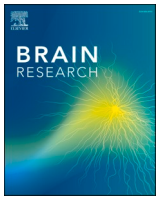
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Research paper

Switching to an allocentric spatial reference frame incurs distinct cognitive processing costs

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ABSTRACT

The ability to acquire, recall, and flexibly use information from first-person (egocentric) and map-like (allocentric) reference frames is essential for human wayfinding and thus, daily life. Prevailing models of the neural systems that support the representation and coordination between reference frames suggest that switching back-and-forth should result in either lower accuracy, slower response time (RT), or both. However, predictions of these models have not been adequately tested for spatial memory of large-scale, naturalistic environments. Inspired by previous work on task switching, we developed a novel task in which participants performed a spatial memory switching task that included trials in both egocentric and allocentric reference frames. Participants learned a large virtual neighborhood by navigating to various target stores. They then completed runs of the memory task, with approximately equal numbers of egocentric and allocentric trials. Critically, we manipulated whether the same reference frame was repeated or switched on a trial-to-trial basis to determine whether there is a cost associated with changing reference frames. Results showed no significant differences in spatial memory accuracy across conditions but significantly slower response times for switching trials. Importantly, simple effects analysis revealed significant reaction time costs only or egocentric-to-allocentric switching. These findings suggest that there may be cognitive differences dependent on the direction of reference frame switching, although our data cannot completely rule out the existence of allocentric-to-egocentric switching costs. Future neuroimaging studies to test predictions generated by our results, particularly when switching to an allocentric frame, will provide crucial insight into human spatial memory function.

1. Introduction

To successfully and efficiently navigate the complex environments encountered in the world, humans and animals must effectively use spatial information relative both to one's own body or viewpoint (egocentric) and the structure or configuration of the environment (allocentric). Since Tolman's classic cognitive experiments in rats, the existence of allocentric and egocentric reference frames and the respective use of place and response strategies for each, respectively, have been documented in a number of species from fruit flies to fish (Goodman, 2021; McAroe et al., 2016; Mussells Pires et al., 2024; Packard & McGaugh, 1996; Rinaldi et al., 2020; Tolman, 1948; Wallach et al., 2018).

A primary theoretical model – proposed by Byrne, Becker, and Burgess (BBB model; Byrne et al., 2007) – posits that egocentric representations are primarily supported by sensory input and posterior parietal regions. In contrast, allocentric representations are primarily supported by the hippocampus and other medial temporal lobe (MTL) structures, where place cells, grid cells, and boundary vector cells are commonly observed (Hafting et al., 2005; O'Keefe & Dostrovsky, 1971; O'Keefe & Burgess, 1996). BBB also postulates that retrosplenial cortex acts as a transformation layer between reference frames via input from head direction cells (Taube et al., 1990). However, there have been few direct tests of the predictions from this model. In a recent review, Alexander and colleagues (2023) outline challenges in what they refer to as "falsifying the transformation hypothesis" – which includes BBB and other models. For example, the definition of what a spatial transformation is at a behavioral or neural level is often vague, and there are few explicit predictions that would allow for falsification (e.g., these models are implicitly agnostic to the symmetry of the transformation process, so presenting evidence for symmetry or asymmetry cannot directly invalidate it). To address this gap, we formalized several

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predictions based on our interpretation of transformation models (although we acknowledge that there are different interpretations) and examined human behavior during a spatial memory task that required trial-by-trial switching between egocentric and allocentric reference frames.

From our interpretation of the BBB framework, we posited the following predictions: (1) a switch cost in processing when redeploying knowledge from one reference frame to another (i.e., switching) compared to continued deployment in the same reference frame (i.e., repeating) and that (2) any switch cost would be the same regardless of the direction of redeployment. There have only been a handful of human behavioral studies on spatial switching, with mixed results. In a visual perception task, Lv and Hu (2020) found increased reaction time for switching compared to repeating with no directional difference between them, at least when information did not conflict across frames. While the perceptual task's design served as an elegant test of egocentric and allocentric frames, the task was effectively two-dimensional (i.e., lacking a depth component) and it is unclear whether these results would transfer to larger three-dimensional spaces such as those BBB aims to explain (e.g., rooms, buildings, outdoor spaces).

Orti and colleagues later developed a more three-dimensional task to assess egocentric and allocentric transformations, whereby participants viewed novel triads of objects on a table and made judgements about an object's position relative to the participant's body (egocentric) or to other objects (allocentric) (Orti et al., 2023; Orti et al., 2024; Orti et al., 2025). Participants made pairs of judgments with the second pair either repeating or switching from the first. They found that when initially biased toward an allocentric frame, participants made more errors and were slower to respond, a selective impairment inconsistent with our predictions from BBB. Notably, in their initial work using this paradigm, Orti and colleagues report significantly slower reaction times for allocentric judgements and participants were less accurate when the initial judgement was allocentric (Orti et al., 2023). This is an important consideration given that previous work has shown participants tend to perform worse on allocentric relative to egocentric spatial memory tasks, specifically for newly learned spatial relationships acquired from viewpoints (Starrett et al., 2023; Zhang et al., 2014). Thus, it remains unclear how participants would dynamically use egocentric and allocentric representations when recalling well-learned spatial relationships.

Relevant to our interest in human navigation, spatial memory may depend crucially on the type of space that is being recalled and whether movement is or is not required for sufficient learning, such as in environmental or vista space (Montello, 1993; Montello & Golledge, 1998). Previous studies of egocentric and allocentric switching have been limited to smaller vista-type spaces, whereas theories of spatial cognition like BBB have focused more on complex environmental-scale spaces such as those navigated in humans' daily lives. Thus, a gap exists in our understanding for how humans dynamically use reference frames to recall information about well-learned, complex environments.

Even accounting for human idiosyncrasies in spatial encoding, task demands during spatial memory retrieval can introduce bias toward egocentric and allocentric representations. The commonly-used judgements of relative direction (JRD) task ("Imagine standing at [A], facing [B]; point to [C]"; Waller & Hodgson, 2006) has been contrasted with the scene- and orientation-dependent pointing (SOP) task (given a viewpoint, orient and point to a target; Wang and Spelke, 2000). The former is typically deemed more allocentric and the latter more egocentric (Starrett et al., 2023; Zhang et al., 2014), but both tasks have some elements of egocentric and allocentric processing. Further, it is likely not possible to measure pure egocentric or pure allocentric knowledge considering how intertwined they are with task demands. Moreover, it is entirely plausible that reference frames – and any dissociable brain regions that support one specific frame – are never used in isolation (Ekstrom et al., 2014; Filimon, 2015; Nett et al., 2025; Starrett & Ekstrom, 2018). As a workaround for this obstacle, Starrett and Ekstrom (2018) suggest conceptualizing a continuum of egocentric-to-allocentric reliance along which tasks can be designed to tap.

Another aspect not addressed by Starrett and Ekstrom (2018) is that tasks probing points along the ego-allo continuum may not all provide identical amounts of spatial information. For example, the JRD provides no visual or spatial information beyond the targets in the prompt, while the SOP usually provides rich viewpoint information as well as the ability to change viewpoints and orient; yet the two are frequently compared as allocentric and egocentric tasks, respectively. A primary goal in designing the present study was to use egocentric and allocentric spatial memory tasks that provided similar amounts of visual and spatial information while being maximally separated along the egocentric-allocentric continuum. In the present study, both egocentric and allocentric tasks provided only two environmental landmarks to establish a heading without any other cues (e.g., streets or other buildings); only the perspective (first-person and top-down, respectively) differed. Previous studies have suggested that allocentric frames could be solved by mental rotation of viewpoints (de Condappa & Wiener, 2016). For the present work, we developed a paradigm that focused on deployment and redeployment (i.e., switching) on a trial-by-trial basis while equating the relative fidelity of egocentric and allocentric knowledge and the spatial cues provided to assess each frame. Critically, we included repeats of and switches to each frame to also test for directional switching differences. If effects were due only to mental rotation, then allocentric performance would not differ between repeat and switch trials. Additionally, if perceptual information – seeing a top-down view on a preceding trial – were to prime participants to expect a particular trial, this could also provide a confounding benefit to repeat trials or impairment to switch trials. To circumvent this, we made it so the likelihood of a repeat or switch was roughly 50%; moreover, any perceptual or format priming in one direction (e.g., an allocentric trial preceded by an egocentric trial; switch-to-allo) would occur in the opposite case as well (e.g., an egocentric trial preceded by an allocentric trial; switch-to-ego).

Given the relationship between proposed spatial transformation circuits in the brain and the successful retrieval of consolidated memories, we sought to examine spatial memory specifically for well-learned environments (Byrne et al., 2007; Daselaar et al., 2006, 2009; de Landeta et al., 2020; Dhindsa et al., 2014; Hussin et al., 2022; Kaboodvand et al., 2018; Maier et al., 2024; Makino & Komiyama, 2015; Patai et al., 2019; Rolls, 2019; Wang et al., 2020). Based on the theoretical framework of the BBB model, our main hypotheses centered on the magnitude (hypothesis 1 or "H1") and symmetry (hypothesis 2 or "H2") of switch costs. For magnitude, we predicted that switching between reference frames would incur significant costs for only spatial memory accuracy (H1a), only response time (RT; H1b), or both (H1c). Since switching should distinctly engage a BBB neural transformation layer, we hypothesized that we would at least observe significantly slower RT with switching (H1b or H1c). What is less clear from BBB is whether information would be lost in the transformation, but a deficit (H1a or H1c) could suggest either a loss of information during transformation or a speed accuracy tradeoff; the latter of which could be ruled out using RT data if necessary. With respect to symmetry, we predicted that switching costs would be equal (i.e., symmetrical) for egocentric-to-allocentric and allocentric-to-egocentric (H2a); there is no explicit reason in BBB why a transformation layer should work differently depending on direction because it relies on the same circuitry and connections, but we would stress, again, that this is indeed an assumption on our part. Thus, we expected that any asymmetries would be explained by differences in performance between egocentric and allocentric tasks. However, absent broader task differences, it is also possible that we might observe directional asymmetries with deficits for either egocentric (H2b) or allocentric (H2c). Based on previous work that reported selective impairments in healthy aging when switching to allocentric strategy use during wayfinding (Harris et al., 2012), we

hypothesized that any asymmetry in switch costs observed in our task would be greater in the egocentric-to-allocentric direction.

2. Method

2.1. Participants

Prospective participants were between the ages of 18–35, with no reported history of psychiatric or neurologic disorders. No formal power analysis was conducted prior to data collection or analysis because there have not been previous studies with similar designs to use as a basis. Previous experiments reporting effects on the JRD pointing task included samples of 24 participants (Peer & Epstein, 2021; Starrett et al., 2019), so our aim was to obtain viable data from at least 30 participants, allowing for 25% attrition. A total of 44 individuals were enrolled in the study. We failed to obtain useable data from 11 participants for the following reasons: One participant indicated during the second session that they did not believe they knew how to correctly solve the allocentric task, two participants reported after the study that they did not remember they were required to submit responses (i.e., most if not all trials timed out), one participant was dismissed due to the testing computer crashing, and seven participants' data files were lost or overwritten before being downloaded from the testing computer despite having successfully completed the study – the latter issues were traced to a member of the study team who had not received proper training in handling the data files for this study. Thus, viable data was obtained from 33 participants (11 male, 22 female) between the ages of 18-31 (M = 21.06, SD = 3.41). Prior to analysis, additional data from four participants were excluded due to below-chance performance on either egocentric or allocentric trials, and data from five participants were excluded due to excessive (>20%) trials where no response was submitted (see below for details). One participant was missing post-experiment questionnaires and surveys, but their data was otherwise viable and therefore included in relevant analyses. Data from a final sample of 24 participants (7 male, 17 female) between the ages of 18 and 31 (M = 21.30, SD = 3.10) were submitted to subsequent analyses. Enrollment status throughout the experimental procedures is shown as a flow chart in the supplemental materials (Fig. S1). All participants provided informed consent prior to participating in any study activities, and all procedures were approved by the Institutional Review Board at the University of California, Irvine.

2.2. Materials

2.2.1. Virtual neighborhood environment

The to-be-learned environment was created in the Unity video game engine (v2019.4.29f1; Unity Software Inc., San Francisco, CA, USA) using the Landmarks package (Starrett et al., 2021) along with freely available 3D model assets for Unity. The environment was 100m × 150m (Fig. 1, panel A) and built to resemble similar environments from other spatial navigation research studies (Starrett et al., 2019, 2023; Zhang et al., 2014). For each participant, eight distinct target stores were randomly selected from 24 possible stores, randomly assigned one of eight visually distinguishable colors, which were drawn from the set of seven easily discernable colors [orange, sky blue, greenish blue, yellow, blue, vermillion, reddish purple] suggested by Wong (2011) with the addition of a shade of violet (Green-Armytage, 2010). Target stores were randomly populated at one of eight predefined locations in the environment (Fig. 1, panel A).

2.2.2. Stimulus presentation

Participants completed the experiment using a Victus by HP 15L Gaming Desktop (HP Inc., Palo Alto, CA, USA) with 32 GB of system memory, a 13th generation Intel Core i5 -13400 processor clocked at 2.50 GHz, and Intel Arc A380 graphics (Intel Corporation, Santa Clara, CA, USA). Graphics were rendered on a 23-inch Apple Cinema HD display (Apple Inc., Cupertino, CA, USA) at a resolution of 1920 x 1200 and refresh rate of 59.95 Hz.

2.2.3. Experimental tasks

The behavioral tasks for the experiment were built in the Unity game engine using the Landmarks package (Starrett et al., 2021) and compiled as a single, standalone executable for the Windows operating system. At the beginning of each experimental session, participants completed a brief target familiarization task in which each of the eight target stores was shown rotating on a black screen. The main portions of the experiment comprised two tasks: a navigation learning task and a memory task, which alternated with each other during the initial learning session.

2.2.3.1. Navigation learning task. Participants were placed at one of eight random starting locations, selected to minimize the visibility of any target store at the beginning of the task. Participants were required to navigate to each of the eight stores in a randomized order. Participants' free movement was continuous, executed via the arrow keys (up/down: forward/backward translations at 3.5 m/s; left/right: yaw rotations at 60 deg/s).

Phases of the navigation learning task are shown in Fig. 1, panel B. Participants received a cue (3 s) indicating which target store they would need to find on a given trial, which was then moved to the top of the screen where it remained during wayfinding. There was no time limit for wayfinding, so the experiment would only progress once the participant arrived at the target store. Participants were required to move onto a circular platform with an arrow indicator oscillating above it, located 10 m from the center of the target store. Upon arriving, the participant's movement was disabled, and they had to rotate to within 1 deg of facing directly toward the target store to end the trial. Participants repeated the cue, navigate, arrive, orient procedure until each of the eight stores had been found. After the initial trial, each trial started at the target location from the previous trial to emulate real-world navigation.

2.2.3.2. Memory task. Participants recalled spatial information by specifying the angular relationships between target stores – which we operationalize as pointing. Half of the memory trials were displayed from a first-person (ego; Fig. 2, panel A) reference frame, while the other half were displayed from a top-down (allo; Fig. 2, panel B) reference frame. For either reference frame, a participant's heading was established using one landmark and its corresponding arrival location (i.e., 10 m directly in front of that target store and facing it orthogonally) from the navigation learning trials. Participants were shown only a virtual desert, a single target store to establish their heading either from their viewpoint (ego) or the center of the screen (allo), and a text cue indicating a second target store to point to (Fig. 2). Participants oriented to the cued target using the left- and right-arrow keys to rotate counterclockwise or clockwise, respectively, and submitted responses by pressing the up-arrow key. Translations were prohibited and rotation speed was 60 deg per second, the same as the navigation learning task. Crucially, the number of times that the reference frame stayed the same (repeat) or changed (switch) from trial to trial was approximately 50%, determined by a permutation algorithm that constrained the maximum number of times the same format could be shown consecutively to three. Thus, the critical features of the task are the reference frame (i.e., ego- vs. allocentric) and whether the trial has the same reference frame as the previous one (i.e., repeat vs. switch). A sequence of trials is shown in Fig. 2, panel C.

2.3. Design

To test our hypotheses about spatial memory switch costs, the experimental design was derived from the memory task and thus used a

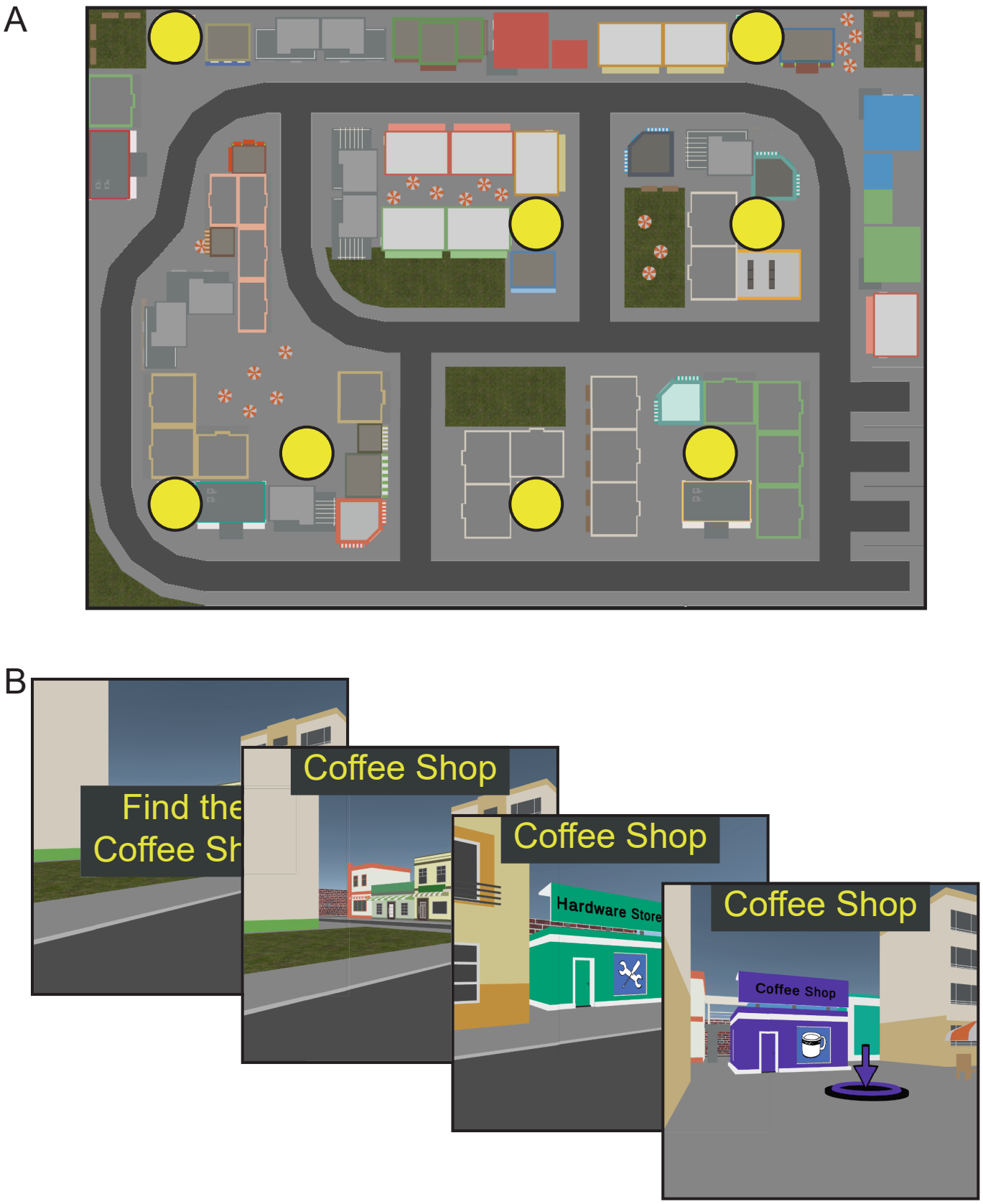


Fig. 1. *Virtual Environment and Navigation Learning Task. Note.* Panel A: An overhead view of the entire virtual neighborhood with circles indicating the target store locations. Panel B: The navigation learning task showing, from left to right, the prompt, the beginning of wayfinding, passing a non-target store, and arriving at the target store.

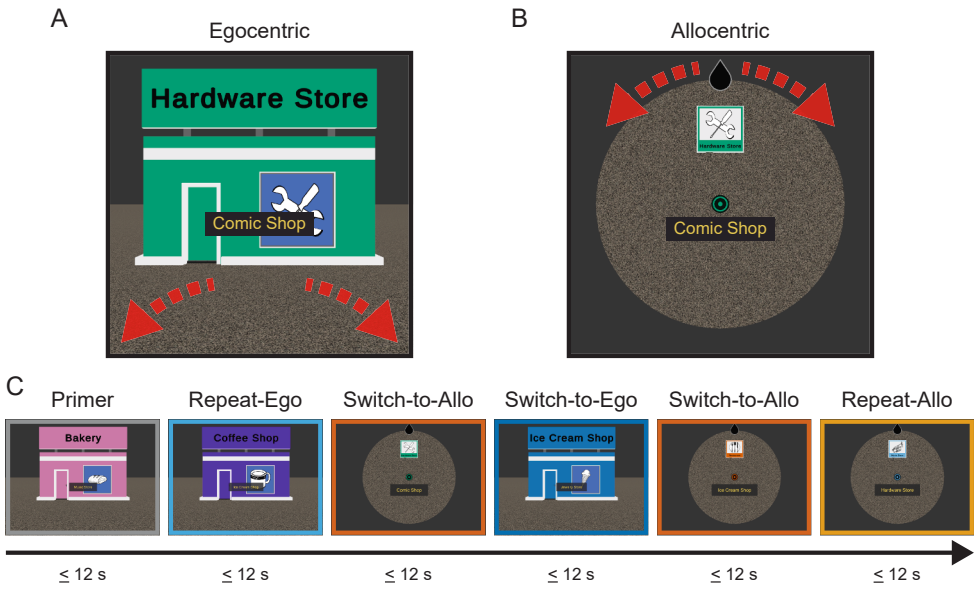


Fig. 2. *Spatial Memory Repeat-Switch Task. Note.* Panel A: An egocentric (ego) reference frame trial. Panel B: An allocentric (allo) reference frame trial. Panel C: A sequence of six trials depicting an initial primer trial as well as each experimental condition of interest (gray: primer, light blue: repeat-ego, dark blue: switch-to-ego, light orange: repeat-allo, dark orange: switch-to-allo). Dotted red arrows in panels A and B, which were not actually seen by participants, illustrate the possible rotation of a participant's viewpoint (ego) or the circle and pointer (allo).

2 (Reference Frame: ego, allo) × 2 (Switching: repeat, switch) fully within-subject design. The Reference Frame manipulation involved displaying the spatial memory task from either an eye-level, first-person perspective (ego) or a top-down perspective (allo). The Switching manipulation involved whether the current trial was the same format as the trial that preceded it or not. This resulted in the following four conditions: repeat-ego, switch-to-ego, repeat-allo, and switch-to-allo (Fig. 2). The primary dependent measures were spatial memory accuracy (absolute angular pointing error) and response time (RT). Absolute angular pointing error on the spatial memory task was calculated as the absolute difference between the correct response orientation and the participants actual response orientation and could range from ($Min = 0°$; $Max = 180°$). RT on the spatial memory task was calculated as the time from trial onset until participants submitted their response, including any rotations (Min = 0.50 s; Max = 12 s). Additional measures of exploratory interest included navigation efficiency (normalized excess path) during the navigation learning task and results from several questionnaires.

2.4. Procedure

The study took place across two sessions, with each lasting 60-90 min. The second session took place at least two and no more than seven days after the first session; this was to provide sufficient time for some degree of systems consolidation, because brain regions associated with coordinating between spatial reference frames (e.g., retrosplenial cortex) have been shown to be important for recollection of consolidated information (Maier et al., 2024; also see Alexander et al., 2023). Session 1 thus served to allow participants to encode the novel virtual environment, which would undergo consolidation prior to session 2 (Daselaar et al., 2009), and familiarize them with the spatial memory tasks.

In the first session, participants provided informed consent prior to being enrolled in the study and then viewed slides instructing them on how to complete the navigation and memory tasks, as well as on the order of tasks and number of trials for each. Regarding the experimental manipulations, participants were only told that there are many tests for measuring spatial memory, and that we were interested in two of them (i.e., participants were not explicitly informed about the Switching manipulation). Participants then completed a practice version of the experimental tasks in an open 50 m × 50 m virtual environment. The practice environment contained four target stores that were not present in the neighborhood. Participants practiced navigating to each of the four practice stores and completed 10 practice trials (5 egocentric and 5 allocentric) of the memory task. The experimenter observed the practice session and answered any questions before beginning the experiment.

Before starting the primary experimental tasks, participants were familiarized with the eight target stores in the neighborhood. Participants viewed each store rotating (30 deg/s) on a black screen; the order was randomized without replacement. (i.e., a store was not viewed again until all other stores had been viewed the same number of times) and repeated until each store had been viewed three times.

Participants then completed four blocks of navigation learning task runs (reaching the location of all 8 stores per run) interleaved with memory task runs (28 trials preceded by 2 primer trials per run). There were 56 possible target pair permutations, randomly distributed across two runs. Each run was repeated a second time, but with the reference frame of each trial reversed (thus each trial was completed in ego and allo format), and the order of the four resulting runs was randomized. This resulted in a total of 112 total memory trials in the first session across the four runs. We chose to include four runs in the initial session because our qualitative assessment of previous studies suggests that many healthy young participants reach asymptotic accuracy performance by this point (Starrett et al., 2019, 2023; Zhang et al., 2014).

Afterward, participants completed several questionnaires before being dismissed. In addition to background and demographic information, participants completed the Santa Barbara Sense of Direction (SBSOD) scale (Hegarty et al., 2002), the computerized Spatial Orientation Task (SOT; Friedman et al., 2020), as well as surveys developed "in-house" to obtain information on video game use as well as experiment-specific feedback and strategies used. The SOT was implemented using a standalone application available from the authors and digital versions of the other questionnaires were created and administered using QuestionPro (QuestionPro Inc., Austin, TX, USA).

In the second session, participants re-read the same instructions from the first session and were refamiliarized with the target stores, this time viewing each store only once. This time, participants completed only a single run of the navigation learning task (8 trials) before completing

eight runs of the memory task (30 trials each; 2 primer trials followed by 28 trials with 6-8 trials per factorial cell per run). Each target pair permutation was presented four times in total (50% allo) for a total of 224 memory trials. After completing the experimental tasks, participants filled out a survey about their impressions of the task, awareness of and difficulty with the Switching manipulation, and strategies used for each trial type before being paid and dismissed.

2.5. Data exclusion

Quantitative criteria for excluding datasets comprised a permutation test to determine whether memory accuracy was better than chance and evaluation of the percentage of trials in which no response was recorded. For permutation tests, a subject-specific null distribution was created for each reference frame task by shuffling the correct answer labels 1000 times and counting the number of times when the median error using the shuffled labels was less than or equal to the observed error to estimate a *p*-value; *p*-values less than .05 were considered to indicate better-than-chance performance. Non-response trials were flagged for removal and data from participants who did not respond on at least 80% of trials were excluded completely. Table S1 shows each participants permutation test *p*-values and timeout proportions for each task. Participants could not submit responses until at least 0.50 s had elapsed. Across all participants only one participant responded in less than 0.70 s, and only on a single trial, so no trials were removed based on a lower threshold for RT. For completeness, the data were reanalyzed without removing any participants based on chance performance or excessive timeouts (N=33; see Results).

2.6. Data analysis

Unless otherwise noted, all analyses were conducted using R version 4.5.1 (R Core Team, 2021) and R-Studio version 2024.12.0+467 (Posit team, 2023) with the following packages: afex v1.4-1 (Singmann et al., 2021), ARTool v0.11.2 (Kay et al., 2021), effectsize v1.0.1 (Ben-Shachar et al., 2020), emmeans v1.11.1 (Lenth, 2021), ggpubr v0.6.0 (Kassambara, 2020), glue v1.8.0 (Hester et al., 2024), hues v0.2.0 (Baumgartner & Dinnage, 2019), lme4 v1.1-37 (Bates et al., 2015), performance v0.14.0 (Lüdecke et al., 2021), rmcorr 0.7.0 (Bakdash & Marusich, 2024), rstatix v0.7.2 (Kassambara, 2021), and core tidyverse packages (v2.0.0 Wickham et al., 2019 – ggplot2 v3.5.2, dplyr v1.1.4, tidyr v1.3.1, readr v2.1.5, purr v1.0.4, tibble v3.3.0, stringr v1.5.1, forcats v1.0.0, lubridate 1.9.4). Absolute angular pointing error on the spatial memory task was calculated as the absolute difference between the correct response orientation and the participants actual response orientation and could range from ($Min = 0°$; $Max = 180°$). RT on the spatial memory task was calculated as the time from trial onset until participants submitted their response, including any rotations ($Min = 0.50$ s; $Max < 12$ s).

Consistent with the factorial design of the experiment, we planned to use a 2 (Reference Frame: ego, allo) × 2 (Switching: repeat, switch) Analysis of Variance as an omnibus test of our main hypotheses. ANOVA models were fit and assessed for violations of statistical test assumptions (see Supplemental Materials). If assumptions were violated we (1) refit the model, aggregating participant data using the median, (2) refit the model, applying a linear transformation to the response variable – a log transform is commonly used for positively skewed data such as those obtained in our task, (3) applied an aligned rank transform to the response variable (Wobbrock et al., 2011); we re-assessed for violations of assumptions at each step and stopped if assumptions for ANOVA were met. When aligned rank transform was used, models were fit using linear mixed effects models, making it more difficult to obtain effect size measures (e.g., partial eta-squared; η_p^2). If these steps did not resolve violations, we planned to conduct pairwise Wilcoxon signed rank-sum tests, due to the lack of nonparametric alternative for two-way fully within-subject ANOVA. In the presence of an interaction effect, we conducted simple main effects analysis comparing switch and repeat trials across reference frames. We also carried out exploratory pairwise comparisons across all conditions and corrected for multiple comparisons using the Bonferroni method.

3. Results

3.1. Primary analyses from session 2

Our main research question related to how switching between reference frames affects consolidated spatial memories for well-learned environments, so our primary analyses were conducted on data from session 2.

3.1.1. Accuracy: absolute angular pointing error

When analyzing absolute angular pointing error from session 2 (Fig. 3, panel A), a Shapiro-Wilk test confirmed that the distribution of residuals from the ANOVA model deviated significantly from a normal distribution ($W = .91$, $p < .001$). Neither aggregating each participant's data using the median ($W = .88$, $p < .001$) nor applying a log-transform ($W = .95$, $p = .001$) resolved the violation (Fig. S2), but an aligned rank transformation allowed us to analyze the results using an ANOVA framework (Kay et al., 2021; Wobbrock et al., 2011). None of the effects reached statistical significance, including the main effect of Reference Frame ($F(1,23) = 1.23$, $p > .250$), main effect of Switching ($F(1,23) = 0.53$, $p > .250$), and interaction ($F(1,23) = 2.24$, $p = .148$). Pointing accuracy results are shown in Fig. 3, panel A. The pattern of results was unchanged when including participants who were deemed to have performed below chance or had an excessive number of timeout trials.

3.1.2. Response time (RT)

For pointing RT (Fig. 3, panel B), a standard within-subject ANOVA was found to be appropriate since residuals did not differ statistically from a normal distribution ($W = .97$, $p = .060$; Fig. S3). The main effect of Reference Frame did not reach significance ($F(1, 23) = 1.63$, $p = .214$, $\eta_p^2 = .07$). There was a significant main effect of Switching ($F(1, 23) = 9.69$, $p = .005$, $\eta_p^2 = .30$), and a significant interaction between Reference Frame and Switching ($F(1, 23) = 4.33$, $p = .049$, $\eta_p^2 = .16$).

We further examined the interaction between egocentric and allocentric switching by testing simple (main) effects of switching within each reference frame. We conducted paired *t*-tests comparing switch and repeat conditions across both egocentric and allocentric reference frames. Participants took significantly longer to respond on switch-to-allo ($M = 5947.96$ ms, $SD = 1093.77$) than on repeat-allo ($M = 5636.49$ ms, $SD = 1177.02$) trials, ($t(23) = 4.00$, $p < .001$, 95% CI [150.52, 472.41], $d = .82$). However, participants' response times on switch-to-ego ($M = 5719.67$ ms, $SD = 1002.91$) and repeat-ego ($M = 5631.51$ ms, $SD = 1031.90$) trials were not statistically different, ($t(23) = 0.33$, $p > .250$, 95% CI [-96.29, 272.61], $d = .20$). RT results are shown in Fig. 3, panel B.

Given that the simple main effect for switch versus repeat on allocentric trials would clearly exceed even the strictest multiple comparisons correction threshold, we chose to conduct exploratory pairwise comparisons for all conditions to examine the full pattern of results while applying a Bonferroni correction (threshold of *p*-uncorrected < .008 for six comparisons). Results for pairwise tests with uncorrected and corrected *p*-values are shown in Table 1.

Given the relatively high *p*-value observed for the Frame by Switching interaction, we performed a post-hoc power analysis using the G*Power application (Faul et al., 2007). For a more accurate power analysis, we explicitly calculated the correlation between repeated measures variables to input into G*Power. The Pearson correlation between mean RT for repeat-allo and switch-to-allo was .95 ($r(22) = .95$, $p < .001$, 95% CI [.88, .98]), resulting in an estimated power of .98 for a

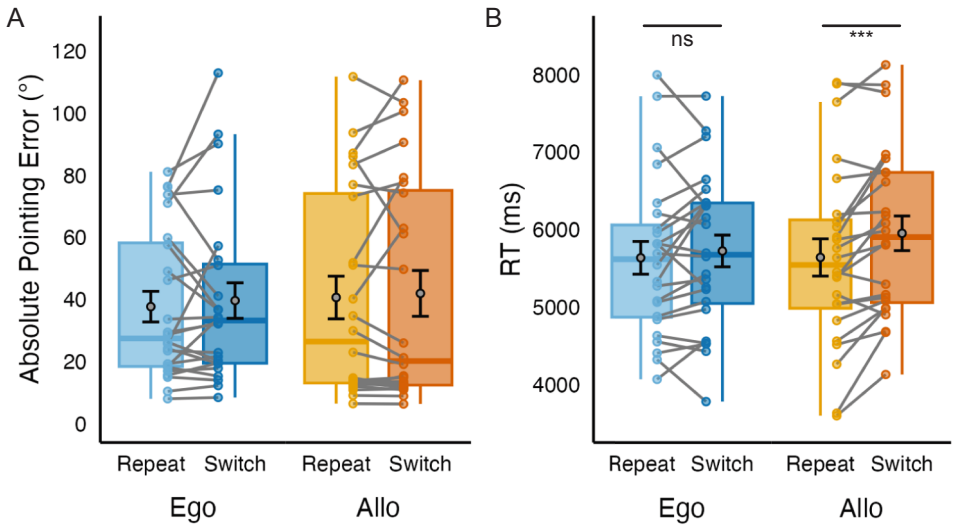


Fig. 3. *Accuracy and Response time Results. Note.* Panel A: There were no differences in absolute angular pointing error across Reference Frame (ego, allo) or Switching (repeat, switch). Panel B: For RT, there was a main effect of Switching and a Frame × Switching interaction effect; simple effects revealed significantly slower RT for trials when switching from ego to allo. Results are shown for trials from each reference frame (ego, allo) grouped by trials where the reference frame was repeated or switched relative to the preceding trial, indicating the four experimental conditions: repeat-ego (light blue), switch-to-ego (dark blue), repeat-allo (light orange), and switch-to-allo (dark orange). Boxes indicate the median and interquartile range. Upper and lower whiskers correspond to the maximum or minimum value, respectively, within 150% of the interquartile range. Gray dots indicate the mean with error bars showing the standard error of the mean. Individual participants' data points for each condition are shown in the corresponding color and connected for each participant across repeat and switch conditions. Ego: egocentric. Allo: allocentric. RT: response time. ns $p > .05$. *** $p < .001$.

Table 1
Pairwise Comparisons across Conditions for Response Time.

Comparison		M_{Diff}	$t(23)$	p	p_{corr}	95% CI	Cohen's d
Switch-to-Allo	Repeat-Allo	311.47	4.00	<.001***	.003**	[150.52, 472.41]	0.82
Switch-to-Allo	Switch-to-Ego	228.29	2.19	.039*	.232	[12.94, 443.63]	0.45
Switch-to-Allo	Repeat-Ego	316.45	3.04	.006**	.035*	[101.00, 531.90]	0.62
Repeat-Allo	Switch-to-Ego	-83.18	-0.70	.490	1	[-328.67, 162.30]	-0.14
Repeat-Allo	Repeat-Ego	4.98	0.05	.964	1	[-217.96, 227.92]	0.01
Switch-to-Ego	Repeat-Ego	88.16	0.98	.333	1	[-96.29, 272.61]	0.20

Note. p_{corr}: p-values after Bonferroni correction for six comparisons.
*$p < .05$. **$p < .01$. ***$p < .001$.

two-tailed test. On the other hand, the weakest effect for switch-to-allo trials was the comparison with switch-to-ego trials, where the significant correlation in RT between conditions ($r(22) = .89$, $p < .001$, 95% CI [.75, .95] resulted in an estimated .57 power. Thus, future studies seeking to replicate our observed interaction effect should recruit a sufficient sample size to power their tests.

3.2. Exploratory analysis from session 2: sense of direction as a covariate

We conducted an exploratory analysis to determine whether sense of direction moderated participants ability to switch between reference frames effectively. Participants' scores on the SBSOD ranged from 2.73 to 5.80 ($M = 4.06$, $SD = 0.90$). We reran the raw RT as an analysis of covariance (ANCOVA) using the afex::aov_ez function in R with the factorize flag set to FALSE, factors specified as factors, and the covariate specified as a continuous value and centered. The overall effect of the covariate was not significant ($F(1, 21) = 2.67$, $p = .117$, $\eta_p^2 = .11$). All results with the SBSOD covariate are shown in Table S2.

3.3. Exploratory analyses from session 1: pre-consolidation learning

To test exploratory hypotheses about spatial switching during learning and prior to consolidation, we repeated the same analyses using data from the first session, which comprised only four runs of the task interleaved with learning by wayfinding, as compared to the eight runs in session 2 with only a single wayfinding refresher prior and no other tasks interleaved.

3.3.1. Accuracy: absolute angular pointing error

Accuracy data was analyzed using the same aligned rank transform ANOVA procedure. Accuracy results mirrored those observed for session 2 with no effects reaching significance: Frame ($F(1,23) = 0.54$, $p > .250$), Switching ($F(1,23) = 0.09$, $p > .250$), Interaction ($F(1,23) = 1.56$, $p = .224$).

3.3.2. Response time (RT)

For RT, none of the planned transformations resulted in models meeting the assumptions of ANOVA, so rank aligned transformation was applied. Like session 2, we observed an interaction ($F(1,23) = 8.58$, $p = .008$) and no main effect of Frame ($F(1,23) = 4.22$, $p = .052$). Unlike for session 2, we did not observe a main effect for Switching ($F(1,23) = 1.92$, $p = .179$). Follow-up pairwise Wilcoxon tests showed that participants were slower to respond on switch-to-allo trials compared switch-to-ego trials. A difference from switch-to-allo trials did not reach significance for repeat-ego trials and did not survive multiple comparison correction for repeat-allo trials. Session 1 RT results are shown in Fig. S4

and Table S3. Results for both accuracy and RT across the entire experiment (all sessions and runs) are shown in Fig. S5.

4. Discussion

In this experiment, we sought to validate behavioral predictions based on our interpretation of a prominent neural model of spatial cognition, the BBB model (Byrne et al., 2007). Specifically, we tested whether switching between memory tasks that rely on primarily egocentric or allocentric reference frames resulted in significant accuracy or RT costs and whether the direction of this switching mattered. Our results partially support the existence of a cognitive transformation process predicted by the BBB model (significantly slower RT with preserved accuracy; H1b). However, this finding comes with the important caveat that this transformation is behaviorally borne out in reference frame switching that is either not bi-directional or at least not symmetrical (significantly slower RT only for the subset of allocentric trials that were preceded by an egocentric trial, absent any overall performance difference across egocentric and allocentric tasks; H2c).

One possible explanation compatible with BBB is that allocentric-to-egocentric switching may still rely on the same processes and brain regions (e.g., retrosplenial cortex), but that inverting this transformation is more computationally demanding, which could perhaps be demonstrated through computational modeling. For example, neural network models tasked with recreating top-down and first-person views revealed latent variables that more closely resembled place-like codes when reconstructing first-person from top-down, while latent variables that more closely resembled head-direction-like codes when the reconstruction was reversed (Xing et al., 2022).

Another, more complex explanation could be that differences in switching direction arise from the degree of afferent or efferent connectivity between posterior parietal cortex and MTL via retrosplenial cortex or another posterior medial region that supports this transformation. For example, macaque retrosplenial cortex features greater efferent and afferent connectivity with the hippocampal formation compared to posterior parietal cortex (Kobayashi & Amaral, 2003, 2007). Future studies using diffusion MRI would provide valuable insight on this question. This anatomical connectivity relationship with the hippocampal formation and posterior parietal cortex is opposite for the posterior cingulate cortex. This suggests that retrosplenial and posterior cingulate cortex may work together to handle bi-directional transformation, but it is difficult to compare these to rodent models, which are the basis for BBB (Alexander et al., 2023). It may also be that other brain regions mediate this process through attention or executive functions. Another possibility is that egocentric-to-allocentric and allocentric-to-egocentric switches are relatively independent of one another, which would be consistent with previous behavioral studies on reference frame abstraction and switching (Harris et al., 2012; Harris and Wolbers, 2014; Lv and Hu, 2020; Orti et al., 2023; Orti et al., 2024; Orti et al., 2025), but inconsistent with the BBB framework. Regardless, future neuroimaging research is vital to determine the specific region, regions, or neural patterns associated with reference frame transformation and switching, while considering directionality.

Another factor to consider for elucidating this process is aging, as previous work has shown effects when reference frames differ across encoding and retrieval (Ladyka-Wojcik et al., 2021). Failure to coordinate across reference frames is thought to underly cognitive decline in both healthy and neurodegenerative aging (Harris et al., 2012; Ijaz et al., 2019; Ladyka-Wojcik and Barense, 2020; Schaat et al., 2020; Tu et al., 2015), yet the behavioral and brain processes that support spatial reference frame switching even in healthy adult humans remain poorly understood. Humans have demonstrated the ability to acquire and utilize both reference frames, seemingly simultaneously, but the degree to which each is used has been observed to vary across task demands, individuals, and experience (Foo et al., 2005; Gramann et al., 2005; Iglói et al., 2009; Nett et al., 2025; Starrett et al., 2023; Vijayabaskaran & Cheng, 2022; Zhang et al., 2014).

A number of spatial memory studies have reported higher memory error for allocentric tasks like the JRD compared to their egocentric counterparts (Starrett et al., 2019, 2023; Zhang et al., 2014). Here we find an interaction where RT in an allocentric frame is greater only when switching from an egocentric frame, absent a main effect of reference frame (egocentric versus allocentric) on accuracy or RT. Given how previous studies have suggested that allocentric tasks may be more difficult than egocentric tasks (e.g., Zhang et al., 2014), it is noteworthy that our effort to equate spatial information available across each reference frame resulted in more comparable performance. While the absence of a main effect of reference frame may seem contradictory to previous studies, we believe this is related to the degree to which the available information was equated across the two tasks. Typically, egocentric tasks provide a full viewpoint for participants, with several variations on its extent (e.g., participants can look around) and duration (some background or landmark information is hidden after a period), while allocentric tasks often provide no visual information from the environment ("Imagine standing at A, facing B; point to C"). In contrast, in both our memory tasks, participants use an established vector between a single visible landmark and a location 10m in front of it, before indicating the relative vector of a second cued target. Equating the difficulty of the tasks increases our confidence in the RT findings being related to switching between reference frames and not to other factors.

4.1. Limitations and gaps to be addressed in future studies

It is important to note, that while our simple effects analysis only revealed a significant response time cost for egocentric-to-allocentric switching, the lack of a significant difference for allocentric-to-egocentric switching is not evidence that there is no cost for this condition. Indeed, the simple effects analysis was triggered by the presence of an interaction with a relatively small effect size near the threshold for statistical significance. If researchers wish to explicitly test for asymmetry in switching, they should consider powering their design to detect the smallest possible effect of allocentric-to-egocentric switching. Our exploratory pairwise comparisons (Table 1) provide some evidence that response time effects were selective for the switch-to-allo condition, but not all comparisons survived multiple comparison correction. Nonetheless, the effect of response time cost for switch-to-allo relative to repeat-allo that we observed was robust and suggest this may be the best test case for brain mechanisms related to reference frame switching. Another consideration is whether an alternative to the navigation learning task (e.g., studying maps) might elicit stronger effects for allocentric-to-egocentric switching instead (Richardson et al., 1999; Starrett et al., 2019, 2023).

While a lack of differences between egocentric and allocentric could indicate a shared strategy (e.g., recall information from an egocentric first-person perspective and project it into a top-down perspective for allocentric trials), we feel this is more likely an effect of removing differences in spatial information typically confounding behavioral comparisons of egocentric and allocentric spatial memory tasks in humans (Zhang et al., 2014). Other studies have use pupillometry in addition to RT as an index for cognitive load or processing (de Condappa & Wiener, 2016; Orti et al., 2025), which was not available in the present study. Extending these results using immersive virtual reality and eye tracking would thus provide richer data to disentangle the cognitive mechanisms underlying these behavioral effects. Disentangling how perceptual affordances (e.g., imagined heading versus a viewpoint) contribute to the deployment of egocentric or allocentric reference frames remains an important question and may have implications for how spatial switching is executed. However, examining this is beyond the scope of the current study aims. Here, we attempted to directly control and equate the amount of visual information presented while encouraging participants to utilize different reference frames (see Han et al., 2012; Han & Becker, 2014; Starrett & Ekstrom, 2018).

Navigation is a complex behavior involving multisensory integration and relying on other cognitive functions such as attention and working memory (Blacker et al., 2017; Garden et al., 2002; He et al., 2021; Li et al., 2024; Meneghetti et al., 2016a; Meneghetti et al., 2016b; Meneghetti et al., 2021; Piccardi et al., 2014; Plancher et al., 2018; Weisberg & Newcombe, 2016). Indeed, our novel spatial memory switching paradigm was inspired by task switching literature, for which working memory is particularly important (Baddeley et al., 2001; Liefooghe et al., 2008; Monsell, 2003). Even for well-learned or consolidated information, working memory may be crucial for manipulating spatial information online across reference frames. Thus, one limitation that should be considered in future studies is the inclusion of measures of working memory such as N-back or span tasks (Burgoyne et al., 2024). Additionally, representations in working memory can be modulated by the focus of attention and whether or not an item will continue to be relevant for future behavior (LaRocque et al., 2013; Lewis-Peacock & Postle, 2008; Rose et al., 2016). Connecting reference frame switching with models of attention, working memory, and even temporal sequencing (for the latter, see Tarder-Stoll et al., 2024) will provide valuable insight for our understanding of spatial transformations in the brain.

Another limitation was that our design may have been more sensitive to task-set differences – recalling various spatial details by drawing more on egocentric or allocentric representations – rather than the actual coordinate transformation (e.g., where observer is the origin for egocentric as opposed to an environmental landmark or anchor for allocentric) of specific spatial details between egocentric and allocentric frames. In our task, switch trials never repeated the same spatial prompt (facing the bookstore, rotate to the gym). Future studies may benefit from comparing this paradigm to perspective taking tasks such as the spatial orientation task (SOT; Friedman et al., 2020; Hegarty & Waller, 2004; Kozhevnikov & Hegarty, 2001) or immersive viewpoint transformation task (iVTT; C. He et al., 2022). Additionally, incorporating directed transformations for the same spatial prompts into our switching task may help disentangle these processes. It will be important to determine whether these are fundamentally different cognitive processes and whether they rely on distinct brain regions or networks.

A methodological limitation of the study was that some data was compromised due to issues with training study team members on proper data collection procedures to ensure participants were complying with task instructions. Quality checks and objective benchmarks for assessing viability, such as permutation tests to assess chance performance, ensured that only high-quality data were analyzed. However, more quality assessments during data collection (e.g., a report on proportion of non-response trials after each run) would serve to prevent such issues.

While we believe the inclusion of both repeat and switch trials for each reference frame should account for participants potential strategy preference, perceptual differences, or mental rotation for one reference frame or another, we cannot definitively disentangle differences due to task-switching more generally from differences due to reference frame switching. To rule this out, future work should compare spatial reference frame switching to task switching in non-spatial memory. In line with this, it is also worth noting that we only tested reference frame switching across separate retrieval episodes. In contrast, models such as BBB were likely formulated to account for within-retrieval transformations, which we did not test. Perhaps one way to partly address this would be having trials that maintain a constant heading across retrieval episodes/trials. Requiring reference frame transformations within a single retrieval episode will require additional new and clever behavioral paradigms, which might not be possible (see Alexander et al., 2023).

4.2. Conclusions

These results advance our understanding of how spatial transformations support the flexible redeployment of information across reference frames in large-scale, naturalistic environments. Inspired by neural models of reference frame transformations (Byrne et al., 2007), we formalized and tested explicit predictions related to trial-by-trial reference frame switching across retrieval episodes. Our findings provide evidence for a significant and selective cost in processing time when shifting to an allocentric frame of reference relative to a previous spatial memory retrieval episode, which has important implications for how humans coordinate spatial knowledge across egocentric and allocentric reference frames as well as the tasks used to assay these representations. These results also raise several exciting questions about how spatial reference frame switching is implemented in the human brain and behavior. Future studies utilizing this or other human reference frame switching paradigms should carefully consider factors such as what type of spatial environment was learned (vista, environmental), how it was learned (directed exploration versus maps), the amount of spatial information available during memory testing, the extent and fidelity of the learned representations, and how the spatial information being assayed may have changed with the reference frame switch (entirely new memory retrieval, new location, or new orientation). The latter example may be a particularly fruitful direction of study, given that executive functions like task sets, strategy-use, and decision making certainly co-occur with the demand for explicit spatial transformation operations; this aspect is not often discussed in the context of the influential BBB model. Our experimental design and results serve to better connect theories of spatial cognition with literature on episodic memory, particularly regarding learning and consolidation of knowledge acquired while navigating (Alexander et al., 2023). Future neuroimaging experiments will provide valuable insight into the neural mechanisms that underly asymmetric cognitive costs of spatial reference frame transformations and switching in regions including retrosplenial cortex. Thus, this work is an important first step in closing the loop between spatial cognition research and neural models of spatial processing.

Open practices statement

The data and analysis code are available at https://osf.io/edbyx/. Unity tasks were built with the open-source Landmarks package available at https://github.com/mjstarrett/landmarks, and precompiled executable applications for Windows or macOS are available upon request. The computerized SOT (as well as the original version of the SBSOD not used in this experiment) is freely available from https://hegarty-lab.psych.ucsb.edu/resources. Printouts of the Video Game Questionnaire, SBSOD, Background Questionnaire, and Post-Experiment Questionnaire that were administered via QuestionPro are included as appendices in the supplemental materials (Appendix S1-S4, respectively). The experiment was not preregistered.

Declarations

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Ethics approval

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards. The study was approved by the Institutional Review Board at the University of California, Irvine.

Consent to participate

All participants gave their written, informed consent prior to their inclusion in the study.

Consent to publish

All participants gave written, informed consent for their de-identified data to be published and shared.

Availability of data and materials

The datasets and code associated with this study were made available upon publication via an Open Science Framework (OSF) repository, https://osf.io/edbyx/. A view-only link to the anonymized repository was made available during the peer-review process, https://osf.io/edbyx/overview?view_only=a2fe69a431f5492fae7b88174b4677bf.

CRediT authorship contribution statement

Michael J. Starrett: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Craig E.L. Stark:** Writing – review & editing, Supervision, Methodology. **Elizabeth R. Chrastil:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.brainres.2026.150637.

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