition, we tested for effects of gravity and body axes alignment during testing (hereafter called gravity-body alignment effect). The gravity-body alignment effect predicts better performance for test trials spent upright, as only then body vertical and gravitational axis are aligned. Please note that predictions for aligned body- and room-vertical axes during testing are identical to the predictions for encoding spatial information in a room-based reference frame.

Effects of consistent axes orientation across learning and testing. The corresponding predictions are summarized in Figure 2C. We tested for effects of consistent orientation of gravity and room axes across learning and testing (hereafter called gravity-room consistency effect). Accordingly, we predicted better performance for test trials in which the visual room was orientated in the same way relative to the direction of gravity as during learning, irrespective of body orientation. For instance, when the visual room was oriented upwards (or sideways) with respect to gravity during learning, best test performance should result with an upwards (or sideways) orientation during testing.

We also tested for effects of consistent orientation of gravity and body axes across learning and testing (hereafter called gravity-body consistency effect). This effect predicts better performance for test trials that the participants performed in the same body orientation as during learning compared to the ones performed in the respective other body orientation. For instance, if the participants learned the layout while lying sideways, better performance was expected for those test trials in which they were lying sideways too, compared to those in which they were upright. Please note that a consistent relationship between the body and the visual room orientation means that participants see the room in the same orientation relative to their body orientation as they saw it during learning. This is exactly what encoding along the egocentric body vertical predicts and these predictions are therefore identical.

Data analysis. The method of choice was to run statistical analyses on each of the two dependent variables (angular error and latency) for each of the hypotheses (reference directions in memory, effects of axes alignment during testing, and effects of consistent axes orientation across learning and testing). All these tests followed a 2 x 2 mixed-factorial design. The first factor was a within-subjects factor and separated the test trials predicted to yield better performance from those predicted yield worse performance according to the predictions of a hypothesis. This factor was called prediction-based factor. By design, fewer test trials that predicted better performance contributed to this factor compared to the other test trials. Since the data of each participant was aggregated across trials, this only indirectly affects the ANOVAs compared to the variance across participants. The second factor was the between-subjects factor learning condition.

We planned to run mixed-effects ANOVAs on each dependent variable for each of the tested hypotheses. We report all main effects for the prediction-based factors of the computed ANOVAs. We only report the main effects of the factor learning condition and the interactions between the two factors if significant. If there were significant interactions, we used follow-up contrasts to analyze them further. These contrasts were obtained using the methods implemented in lsmeans (Lenth, 2015). We report η_G^2 as effect size measure for ANOVAs following Bakeman's (2005) recommendations. We tested whether speed-accuracy trade-offs occurred for significant effects regarding the tested hypotheses by correlating the corresponding error and latency data.

Since the predictions for the body vertical and the visual room vertical as reference directions in memory were identical in Experiment 1 (Figure 2A), we planned to run a single ANOVA to test the predictions of these hypotheses. We also planned to conduct a single ANOVA for both body-gravity (alignment and consistency) effects. The body-gravity alignment effect is contrasting the body upright with the lying sideways condition during testing. Thus, if the ANOVA reveals a significant main effect of body orientation during testing, this shows that a body-gravity alignment effect has occurred. A significant interaction with the factor learning condition (upright vs. lying sideways during learning) may indicate a consistency effect, where better performance occurs when the body position during testing matches the position occupied during learning.

The figures showing the results of the ANOVAs only contain the results for the prediction-based factors. The bars show the mean difference in performance between the test trials predicted to yield better performance and the respective others. The error bars indicate the standard error of the mean of this difference. Please see Figure 4 for a visual explanation of how the data for the plots were obtained. Supplementary Figures 1 to 3 show the data across all body and visual room orientations used during learning and testing.

Insert Figure 4 about here

The presented objects' layout consisted of intrinsic axes, i.e. rows and columns. Meilinger et al. (2013) showed that participants tend to use verbal description along those intrinsic axes during encoding and that this description, or the intrinsic axes themselves, produce a W- or saw-tooth-pattern in the performance curve for different (imagined) views during memory recall. Tests on views aligned with the intrinsic axes yield better performance than non-aligned, or oblique views (Mou & McNamara, 2002) and it was suggested that this is due to more simple transformations for the aligned perspectives (Street & Wang, 2014). These effects occurred also in our experiments. However, as we were not interested in these effects, we ran linear mixed effects models with the W-contrast as a predictor for both dependent variables (after removing outliers) and performed further analyses on the residuals of these models, therefore subtracting the W-shape from our data. To this end, we created a W-shape factor separating the room orientations of 0°, 90°, 180°, and 270° from the remaining ones.

Results and Discussion

Insert Figure 5 about here

The results of our analysis for Experiment 1 are shown in Figure 5. 1.9 % of the error and 3.8 % of the latency data (5.39 % in total) were marked as outliers (exceeding three SDs of the overall mean, with outliers being removed independently for each dependent variable) and excluded before subtracting the W-shape and further analyses. Analogous to the Predictions section, we split the results of Experiment 1 into three sections.

Reference direction in memory. The results for the references directions used in memory are shown in the left panels of Figure 5. Since the predictions for the body and visual room axes were identical for Experiment 1 (see Figure 2A), the shown bars regarding these hypotheses are identical. The ANOVA with the body/room prediction-based factor yielded a significant effect for angular error, $F(1, 18) = 4.78$, $p = .042$, $\eta^2_G = .15$, but not for latency ($F < 0.44$). In terms of the body/room hypotheses, angular error and latency correlated positively ($r = .751$, $p < .001$), indicating that no speed-accuracy trade-off occurred but that an increase in error also led to an increase in latency and vice versa. The ANOVA for the gravity hypothesis did not lead to a significant main effect of the prediction-based factor, neither for angular error nor for latency, Fs < 2.33, ps $> .144$, $\eta^2_G < .09$.

The main effect regarding the body/visual-room hypotheses indicates that participants were more accurate when tested with a visual room-body relationship that matched the room-body relationship experienced at learning (stored in memory). Because the body and the visual room vertical had identical performance-related predictions, the obtained evidence does not distinguish whether participants selected the body vertical or the visually presented room vertical as the reference direction in memory of vertical object locations. The nonsignificant gravity-based main effect suggests that a reference direction based on gravity, as tested in this experiment, might not have been used in memory for vertical spatial layouts. Noteworthy, the selection of an egocentric reference frame for a vertically presented stimulus would be in line with previous findings (Kushiro, Taga, & Watanabe, 2007), and would extend these from a perception to a spatial memory task.

Effects of axes alignment during testing. The middle panels of Figure 5 show the results of the tested effects of axes alignment at memory retrieval. The ANOVA testing the gravity-room alignment effect did not yield a significant main effect for either of the two dependent measures (*F*s < 0.02). This indicates no effect on retrieval for situations in which the visual room is in its canonical orientation to gravity (visual room vertical aligned with gravity) regardless of body orientation.

The ANOVA testing both, the gravity-body axes alignment and consistency effects, revealed a significant main effect for angular error, $F(1, 18) = 5.04$, $p = .038$, $\eta^2_G = .20$, indicating an advantage for body-upright testing, but no consistency effect as the interaction was not significant, $F(1, 18) = 3.70$, $p = .070$, $\eta^2_G = .16$. For latency, no significant main effect and no significant interaction were present, *F*s < 1.69, *p*s > .211, $\eta^2_G < .09$. Angular error and latency correlated positively ($r = .615$, $p < .001$), indicating that an increase in error also led to an increase in latency, and vice versa. These results show that participants were more accurate in recalling spatial relations when tested in an upright body orientation compared to when lying sideways, irrespective of the visual room orientation relative to gravity during testing and regardless of the body orientation during learning. This alignment effect suggests either that an alignment of the body vertical with the direction of gravity helped during recall or that a misalignment impaired recall performance.

We do not believe the concern that this body upright advantage could be caused by difficulties in using the gamepad while lying sideways, as although participants were lying on their left arm during these test conditions, limitations in mechanical control of the gamepad are unlikely. Participants only needed their left thumb to control the joystick of the gamepad and used their right thumb to control the button. We also consider it unlikely that participants were confused by how the joystick operated while lying down. The gamepad controller output was rotated in the lying sideways test conditions so that the gravitational up/down axis on the gamepad was linked to the up/down controlling on the VR board. Participants did not report any problems with controlling the gamepad when lying sideways. Please note that we tested the used setup of controls in pre-tests, where participants clearly preferred the gravity-relative to the gamepad-relative control.

Effects of consistent axes orientation across learning and testing. The right panels of Figure 5 contain the results of the tested effects of consistent axes orientation across learning and testing. The ANOVA testing the gravity-room consistency effect did not show any significant results for either of the two dependent measures (*F*s < 0.31).

As stated above, the ANOVA testing gravity-body axes alignment and consistency effects revealed no significant interactions with the factor learning condition. This indicates that a consistent relation between the gravity and visual room axes as well as between the gravity and body vertical axes across learning and testing did not affect memory retrieval.

Experiment 2

Experiment 1 revealed that participants either used the body or the visual room vertical as a reference direction for encoding vertical object locations but could not distinguish between the two. Experiment 2 aimed to distinguish the influence of body- and visual room-based vertical axes in establishing the frame of reference in memory. It used the same paradigm as in Experiment 1, except for the introduction of a 90° offset between the body and visual room orientations during learning enabling us to achieve the desired differentiation. In addition, we aimed to corroborate the findings concerning the axes alignment and consistency effects.

Methods

A different group of twenty naïve subjects (7 male), age ranging from 19 to 59 (*M* = 29.05, *SD* = 10.46) participated. Recruitment, material, procedure, instructions, design, and analysis were identical to Experiment 1 except for the following: During learning, we introduced a 90° offset between the body and room orientations. Participants who learned in an upright position saw the room rotated 90° clockwise relative to gravity. Participants who were lying on their left side during learning saw a non-rotated room, aligned with gravity. The predictions concerning the tested hypotheses are summarized in Figure 6. For detailed explanations of how these predictions were derived in general, please see Experiment 1, Predictions.

Insert Figure 6 about here

Results and Discussion

Insert Figure 7 about here

2.2 % of the error and 3.4 % of the latency data (5.43 % in total) were marked as outliers and excluded from the analysis. We report the result for (1) the reference direction in memory, (2) the effects of axes alignment during testing and (3) the effect of consistent axes orientation across learning and testing in the following.

Reference direction in memory. The left panels of Figure 7 show the results of the reference direction used in memory, for angular error (top) and latency (bottom). The ANOVA with the gravity prediction-based factor exhibited an effect for latency, $F(1, 18) = 14.49$, $p < .001$, $\eta_G^2 = .36$, but not for error, $F(1, 18) = 1.61$, $p = .221$, $\eta_G^2 = .06$. A positive correlation was obtained when correlating error and latency ($r = .426$, $p = .006$), indicating that no speed-accuracy trade-off occurred. This suggests that participants reacted quicker when their body was aligned with the reference direction of the mental representation defined by the direction of gravity during learning.

However, similar effects can be reported for the ANOVA that tested the body vertical hypothesis, with a significant effect on latency, $F(1, 18) = 6.08$, $p = .024$, $\eta_G^2 = .19$, but not on error, $F(1, 18) = 0.21$, $p = .651$, $\eta_G^2 = .01$. Additionally, with the body-based prediction factor, we found a main effect for learning condition, $F(1, 18) = 7.71$, $p = .012$, $\eta_G^2 = .13$, showing that participants were slower in recalling the spatial locations, if they have learned them in a lying sideways body posture. Further, an interaction between the body-based factor and the learning condition was present, $F(1, 18) = 6.95$, $p = .017$, $\eta_G^2 = .21$, indicating that the body-based factor showed a larger difference for participants who learned the locations in an upright body posture, $t(18) = -3.61$, $p < .003$, than when lying down ($t < 0.13$). Again, a positive correlation was obtained between angular error and latency ($r = .347$, $p = .028$), indicating no speed-accuracy trade-off. This shows that participants were quicker when tested with a visual room that was orientated in the same relation to the body as was the case during learning, which suggests the selection of an egocentric reference direction. The room-based prediction factor did not reach significance for both angular error and latency (Fs < 0.89).

The above results concerning the selected reference direction suggest that participants used either the body vertical or the direction of gravity and not the visual room vertical in spatial memory for vertical locations. These findings vary from those of Experiment 1 in such that now this makes room to rule out the visual room vertical, but not the direction of gravity. In one of the learning conditions of Experiment 2 (where the participants were upright during learning), the predictions for both the body and the gravity axes were identical and therefore we cannot disentangle, which of the two axes was used in this condition. In the other condition, when participants learned the layout while lying sideways, the predictions differed, and the results make room for a more meaningful conclusion. The observed interaction concerning the body-based prediction factor suggests that participants did not select their body vertical as a reference or selected it less often in this condition. No such interaction (but a main effect) was present for the gravity-based prediction factor, which indicates that participants relied on gravity than on their body when they were lying sideways during learning. What might be the reason for this? We think that gravity might be selected in cases in which the own body vertical is less salient due to misalignment with the location layout and the direction of gravity (as was the case in the learning condition participant spent lying sideways). This is in line with findings of a previous study, in which reclined participants could recognize point-light walkers more accurately when the walkers were upright and aligned with gravity, regardless of the room orientation, and while the body vertical axis was misaligned and therefore rather uninformative (Chang, Harris, & Troje, 2010). Noteworthy, the selection of gravity would also be in line with previous findings regarding gravity-based reference frames for vertical objects and arrangements (Bernardis & Shallice, 2011; Pani & Dupree, 1994), and would extend these from a spatial span and perception task to a long-term spatial memory task.

Effects of axes alignment. The middle panels of Figure 7 show the results of the tested effects of axes alignment during memory retrieval. The ANOVA testing the gravity-room alignment effect did not yield a significant main effect, neither for angular error nor for latency, *F*s < 0.20, *p*s > .670, η^2_G < .02.

The ANOVA testing the gravity-body alignment and consistency effects revealed a significant main effect for angular error, $F(1, 18) = 9.53$, $p = .006$, $\eta^2_G = .34$, but no significant interaction with learning condition, $F(1, 18) = 0.10$, $p = .755$, $\eta^2_G = .01$. This indicates higher accuracy when tested upright than when lying sideways, irrespective of the learning condition or the visual room orientation during testing. No effects on latency were present (*F*s < 0.53). When correlating angular error and latency, a positive but not significant correlation was obtained ($r = .122$, $p = .454$), which suggests no speed-accuracy trade-off. These results corroborate the findings of Experiment 1 concerning the body-gravity alignment effect.

Effects of consistent axes orientation. The right panels of Figure 7 contain the results of the tested effects of consistent axes orientation across learning and testing. The ANOVA testing the gravity-room consistency effect did not show any significant results for both measures, *F*s < 2.05, *p*s > .169, η^2_G < .08.

The ANOVA testing both, the gravity-body axes alignment and consistency effects, revealed no significant interactions with the factor learning condition. Thus, as in Experiment 1, there were no consistency effects on memory retrieval.

Experiment 3

We found varying results concerning the reference direction in memory of vertical spatial layouts in the previous two experiments. Whereas evidence for the body vertical was present in both experiments, we cannot rule out the selection of allocentric visual room or gravity-based axes yet. At least two reference axes were aligned in every learning condition of Experiment 1 and 2 (see Figures 2 and 6, Learning conditions), with identical predictions for two of the reference directions in several conditions. In Experiment 3, we made all potential reference directions misaligned with each other during learning to achieve independent predictions for each of them. Again, we tested for consistency and alignment effects during memory recall and additionally intended to test effects of aligned reference axes during the time of learning.

Methods

Ten naïve subjects (5 male) aged from 19 to 56 years old (*M* = 28.5, *SD* = 10.72) participated. Again, recruitment, material, procedure, instructions, design, and analysis were identical to the previous experiments, except for a different condition during learning. Participants learned the layout of objects while lying on their side and with the room in VR rotated by 135° in a clockwise direction relative to gravity. We chose this rotation to yield the biggest overall difference of the gravitational, body, and visual room vertical axes. This Experiment consisted of one learning condition only. Since in the previous experiments, every single condition included ten participants, we limited the number of participants to ten in the condition of this experiment as well. The predictions concerning the tested hypotheses are summarized in Figure 8. For detailed explanations of predictions, please see Experiment 1, Predictions. Since there was only one learning condition in Experiment 3, we simply conducted paired t-tests on the dependent variables for each of the hypotheses. We report Cohen's *d* as an estimate of effect size.

Insert Figure 8 about here

Results and Discussion

Insert Figure 9 about here

1.9 % of the error and 5.3 % of the latency data (7.19 % of the data in total) were marked as outliers and excluded from the analysis. We report the result for (1) the reference direction in memory, (2) the effects of axes alignment during testing and (3) the effect of consistent axes orientation across learning and testing in the following. In addition, we report (4) results regarding the effects of axes alignment during learning.

Reference direction in memory. The left panels of Figure 9 show the results of the reference directions used for encoding, for angular error (top) and latency (bottom). The t-tests for the body-based hypothesis was significant for latency, $t(9) = -2.48$, $p = .035$, $d = -1.11$, and showed a strong trend for an effect for angular error, $t(9) = -2.16$, $p = .060$, $d = -0.96$. Correlating angular error and latency revealed a positive but not significant interaction ($r = .356$, $p = .123$), which suggests no speed-accuracy trade-off.

The t-test targeting the gravity-based hypothesis did not reach significance for either angular error or latency, ts < 0.44, ps > .677, ds < .20. In the case of the visual room-based hypothesis, the t-test was not significant for both angular error and latency, ts < 1.38, ps > .202, ds < .62. These results indicate a clear support for the selection of the body vertical for encoding vertical layouts in memory with latency and by trend with error and do not support the hypotheses of encoding relative to the visual room vertical or the direction of gravity.

Effects of axes alignment during testing. The middle panels of Figure 9 show the results of the tested effects of axes alignment during memory retrieval. The t-test testing the gravity-room alignment effect did not reach significance for both dependent variables, ts < 0.45, ps > .667, ds < 0.21.

The body-gravity consistency and alignment effects are defined by the same difference, but with opposite directions. Thus, we were required to perform only a single *t*-test for each measured variable. Neither of these conducted tests reached significance, *t*s < -1.40, *p*s > .196, *d*s < -0.63. However, the directions of differences are in favor for an alignment effect like in Experiment 1 and 2. Effect sizes are even similar to the ones of the other two experiments. We think that only the reduced number of participants was responsible for falling short of replicating the previously found effect.

Effects of consistent axes orientation. The right panels of Figure 9 contain the results of the tested effects of consistent axes orientation across learning and testing. The *t*-test testing the gravity-room consistency effect did not reach significance for both dependent variables, *t*s < 2.18, *ps* > .056, *ds* < 0.99. However, the effect on latency was only marginally not significant and the effect size indicates a strong effect. This suggests better memory recall when tested with the same visual room orientation relative to gravity as seen during learning, irrespective of the body orientation during testing. However, since this gravity-room consistency effect was not present in the previous experiments the general validity of it is questionable. The above results regarding the gravity-body alignment effect already showed that no such consistency effect occurred. These results corroborate the findings of Experiment 1 and 2.

Effects of axes alignment during learning. We tested whether aligned axes during learning influenced performance in the following testing phases. Since we assigned every participant in our study to one learning condition, this test had to be a group comparison across all five learning conditions of all three experiments. Together with the learning condition of this experiment, the learning conditions covered all combinations of alignment between the three vertical axes (i.e., none, body and visual room aligned, gravity and visual room aligned, gravity and body aligned as well as gravity, body and visual room aligned).

We ran a single ANOVA including every single combination of aligned axes (excluding interactions) during learning for both measures, angular error, and latency. This procedure did not produce any significant effect for neither, angular error nor latency (*F*s < .29). This finding indicates that aligned axes during learning did not influence memory encoding.

However, there was an effect of learning condition in the ANOVA of Experiment 2 testing the body-based hypothesis, where participants were slower in recalling the spatial locations when they had learned them in a lying sideways body posture compared to when they were being upright.

General Discussion

The present study investigated the selection of reference frames in spatial memory of vertical locations, where salient allocentric directions are always present (i.e., the direction of gravity and the visual vertical) contrary to the typically tested horizontal spatial memory. The tested reference frames differed in terms of reference direction, namely, an egocentric body vertical, an allocentric visual room vertical, or an allocentric gravitational reference axis. In addition, we tested potential processing advantages from aligned (i.e., when they are in their canonical relationship) body, gravity, or visual room vertical axes as well as the consistency effects when axes orientations were identical across learning and testing.

Reference frames in memory

Prior studies on long-term spatial memory for vertical space did not disentangle whether the selected reference frame for encoding was of egocentric or allocentric nature, as they did not dissociate the body orientation from the visual room or gravitational vertical axis (Hintzman et al., 1981, Experiment 5; Tlauka & Nairn, 2004). In Experiment 1, we dissociated the direction of gravity from the body and the visual room vertical, while body and visual room were always aligned during learning. Participants showed more accurate retrieval when their body was aligned with the visual room axis during testing, regardless of the alignment with gravity. According to the predictions, this suggests that the participants selected the body or the visual room vertical as reference axis in memory. In Experiments 2 and 3, an offset between the body vertical, the visual room vertical and the gravity axis during learning rendered the predictions for each of the possible reference directions distinguishable. We found quicker retrieval performance when the relationship between the body and visual room was the same as during learning, irrespective their relationship with gravity. According to the predictions, these results indicate that vertical locations were encoded along the egocentric body vertical axis.

It may be surprising that the gravitational axis and the visual room vertical had altogether a weak influence on reference frame selection for memorizing vertical spatial relations. For horizontal spatial memory, humans are capable of using salient allocentric reference frames in memory (e.g., Kelly et al., 2013; Mou & McNamara, 2002; Mou et al., 2007; Shelton & McNamara, 2001; Street & Wang, 2014). The direction of gravity and the visual room vertical provide highly salient orientation cues, which are–in the case of gravity–used for various other tasks as well (Bernardis & Shallice, 2011; Kluzik, Horak, & Peterka, 2005; Lacquaniti et al., 2015; Pani & Dupree, 1994). One may argue that the weak influence observed in our study is because the experimental manipulations of the allocentric vertical reference axes were not strong enough and therefore the allocentric axes themselves not salient enough to affect the selection of reference frame. However, some participants appeared to have used gravity as a reference in the second learning condition of Experiment 2. In this condition, gravity was possibly a more salient reference than the own body vertical, because it was aligned with the location layout while the body was misaligned with the visual room and gravity and therefore rendered as rather uninformative (Chang et al., 2010).

Consequently, our experimental manipulations of the vertical axes orientations were, in this case, salient enough and indeed influenced participant's selections. It also implies that the spatial cognitive system flexibly selects between the various frames of references for spatial memory of vertical locations in specific situations and that it is not bound exclusively to an egocentric reference system. However, when gravity was not aligned with the visual room during learning, participants again selected an egocentric reference frame (Experiment 3). This suggests that egocentric reference frames are preferred in vertical memory if the direction of gravity does not represent a more salient alternative.

At large, our findings indicate that humans predominantly select an egocentric reference frame defined by the body vertical axis for spatial memory of vertical object locations perceived from a single point of view. Such an egocentric representation was associated with view-based representations in the past (Christou & Bülthoff, 1999; Diwadkar & McNamara, 1997). Participants might have stored an egocentric view of the objects' layout and performed best when the view of the visual room relative to their body during testing was most like the view stored in memory.

Results of previous studies using horizontal layouts indicate that when multiple views on the to-be-studied layout are experienced during learning, humans select a reference frame that is aligned with salient environmental or layout intrinsic axes. Importantly, although participants might initially use an egocentric reference frame, they appear to restructure their memory around salient allocentric axes after experiencing additional perspectives (Kelly & McNamara, 2008; Kelly et al., 2013; Shelton & McNamara, 2001). With different views on a vertical location layout during learning, the saliency of the ego- and allocentric reference frames might vary and humans might choose the most salient allocentric option from multiple experienced perspectives as well. For instance, when learning a layout in an upright *and* in a lying sideways body orientation, a gravity-based reference frame might be the most salient alternative in the lying sideways condition and, depending on the sequence of body orientations, participants might initially select it or restructure an egocentric memory. The results regarding the selection of gravity as a reference in Experiment 2 hint towards this conjecture. Consequently, allocentric reference frames in spatial memory of vertical locations might exhibit greater influence with multiple learning views.

Besides, the roles of allocentric reference frames might also vary with the size of the environment where the objects are placed in (Burgess, 2006; Wolbers & Wiener, 2014). For instance, different reference frames might be selected in environmental spaces that require navigation compared to vista spaces (Meilinger, Strickrodt, & Bülthoff, 2016). If an environmental space comprising multiple rooms and corridors must be memorized through navigation, the space is usually lacking a common visual context rendering it impossible to represent it by a single view-based representation, which might lead to the selection of allocentric reference frames. Future research should examine the impact of environmental spaces and multiple views during learning on reference frame selection in spatial memory of vertical locations.

Effects of axes alignment during learning and testing

We tested for effects of aligned (i.e., they are in their canonical relationship) body vertical, gravity, or visual room vertical axes during learning or testing. In Experiment 1 and 2, the upright body posture during testing (i.e., aligned body vertical and gravity axis) yielded more accurate memory recall compared to when participants were lying sideways. The effect size was similar in Experiment 3–but probably due to half the number of participants tested–this difference was not significant. Contrary to testing, we did not observe a general advantage of any aligned vertical axes during learning when comparing the learning conditions across experiments. Unlimited learning time and learning to criterion might have occluded potential effects during learning. However, we found a difference between the learning conditions in Experiment 2, which showed quicker recall after learning the environment in an upright compared to a lying sideways body posture. Consistent with a previous study using a three-dimensional path-memorization task (Vidal & Berthoz, 2005), these results indicate a memory processing advantage in an upright body position. Our results extend these prior findings to memory recall of locations as well as to learning object configurations within a vista space, where the whole space can be perceived without any translational self-movement. We did not find an effect of aligned visual room vertical and gravity axis at learning or at testing, which further emphasizes the dominant role of the egocentric body-based axis in spatial memory.

Body upright advantages are found also in other tasks, for example, vestibular and sometimes visual heading discrimination (Hummel et al., 2016; MacNeilage et al., 2010) as well as visual distance estimation (Harris & Mander, 2014). Arguably, they indicate a general processing advantage when the body vertical and gravity axes are aligned (Barnett-Cowan & Bülthoff, 2013; Vidal & Berthoz, 2005). Where might this advantage come from? Humans keep an upright head posture throughout most of their wake times (Pozzo, Berthoz, & Lefort, 1990) and their brain seems to establish mental representations of the body with the prior of an upright head posture (MacNeilage, Banks, Berger, & Bülthoff, 2007; Mittelstaedt, 1983; Schwabe & Blanke, 2008). Restraining head movements can yield more parsimonious (fewer parameters required) and robust (no singularities) self-to-environment representations (Finkelstein et al., 2015), reducing orientation and navigation to yaw rotations (around the vertical axis) as well as translations along horizontal coordinates. Thus, human spatial processing might be tuned to or work best with an upright body and head posture. However, what is the nature of the processing costs when the body vertical and the direction of gravity are not aligned? While we are not able to give a conclusive answer, we can exclude some explanations based on our and other data.

Firstly, we think that the processing costs are not due to the preference of the spatial system for yaw over roll or pitch rotations (Creem, Wraga, & Proffitt, 2001; Vidal, Amorim, & Berthoz, 2004). In a previous study, we did not find a difference in spatial memory retrieval when comparing horizontal layouts with yaw rotations and vertical layouts with roll rotations (Hinterecker et al., 2018). Furthermore, the present experiments only incorporated roll rotations and our findings can therefore not originate from differences in multiple rotation axes.

Secondly, we do not think that the processing costs are caused by different encoding processes for the horizontal and the vertical plane, as proposed for navigational memory (Jeffery et al., 2013). Since we only tested locations distributed on a vertical plane in this study, preference for spatial planes cannot explain the present findings. Furthermore, the results of our previous study (Hinterecker et al., 2018) did not reveal differences between spatial memory for layouts distributed on a horizontal or vertical plane perceived from a single view.

Thirdly, we do not think that it is likely that the body upright advantage originates from a habitual context advantage. That is, if the environmental context is as in situations encountered most of the time, performance is better compared to untypical contexts. Accordingly, one would not only expect better performance when being upright (as this is the posture in which we interact with the environment most of the time), but also better performance when the visual room vertical and the objects in the room are aligned with the direction of gravity (as usually is the case, unless visiting a trick cabinet). As we did not observe the latter effect of aligned room vertical and gravity axes, a habitual context advantage seems unlikely.

Fourthly, we also consider interference between two location representations (one body-relative and one gravity-relative) as unlikely. There are indications that the representation of the currently perceived environment may interfere with a differently oriented and imagined (Avraamides & Kelly, 2010; Kelly, Avraamides, & Loomis, 2007; May, 2004), or recalled (Meilinger & Bülthoff, 2013; Riecke & McNamara, 2017) representation of the same or of a similarly structured environment. However, in the present experiments, an interference causing the observed alignment effect would encompass two memorized representations (body- and gravity-based) and not a perceptual versus a non-perceptual representation. This would require memorizing and encoding locations in long-term spatial memory twice and not just once, which we think is highly unlikely. Noteworthy, a potential interference is also not able to explain why evidence for body-relative memory was observed in all experiments and evidence for gravity-relative memory only in Experiment 2, as such interference should be present in all experiments.

From our perspective, a likely viable model for the upright body advantage consists in a selection conflict between body- and gravity-based reference frames (Vidal & Berthoz, 2005). During learning, participants do not encode locations multiple times, but might be unsure relative to which reference frame they specify locations when lying sideways and with gravity being a salient alternative to the own body. This might have been the case in the second learning condition of Experiment 2 (Figure 6), where the visual room was upright and aligned to gravity, while the body vertical was not. The selection conflict between the gravity- and body-based reference frames might have impaired encoding, thereby leading to a decreased recall performance compared to the condition participants sat upright during learning (as suggested by a main effect of the factor learning condition in Experiment 2). In all other experiments and conditions, no such conflict was present, as gravity might not have been a salient enough alternative. This argument suggests that spatial encoding is impaired if the own body is not aligned with gravity as usual and with gravity being a salient alternative as a reference direction. It points towards a general body upright advantage during learning since in these situations no such selection conflict occurs.

This body upright advantage is in line with the study of Vidal and Berthoz (2005), where participants showed a body upright advantage during learning too. In their study, the advantage was higher for field-dependent participants, which have difficulties in suppressing external reference frames (measured in a rod and frame test) in favor of an egocentric reference frame (Vidal & Berthoz, 2005). It is conceivable that a conflict between egocentric and gravity-based reference frames affected such individuals more severely leading to a stronger body upright advantage than for participants who are better in concentrating on an egocentric reference frame. In addition, this conflict can explain why some participants might have selected the gravity-based over the body-based reference direction for encoding in Experiment 2, and why the egocentric reference axes dominated in the other conditions.

A reference frame conflict could explain the body upright advantages not only during learning but also during testing. In our experiment, participants were required to move target objects across the board during recall using a gamepad. While lying down sideways, object control might have suffered from a selection conflict. Controls can function relative to the own body or relative to gravity. The latter was the case in our experiments, which means that when lying sideways on their left side, turning the joystick to the egocentric right moved the target object upwards on the screen with respect to gravity. Thus, in a lying position, a conflict between the gravity-based and body-based controls might have occurred. In contrast, with the body being upright, no conflict occurred, as the egocentric and the gravitational control directions were aligned, which could explain the comparably better performance. In accordance with previous work (e.g., Vidal & Berthoz, 2005) we think a reference frame conflict is the most plausible explanation.

To sum up our considerations, a selection conflict between body- and gravity-based reference frames can explain the body upright advantage during learning and testing found in our and other experiments (e.g., Vidal & Berthoz, 2005), and it can explain why we observed additional gravity-relative encoding in Experiment 2 only. It provides a better explanation than alternative considerations based on interference between memory traces, habitual context transformation differences, rotation advantages around certain spatial axes, or better encodings along certain spatial planes. Further research must examine the exact mechanisms in more detail.

Effects of consistent axes orientation across learning and testing

We tested whether consistent axes orientation during learning and testing affected recall performance and whether such consistency acted as a relevant context. Context effects (Smith & Vela, 2001), as an instantiation of the more general principle of encoding specificity (Tulving & Thomson, 1973), predict memory retrieval as a function of the similarity between the encoding and retrieval situations. If the similarity is high, the memory retrieval will be better compared to situations with great dissimilarity. Context effects were shown for objects accompanying targets (Bloch & Vakil, 2017), bodily states (Goodwin, Powell, Bremer, Hoine, & Stern, 1969), and environments such as underwater versus on the surface (Godden & Baddeley, 1975). Here, we examined whether vertical axes orientation counts as context as well. Surprisingly, our results suggest that the orientation of the body or the visual room vertical with respect gravity did not seem to count as a context. We did not observe any significant advantage when the room or the body axis had the same orientation relative to gravity during learning and testing. Please note that the observed egocentric encoding is a consistency or context effect between the visual room vertical and the body-based reference axis. Participants recall configurations better when they are oriented relative to the room comprising the memorized layout in the same way as they were during learning. Accordingly, the orientation of a layout relative to the body is a relevant context that is encoded. In theory, participants could abstract from the perspective in which they experienced the layout when memorizing object configurations. However, they clearly did not do so, as the results on the selected egocentric reference axis show.

Discussing the underlying assumptions and setup of this study

The assumptions underlying the tests for reference frames in vertical spatial memory were based on common assumptions underlying horizontal spatial memory (e.g., McNamara et al., 2008). They assumed better memory recall when the reference direction established in memory is aligned with the body vertical axis. For example, if locations are encoded along the gravity axis in memory, better retrieval was expected when the body vertical is aligned with the gravity-based reference direction in memory during testing (Figure 3C). One concern is that these assumptions presume that spatial memory using an allocentric gravity-based reference frame is sensitive to the body orientation at recall but is not sensitive to the actual direction of gravity. Encoding spatial locations along gravity might be independent of the body orientation during both encoding and recall. Instead, better recall might occur when the encoded layout must be retrieved in the same orientation with respect to gravity as during learning. In fact, we also tested this possibility. The predictions regarding the effects of consistent gravity and visual room vertical axes orientation across learning and testing can be interpreted as encoding along gravity in memory assuming that recall is insensitive to the body orientation but sensitive to the direction of gravity during testing. In fact, a marginally not significant result with latency in Experiment 3 appeared to be in line with this. However, there were no results regarding this effect in Experiments 1 and 2. Thus, this possibility of a gravity-based reference frame in vertical spatial memory does not hold true for humans.

In addition, our setup led to predictions that did not dissociate between encoding locations in a room-based reference frame and an alignment effect between the body vertical and the visual room vertical axes during testing. To create distinct predictions for these two hypotheses, the spatial layout must be decoupled from the visual room during testing. This means, for instance, rotating the visual room by 90° does not necessarily change the orientation of the spatial layout. Doing this systematically leads to test situations in which a remembered layout encoded in a visual room-based reference frame must be retrieved in an orientation where the body vertical is aligned with the reference direction in memory, but where the visual room vertical axis during testing is not aligned with the body vertical, and vice versa. Since we did not introduce such an experimental manipulation, any effects in line with predictions of the visual room-based reference frame also could be explained by effects of axes alignment between the visual room vertical and the body vertical. However, in reverse, observation of no such effects would suggest that neither hypotheses hold true for humans. This was the case in our study.

Conclusion

The present study, for the first time to our knowledge, disentangled the selection of reference frames for long-term spatial memory of vertical layouts based on the body vertical, the direction of gravity, and the visual room vertical axes. Despite the highly salient environmental reference axes, spatial memory of small-scale layouts in the vertical dimension is primarily represented relative to the body vertical. Gravity can be selected as a reference direction when it represents a more salient alternative than the body vertical axis. Moreover, a body upright advantage was observed when retrieving vertical spatial memory, with recall (and to some extent also encoding) being superior compared to when the body is lying sideways. A selection conflict between gravity and the body vertical axes best explains this finding.

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Figures

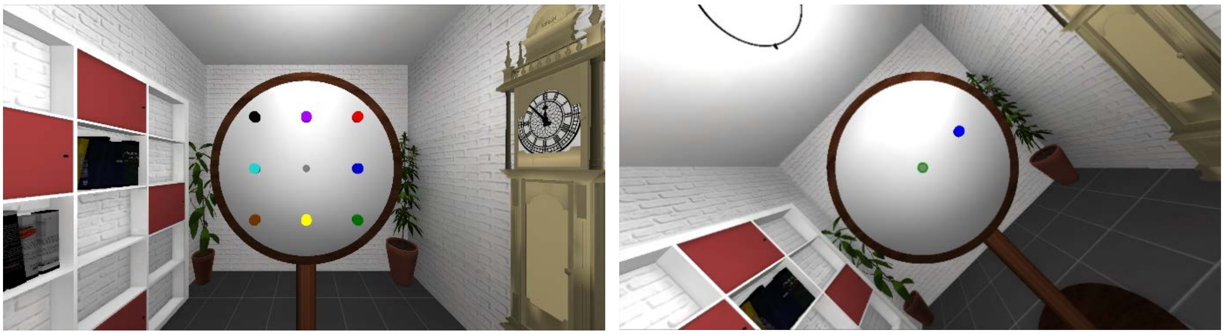

Figure 1. Participants' viewpoint in the virtual environment. In a learning phase (left panel), participants memorized the object layout in either a sitting upright or lying sideways body orientation. In the subsequent testing phases (right panel), we asked participants to reposition a target object (here green object) with the help of two reference objects (here grey and blue) in one out of eight visual room orientations (45° counterclockwise rotation shown). They conducted the test phase in both body orientations.

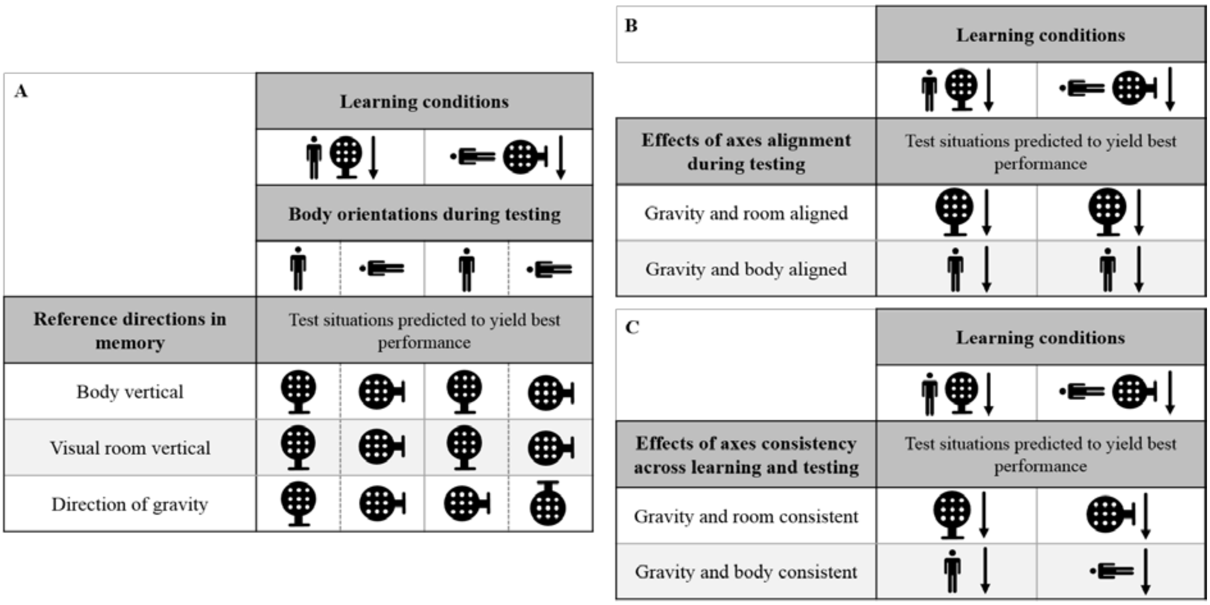

Figure 2. Predictions for best test performance according to the tested hypotheses in Experiment 1. The different vertical axes are depicted by a body icon for the body vertical, a vertical board icon for the visual room vertical, and an arrow for the direction of gravity. ***A***, predictions according to the tested *reference frames in memory* that differ in terms of reference direction. The predictions are explained briefly in the following. For each reference direction, we predicted visual room orientations (depicted by the vertical board icon in the corresponding column) to lead to better test performance compared to the remaining room orientations for a particular learning condition and for a particular body orientation during testing. In detail, if the body vertical is used as a reference during encoding, better recall performance is expected for test trials in which the visual room is in the same orientation with respect to the body as during learning (irrespective of either relation to gravity). If the visual room vertical or gravity axis is used as a reference direction, the body orientation does not matter during encoding. However, the crucial assumption is that performance should be better for trials in which the body (or egocentric viewpoint) and the reference direction of the memory representation are aligned during recall. In the case of the visual room vertical, this means that participants should perform better when the body is aligned with the visual room during testing. For gravity, the same visual room orientation

relative to gravity should yield best performance when tested in upright body position. When tested lying on the side, an orientation rotated by 90° counter-clockwise with respect to the orientation during learning should yield better performance. Note that the orientation of the gravity-based reference direction in memory with respect to the actual direction of gravity is irrelevant during recall. ***B***, predictions according to the tested *axes alignment effects* during testing. The gravity-room alignment effect predicts better performance for trials in which the visual room was upright and aligned with gravity during testing irrespective of the body orientation. The body-gravity alignment effect predicts better performance for trials spent upright and therefore with the body vertical and direction of gravity being aligned regardless of the room orientation. ***C***, predictions according to the tested *consistent axes orientation effects*: The gravity-room consistency effect expects better performance for those test trials in which the room was orientated in the same way relative to gravity as during learning, irrespective of the body orientation. The body-gravity consistency effect expected better performance for trials that the participants performed in the same body orientation with respect to gravity as during learning, regardless of the visual room orientation.

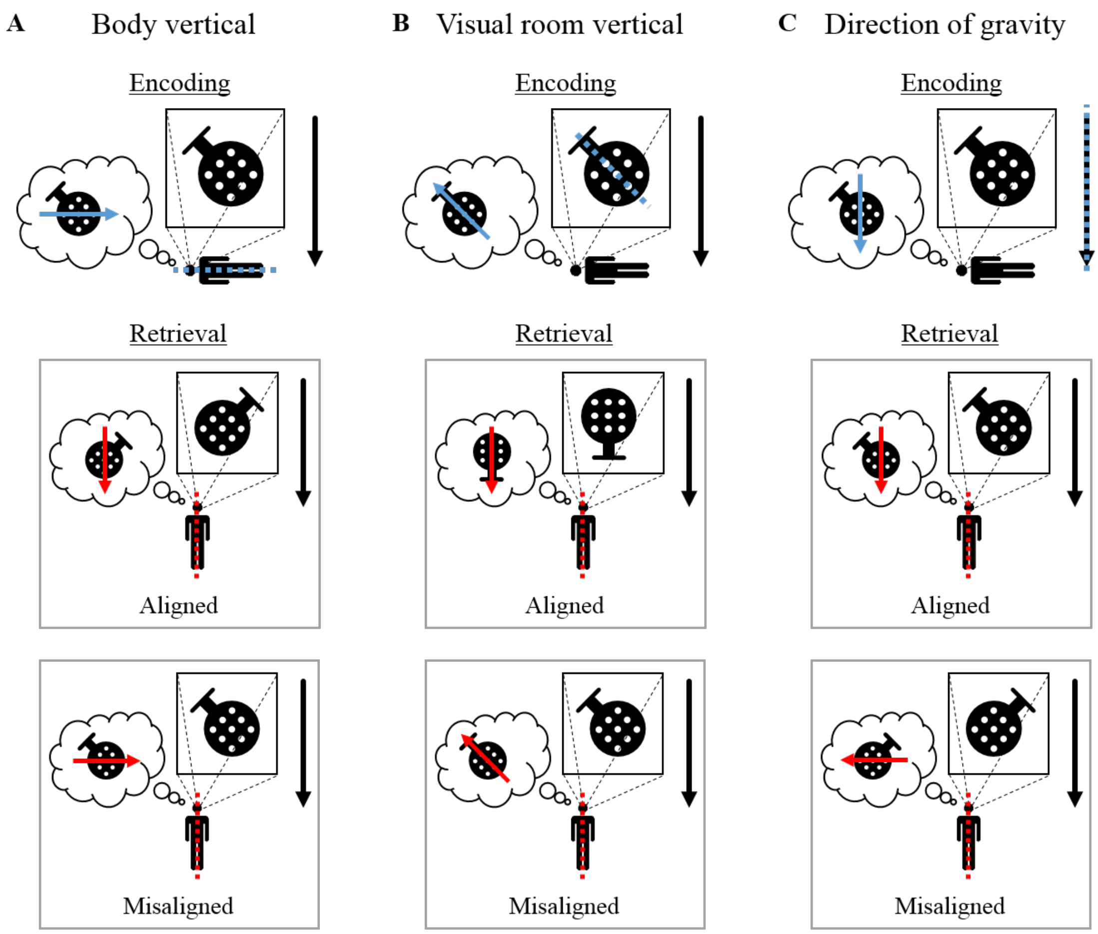

Figure 3. Exemplary best-performance predictions for body vertical (depicted by the human-like figure), visual room vertical (depicted by the board orientation), and direction of gravity (depicted by the black arrow pointing downwards). The same learning (encoding) scenario, as well as two recall examples, are shown for all three axes. In the example for encoding, the participant is lying sideways with the room rotated by 135° clockwise relative to gravity (as in Experiment 3). During retrieval, the participant is upright and is presented with different layout orientations. Here, the first retrieval cases (upper blocks) always show an example where performance should be better due to an alignment of the memories reference direction with the body compared to the second scenario (lower blocks), in which performance should be worse due to misalignment with the reference direction in memory. ***A***, during encoding, the participant sees the room containing the board and uses the body vertical (indicated by the

dashed blue line) as a reference direction in memory (depicted by the cloud). The solid blue arrow indicates the reference direction of the memory representation. In the first retrieval example, the room is rotated by 225° clockwise. The reference direction (indicated by the red arrow) is aligned with the upright body vertical (indicated by the red dashed line), which should yield better performance compared to the second scenario. In the second scenario, the visual room is presented in the same orientation with respect to gravity as during encoding. However, the participant is now in an upright position and therefore the reference direction in memory and the body vertical are not aligned. ***B***, the participant uses the visual room vertical as a reference during encoding of the presented objects' layout. In the first retrieval scenario, the alignment between the reference direction in memory defined by the visual room vertical and the participants' body is given, and better recall performance should occur accordingly. Worse performance should occur in the second scenario, as the axes are misaligned. ***C***, the participant uses the direction of gravity as a reference during encoding. For the upright body position, better recall performance is expected if the visual room has the same orientation as during encoding (as is the case in the first retrieval scenario). In the second scenario, the visual room is rotated differently leading to a worse recall performance. Importantly, the orientation of the gravity-based reference direction in memory with respect to the actual direction of gravity does not play a role during recall.

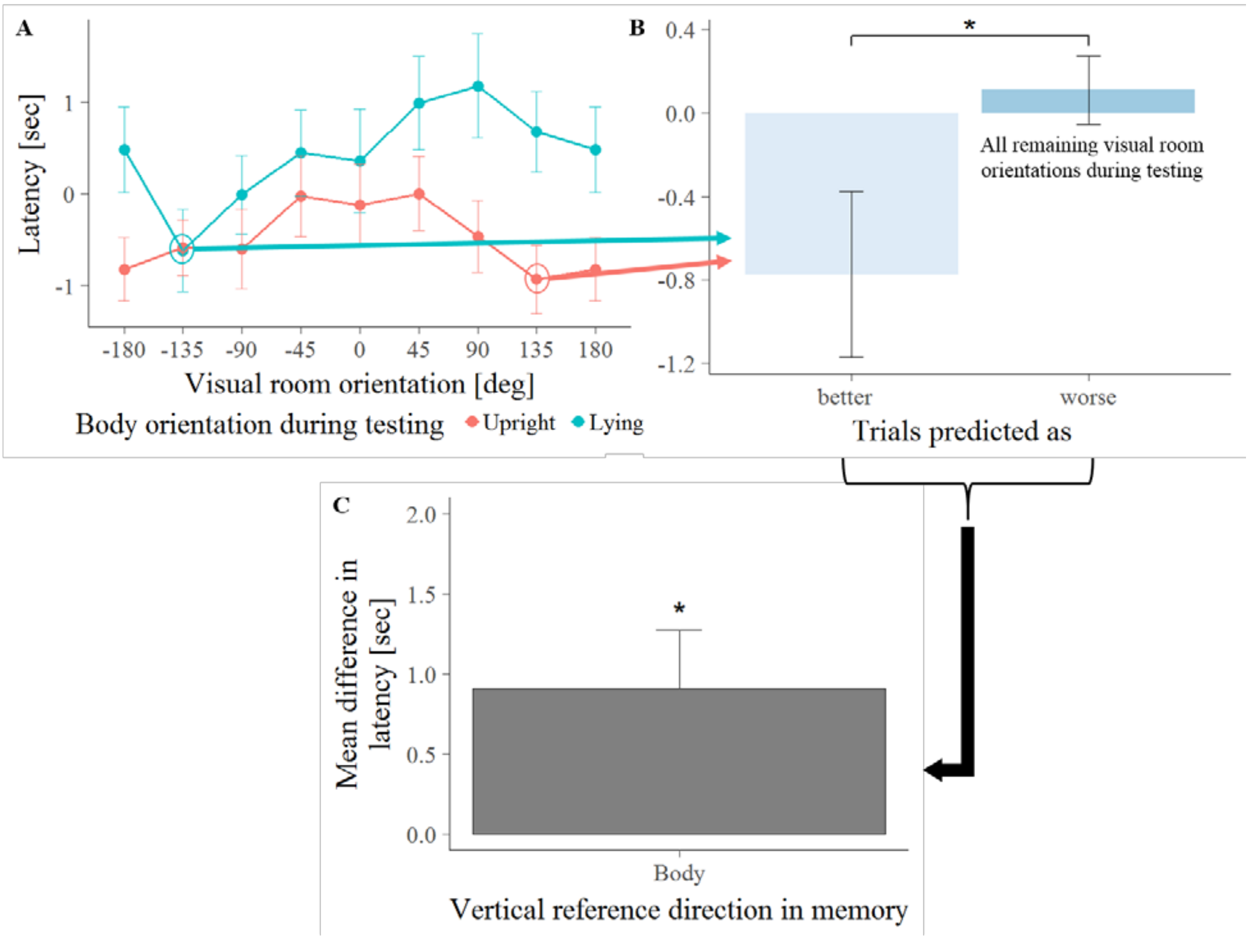

Figure 4. A visual explanation of how the data for the plots were obtained in the example of using the body vertical as reference direction in memory. ***A***, standardized latency data (of Experiment 3) shown as a function of the visual room and body orientation relative to gravity during testing after controlling for the effects of intrinsic layout axes. For each body orientation occupied during testing, one test trial was predicted to yield better performance compared to all remaining test trails. Here, these test trials are indicated with colored circles (reddish circle for upright, greenish circle for lying sideways body position) according to the predictions of the body-based reference frame (see Figure 8). ***B***, bars showing mean latency data for test trials predicted to yield better performance (light blueish bar) and those predicted to yield worse performance (dark blueish bar) according to predictions of the body-based reference frame. These values were tested for difference (using ANOVAs in Experiments 1 and 2, and t-tests in Experiment 3). ***C***, in the article, we present only a single bar showing the

mean difference between the predicted better and predicted worse test trials (here between the two bars shown in **B**), where a positive value indicates a difference in accordance with the respective predictions. The asterisk above the bar indicates whether the statistical test comparing the better versus worse trials reached significance.

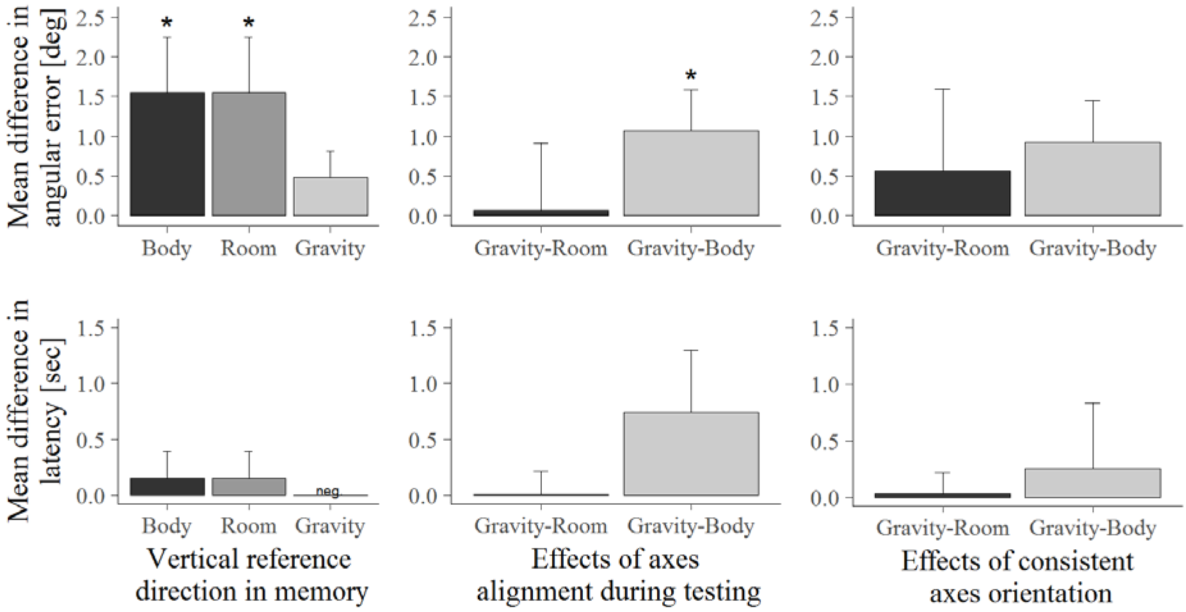

Figure 5. Experiment 1 effects of the tested hypotheses according to Figure 2, i.e., vertical reference directions in memory (left panels), effects of axes alignment during testing (middle), and effects of consistent axes orientation across learning and testing (right) for angular error (top panels) and latency (bottom). Bars show the mean difference (and standard errors of this difference) between trials predicted to yield better performance and the respective other trials, according to the respective hypothesis depicted on the x-axis. Negative differences, where the effect is in the opposite of the predicted direction, are not shown (indicated by a “neg.” label), here only for the reference direction based on gravity with latency. Asterisks mark a significant difference in line with the respective prediction.

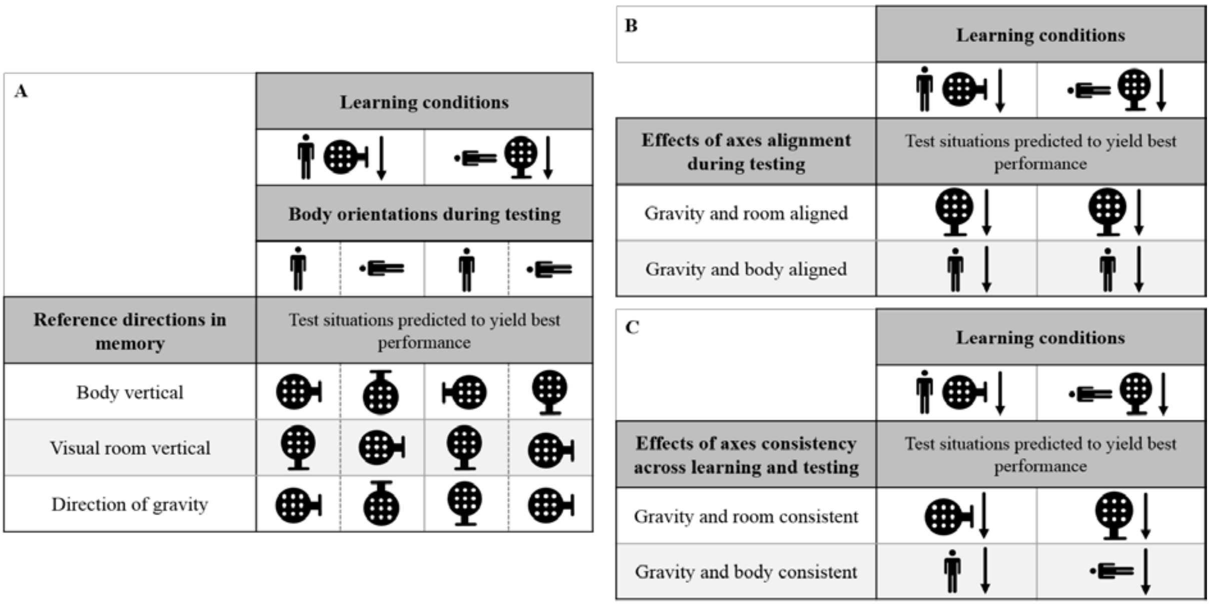

Figure 6. Predictions for best test performance according to the tested hypotheses in Experiment 2. ***A***, predictions according to the tested reference frames in memory that differ in terms of reference direction. ***B***, predictions according to the tested axes alignment effects during testing. ***C***, predictions according to the tested consistent axes orientation effects.

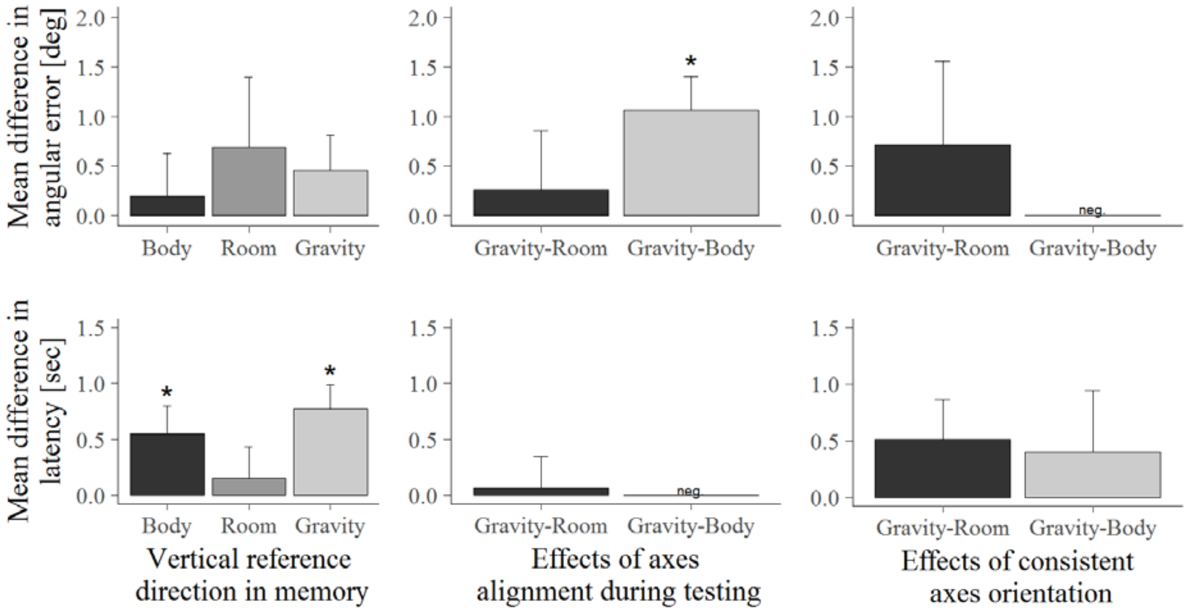

Figure 7. Experiment 2 effects of the tested hypotheses according to Figure 6.

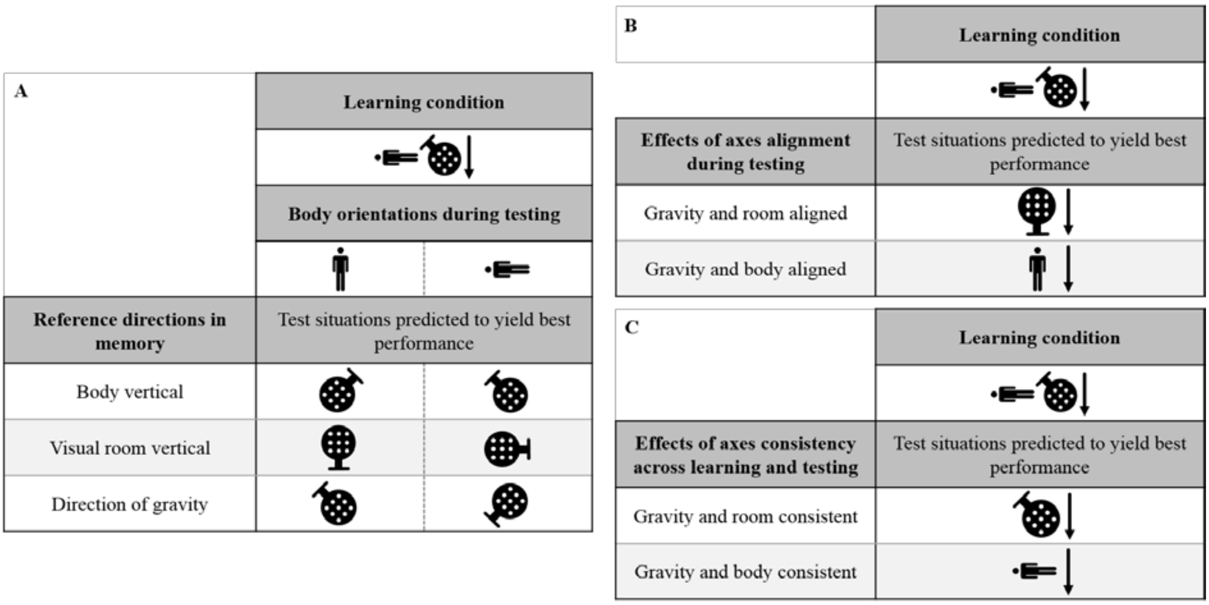

Figure 8. Predictions for best test performance according to the tested hypotheses in Experiment 3. ***A***, predictions according to the tested reference frames in memory that differ in terms of reference direction. ***B***, predictions according to the tested axes alignment effects during testing. ***C***, predictions according to the tested *consistent* axes orientation effects.

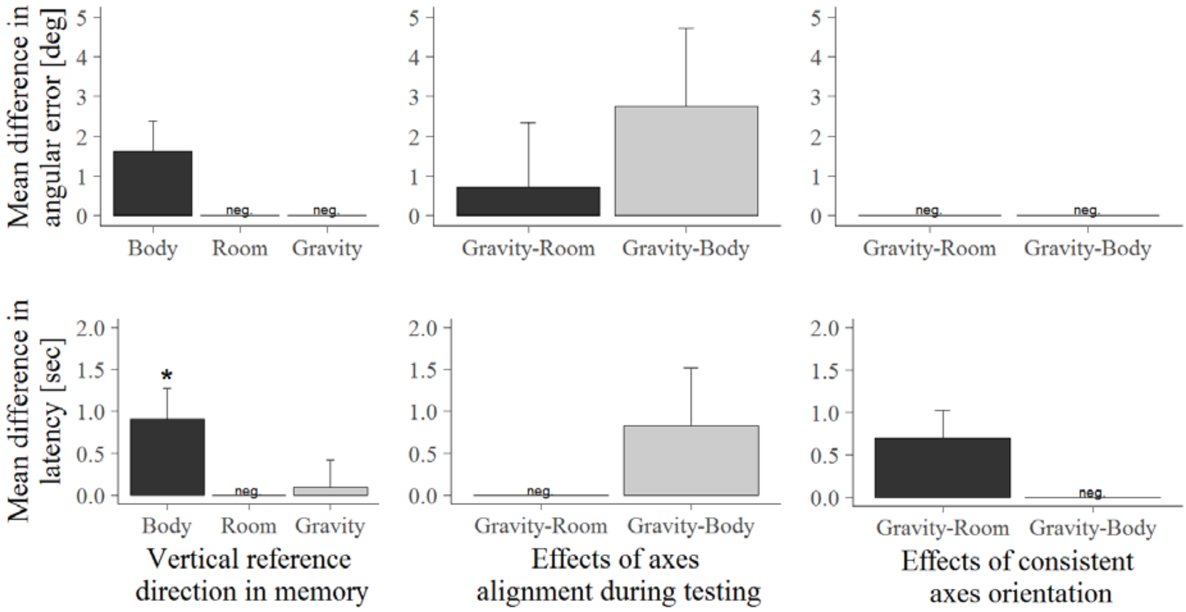

Figure 9. Experiment 3 effects of the tested hypotheses according to Figure 8.