

Naturalistic movements enrich episodic memories but not their spatiotemporal structure[☆]

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ABSTRACT

It remains unclear how episodic memories, our memories for past events, are generated from the rich sensory details encompassing everyday experience. Here, 40 healthy young participants navigated in a large-scale virtual environment under two conditions: an immersive-ambulatory condition, in which participants walked on a treadmill with full-body motion and head turns, or a restricted-movement condition, in which participants used a hand-held joystick to control gaze and position in virtual-reality while standing still. Participants then freely recalled their experience navigating in the virtual town. Analysis of verbal narratives revealed a double dissociation such that ambulation resulted in more detailed episodic elaborations, particularly those grounded in a first-person perspective, whereas restricted movement promoted more generalized spatial elaborations, particularly those not anchored to participants' point of view. These findings suggest that bodily cues contribute to the construction of episodic memory, while their absence may redirect attention toward external features of the environment. Participants also judged the relative direction of landmarks (space) and reproduced the amount of time they had spent navigating (time); however, objective indicators of spatiotemporal memory did not vary based on condition and, with one exception, did not correlate with subjective measures of memory quality. Together, these results suggest that the construction of vivid episodes is not necessarily tied to the precision of spatial and temporal encoding.

1. Introduction

How episodic memories are generated from the rich sensory details that encompass our everyday experiences remains unclear, for example, remembering the last time we had dinner with a friend. Tulving's original formulation of episodic memory suggested its fundamental rooting in space and time, and emphasized first-person mental time travel as a foundational property (Tulving, 1993, 2002). For example, an episodic memory could involve remembering the restaurant where we met a friend recently and being able to re-experience some of the event. According to this and related models (Bellmund, Gärdenfors, Moser, & Doeller, 2018; Buzsáki & Moser, 2013; Chandra, Sharma, Chaudhuri, &

Fiete, 2025; Eichenbaum, 2017; Ekstrom & Ranganath, 2018; Hassabis & Maguire, 2007), space and time should serve as a scaffold for organizing episodic memory, with these two important dimensions acting as a diagnostic feature of rich event-related recall. Another model of episodic memory suggests the importance of sensory and conceptual "channels," emphasizing the importance of how these channels are integrated, with spatial and temporal information comprising two of many channels (Rubin, 2006). Although episodic memories are commonly associated with specific instances in space and time, non-spatiotemporal details could be sufficient to enhance memory quality through external (sensory) or internal (conceptual) organization (Fan, Sokolowski, Rosenbaum, & Levine, 2023; Kensinger & Schacter, 2006; Rubin &

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Umanath, 2015). Resolving the basis for episodic memory formation remains an important yet largely unresolved question in psychology.

While aspects of space and time are undoubtedly important to episodic memory (e.g., remembering the restaurant where you met your friend and the order of events involved), defining what is meant by “space and time” has been more difficult (Ekstrom & Hill, 2023; Gauthier & van Wassenhove, 2016a, 2016b). The fields of spatial navigation and time perception offer well-tested and developed measures of space and time (Brown, 1997; Glicksohn & Hadad, 2012; Huffman & Ekstrom, 2019a; Waller & Hodgson, 2006) although how these relate to the episodic memory elaborations (scored using methods like the autobiographical interview [AI], see Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002) is less clear (Ekstrom & Hill, 2023; Fan, Abdi, & Levine, 2021; Fan et al., 2023; Levine et al., 2002). For example, spatial navigation research has often employed measures of path accuracy (e.g., path directness) and knowledge about the relative directions of landmarks (termed the “judgments of relative direction task,” JRD task) as a means of determining spatial knowledge (Huffman & Ekstrom, 2019a; Waller & Hodgson, 2006). Similarly, the field of time perception has relied on measures of temporal interval duration (often measured with the temporal error ratio, a measure of accuracy, and the coefficient of variation (CV), a measure of precision; Mioni, Stablum, McClintock, & Grondin, 2014). Based on the idea of the cognitive map, some models of navigation and episodic memory assume a close correspondence between knowledge gained through navigation and the development of episodic memory (Bellmund et al., 2018; Chandra et al., 2025; Gauthier et al., 2020). Yet, how these widely employed dependent measures of space and time, which index spatial knowledge and temporal perceptual memory, relate to the spatiotemporal organization of episodic memories, remains unclear.

To address these issues, we designed a paradigm in which participants freely navigated a large-scale virtual environment, allowing us to carefully track their movements in space and control what they experienced visually. Participants were then probed on spatial and temporal knowledge using the JRD and temporal interval reproduction tasks, followed by spontaneous verbal elaboration of the most recently experienced route. Participants were assigned to two different conditions: one in which they navigated by walking on an omnidirectional treadmill, providing them with a rich set of body and head movements, and a second in which they navigated the same environment but with a handheld controller, restricting vestibular and proprioceptive input. Our primary hypothesis was that sensory input would play a fundamental role in enriching episodic memories, such that subjects in the immersive-ambulatory (IA) would exhibit more detailed episodic memories than those in the restricted-movement (RM) condition. Such an effect might be explained by naturalistic movement conferring a benefit to spatiotemporal encoding (Holmes, Newcombe, & Shipley, 2018; Taube, Valerio, & Yoder, 2013), or alternatively by a direct effect of proprioceptive input on episodic memory (Fig. 1C). Adjudicating between these two possibilities, our second main hypothesis relates to potential overlap between spatial navigation, time perception, and episodic memory. If these three constructs share significant overlap (Buzsáki & Moser, 2013; Chandra et al., 2025), then we expect a correlation between the evolution of spatiotemporal knowledge and the extent of episodic detail in participants’ free recall narratives. Alternatively, we may find that spatial and temporal knowledge develop independently of episodic richness, consistent with models emphasizing the partial independence of episodic memory from navigation (Ekstrom & Hill, 2023; Fan, Abdi, & Levine, 2021). Such a dissociation would also align with models highlighting the reconstructive nature of episodic memory (Iriye & St Jacques, 2021; Schacter, Addis, & Buckner, 2007) and the extent to which distortions of temporal structure (e.g., dilation or compression) can be adaptive for future-planning (Friedman, 1993; Schacter, Guerin, & St. Jacques, P. L., 2011). Overall, resolving these issues is fundamentally important to understanding how episodic memory relates to sensory and spatiotemporal dimensions of experience.

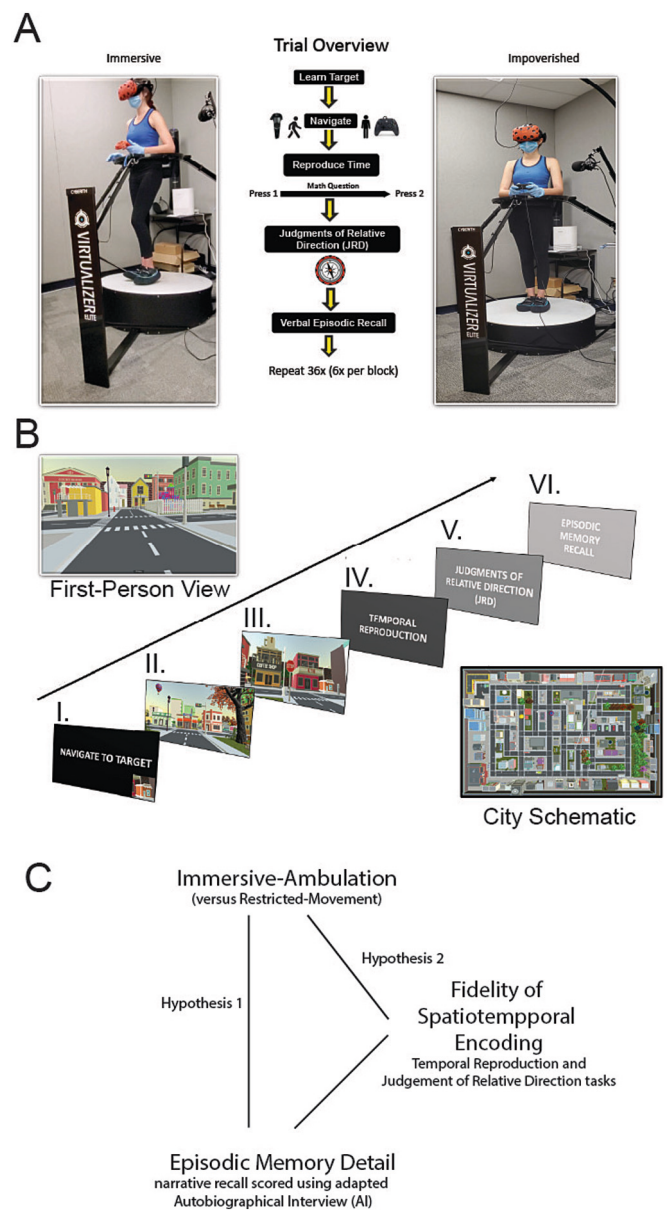


Fig. 1. Study Design. (A) Participants completed the experiment in one of two navigation conditions: the immersive ambulatory (IA) condition (left), or the restricted movement (RM) condition (right). Both conditions featured a head-mounted display (HMD) rendering the virtual environment, but only the IA condition allowed for ecologically valid, self-directed ambulation. (B) Overview of the trial phases. Each trial comprised five key steps: (I) Target Learning, in which participants memorized the location of a target landmark; (II) navigation, in which participants attempted to reach the target, shown in (III), within a virtual town; (IV) temporal reproduction, in which participants estimated duration by holding a button for as long as they perceived the navigation to have taken; (V) judgments of relative direction (JRD), in which participants mentally oriented themselves within the town and pointed to other landmarks; and (VI) episodic verbal elaboration, in which participants verbally recounted their navigation experience. (C) The paradigm was designed to reveal whether naturalistic head and ambulatory movements (between-groups manipulation) result in more detailed episodic memory of recent experience of navigating a virtual town (hypothesis 1), with scores related to episodic memory derived from a grading schema adapted from the Autobiographical Interview (AI). Improved episodic detail in the immersive ambulatory (IA) condition may be explained by a benefit of proprioceptive input to spatiotemporal encoding, which would result in participants in the IA condition exhibiting improved performance on tests of spatiotemporal memory such as temporal reproduction and judgements of relative direction tasks (hypothesis 2).

2. Methods

2.1. Participants

Forty healthy young participants were recruited for this study, with equal numbers (20) assigned to each of the two experimental conditions (IA vs. RM). Participants were compensated \$20/h for their time. The final sample consisted of 24 females and 16 males, balanced across conditions, aged 18 to 30 years. All participants provided informed consent in accordance with the Institutional Review Board at the University of Arizona.

2.2. Materials and apparatus

The virtual environment for this study was a simulated town created using the Landmarks 2.0 software package (Starrett et al., 2021) within the Unity version 2.0 game engine (Unity Technologies, San Francisco, CA). The town layout incorporated multiple landmarks and designated target locations, allowing for an IA navigation experience. Across trials, participants were assigned randomized starting locations within the town, with 64 possible start locations. This ensured that they approached each target from multiple distinct start points. The target identities (e.g., grocery store, gas station) varied each trial, thereby involving new routes every trial.

As shown in Fig. 1A, participants experienced one of two navigation conditions: a treadmill-based navigation condition (immersive ambulatory, IA) or a joystick-based navigation condition (restricted movement, RM). Participants were prospectively assigned to either condition in a counterbalanced manner. In both conditions, participants wore an HTC Vive head-mounted display (HMD) to view the virtual environment. Participants in the IA condition navigated by physically walking on a Cyberith Elite 2.0 treadmill (Starrett, Stokes, Huffman, Ferrer, & Ekstrom, 2019), allowing for ecologically valid self-directed motion through the virtual town. In this treadmill-based setup, view direction was controlled naturally by head movements, providing vestibular and proprioceptive cues that closely resembled real-world navigation. In the RM condition, participants used a hand-held Xbox-controller to direct their movement in the virtual town. The controller's left thumbstick controlled translational movement while the right thumbstick controlled rotational view. Critically, head tracking technology was disabled to prevent participants from adjusting their view direction in the HMD. As such, both conditions permitted self-directed movement, with the critical difference being a much greater range of head and body movement in the IA condition.

2.3. Procedure

The experimental procedure began with 6 practice trials, during which participants used an on-screen target-guided compass to navigate between specific targets. This practice phase familiarized participants with the layout of the virtual town and treadmill or joystick movement. Following the practice session, participants completed 36 trials across 6 blocks of navigating to prompted targets. Each trial encompassed five key phases: target learning, navigation, temporal reproduction, judgments of relative direction (JRD), and verbal episodic elaboration (Fig. 1B).

At the beginning of each trial, participants were presented with a target location and were required to reach the designated location from memory. A maximum of 5 min were allotted for each navigation attempt. If a participant exceeded this time, a compass appeared on the screen directing them to the target. Trials in which participants relied on compass guidance were considered failures and were excluded from further analysis. The exclusion rate did not differ by condition, with participants in both IA and RM completing an average of 31/36 trials.

After reaching the target, participants performed a temporal reproduction task to estimate the duration of their navigation. For this task,

they were instructed to hold down a button on the hand-held controller for as long as they subjectively remembered navigating. This provided an estimate of temporal interval and was used to generate performance measures related to time. This included the temporal error ratio, which reflected the accuracy of the temporal interval estimate on a given trial, and the coefficient of variation (CV), which reflected the degree of variance in temporal estimates across trials (Mioni et al., 2014).

Following the temporal reproduction task, participants performed the judgments of relative direction (JRD) task, which probed spatial memory. In this task, participants responded to prompts that required them to mentally position themselves at a specific landmark in the virtual town and point to another location based on this imagined orientation. For example, a prompt might read: "Imagine yourself standing in front of the grocery store, facing the pet shop. Now, point to the post office." Participants then used their controller to adjust a compass arrow pointing to where they thought the final object was (e.g., post office), with lower absolute angular error (degrees) being associated with better spatial memory. This measure has also been taken as a reflection of allocentric spatial knowledge and correlates strongly with map drawing accuracy (Huffman & Ekstrom, 2019a).

The final phase of each trial involved episodic verbal elaboration (i.e., free recall) in which participants verbally recounted their navigation experience. Participants were prompted to recall aloud everything they remembered about navigating to the previous target. These verbal reports were later analyzed using the autobiographical interview (AI) scoring method (Levine et al., 2002), which categorized verbal content into several categories. These included episodic details (such as references to specific times, places, and perceptual experiences), and semantic or miscellaneous details (such as general allocentric or semantic references, or references to non-event details or emotions).

2.4. Scoring of verbal episodic elaborations

We adapted the system for scoring the episodic quality of verbal free recall originally developed by Levine et al. (2002). This scoring system categorized segments of verbal recall into two broad categories: episodic details, which pertain directly to specific autobiographical events anchored in space and time, and semantic/miscellaneous details, which include generalized semantic knowledge or other miscellaneous content not tied to the main event that is being probed. Unlike Levine et al. (2002), however, which focused on memory for salient autobiographical events (e.g., "seeing a famous person"), our study examined memory for navigating a virtual environment after a brief delay. We thus adapted the original grading system to better capture the nuances of memory recall in our task. While maintaining the broad category distinction between episodic and non-episodic elaborations, we added subcategories relevant to navigation such as egocentric (capturing memory for body-based perspective, e.g. "I turned left at the park") and allocentric (capturing memory for coordinates or 'birds-eye' perspectives of external landmarks, e.g. "The park was south of the school"). Egocentric details were included within the larger episodic category, as they entailed event-specific memory tied to first-person experience. Allocentric details, in contrast, were included in the larger semantic/miscellaneous category as they reflected generalized, schema-like spatial knowledge that was likely abstracted across multiple encounters with landmarks in the environment. No sub-category counted towards both the broader episodic and semantic/miscellaneous categories and these categories were therefore independent from one another. See Table 1 for a full list of subcategories within the broader episodic and semantic/miscellaneous categories. Further details on how this grading system deviates from the original AI, as well as sample graded memory recall transcripts, can be found in supplemental materials.

To account for the fact that differences in episodic memory quality are reflected not only in the tally of verbal elaborations but also in the detail contained in each elaboration, we rated each elaboration on a 1-to-3 scale. A score of 3 reflected richly detailed, specific content tied to a

Table 1

List of verbal free recall components contributing to episodic (event-specific) and semantic/miscellaneous (non-event specific) memory, adapted from Levine et al. (2002) to address the specific demands of evaluating memory recall in a virtual navigation context. Categories marked by * were not in the original Levine system for grading autobiographical memory interviews (AMI).

Broad Category	Subcategory	Description
Episodic	Visual	References to visual details of the environment (e.g., “I saw a large tree”).
Episodic	Place/Spatial	References to specific locations or spatial landmarks tied to the event (e.g., “I reached the gas station”).
Episodic	Time/Duration	Mentions of temporal elements, such as time of day, sequences, and elapsed time (e.g., “It took about two minutes to reach the park”).
Episodic	Egocentric*	References to the subject’s bodily movements or egocentric spatial orientation during navigation (e.g., “The bank was to my left”).
Episodic	General Event	Broad descriptions of the virtual reality experience without anchoring to specific places, times, or sensory details (e.g., “I spawned in the Virtual Town”).
Semantic/Misc.	Semantic	Generalized, factual knowledge, typically of the environment, but not necessarily reflecting a map-like frame of reference (e.g., “The bank is near the park”).
Semantic/Misc.	Allocentric*	Spatial references using an objective or map-like frame of reference (e.g., “The bank was north of the park”).
Semantic/Misc.	Emotion/Thought (Memory Confidence)	Subjective statements about memory confidence or emotional evaluation of recall (e.g., “I’m not sure where I was at that point”).

unique moment in the navigation experience, whereas a score of 1 reflected vague or generic statements. For instance, an episodic detail such as “I saw a car” received a score of 1, while “I saw a blue police car as I turned the corner near the diner” was rated a 3 due to its visual detail and spatiotemporal grounding. Semantic/miscellaneous details were rated using the same scale, acknowledging that generalized statements can still vary in complexity (e.g., “The park was somewhere near the store” vs. “The park was north of the school and east of the bank”). Final memory scores were calculated by summing ratings within episodic and semantic/miscellaneous categories, as well as their constituent subcategories. Unlike the original AI, which features a more free-form recollection prompt, this paradigm prompted participants to recall a specific recent experience. The potential for freely recalled verbal statements to contain both internal and external details motivated our decision to analyze verbal subcategories (e.g., egocentric vs. allocentric) as dependent variables of interest. This was also relevant to our broader question about how spatial navigation, which can include allocentric and egocentric strategies, relates to episodic memory. By separating allocentric and egocentric components of responses, this approach allowed for a more precise comparison of the difference in memory quality between conditions, rather than relying solely on the broader episodic versus semantic distinction, which was sometimes ambiguous at the sentence level. Nonetheless, we included “egocentric” details in the broader episodic category because this represented single event experiences while “allocentric” elaborations were included in the broader semantic/miscellaneous category because they were typically extracted over many different experiences.

Graders were blind to participants’ condition and there were zero counts of participants in the RM condition mentioning ‘joystick’ or subjects in the IA conditioning mentioning ‘treadmill,’ which might have revealed condition.

2.5. Analysis

2.5.1. Variables

Two graders parsed participants’ verbal episodic elaborations and tallied the scores associated with subjective elaborations across each AI subcategory (e.g., visual, allocentric). Aggregate sums of episodic and semantic/miscellaneous ratings were used as primary variables of interest in analyses. A permutation-based statistical test compared compared aggregate episodic and semantic/miscellaneous cumulative scores between graders. Inter-rater reliability, assessed via intraclass correlation (ICC), indicated statistically significant agreement ($ICC = 0.827$, 95 % CI = [0.796,0.853], $p < .001$) for episodic and semantic category scores across all trials and subjects. For new subcategories related to navigation, agreement was higher for egocentric ($ICC = 0.737$, 95 % CI = [0.673,0.789], $p < .001$) than allocentric elaborations ($ICC = 0.438$, 95 % CI = [0.271,0.562], $p < .001$). Objective measures included absolute angular pointing error in the JRD task, excess path based on the navigation data, temporal reproduction accuracy, coefficient of variation (CV), and temporal order accuracy, which was based on the order of mentioned locations during free recall. Details pertaining to calculation of objective indices can be found in supplemental methods.

2.5.2. Analysis

We employed a mixed-effects approach to examine how the two conditions (IA vs. RM) influenced episodic versus semantic memory styles. Specifically, we tested the effect of condition on the cumulative scores for episodic vs. semantic/miscellaneous elaborations per trial, while accounting for participant variability as a random effect. Rather than treating scores for episodic and semantic/miscellaneous elaborations as separate dependent variables, we structured the data such that each trial contributed to two observations—one per memory category—allowing for direct comparisons within a unified model. Condition (IA vs. RM) and memory category (episodic vs. semantic) were modeled as fixed effects. The interaction-term (condition $\times$ memory category) was included to potentially reveal whether conditions were associated with a double dissociation in recall style (episodic vs. semantic dominance differing by condition).

Following this aggregate-level analysis, we conducted separate mixed-effects models to examine condition effects on specific AI subcategories, treating subcategory-specific cumulative scores as dependent variables. Additionally, we tested whether memory styles evolved over time by including block (range: 1–6) as a predictor, assessing condition $\times$ block interactions as potential indicators of gradual shifts in reliance on episodic versus semantic elaborations. Finally, we applied the same mixed-effects approach to analyze the five objective measures—excess path, temporal order, JRD accuracy, temporal error ratio, and coefficient of variation (CV)—using condition as a fixed effect and participant as a random effect where applicable. False discovery rate (FDR) corrections to coefficient p -values accounted for multiple comparisons across AI subcategories and objective measures.

We further examined the relationship between subjective and objective measures by constructing correlation matrices to assess whether specific components of memory recall predicted spatial or temporal accuracy. Subject-wise averages of AI subcategories (e.g., visual, allocentric) and objective performance measures (e.g., excess path) were compared across 40 pairwise correlations, with FDR corrections applied for multiple comparisons.

To explore latent structures within memory recall, we conducted a principal component analysis (PCA) on eight AI subcategories, focusing on whether the resulting clusters aligned with experimental condition (IA vs. RM) or individual differences beyond condition. Subcategory scores were mean-centered and scaled (z-scored), and components were retained based on eigenvalues exceeding 1 and cumulative variance thresholds. We used k-means clustering to visualize memory patterns and assess whether subcategories formed distinct clusters corresponding

to condition or baseline individual differences in memory style. Further details on modelling procedures are provided in the supplemental materials.

3. Results

3.1. The immersive ambulatory-immersive (IA) condition enhanced event-specific verbal elaborations while the restricted-movement (RM) condition favored generalized and non-event details

We first tested the hypothesis that the condition manipulation (IA vs. RM) would influence the cumulative ratings of episodic vs. semantic/miscellaneous elaborations immediately following completion of the route. A mixed-effects ANOVA predicting the sum of subjective elaboration scores on a trial as a function of condition (IA vs. RM) and

category (episodic vs. semantic) revealed a main effect of category ($F(1,2423.95) = 167.16, p < .001$) and a significant interaction between condition and memory-category ($F(1,2423.95) = 361.46, p < .001$). Regarding the main effect of category, a post-hoc t -test revealed a greater likelihood for episodic as opposed to semantic/miscellaneous elaborations during free recall (4.47 episodic – semantic/misc., $t(2424) = 12.93, p < .001$). Regarding the interaction, post-hoc t -tests revealed a double dissociation (Fig. 2A) such that IA participants were more likely to make episodic elaborations (11.2 episodic – semantic/misc., $t(2424) = 22.96, p < .001$) and an opposing tendency for RM participants to make more Semantic/Miscellaneous elaborations (-2.1 episodic – semantic/misc., $t(2424) = -4.30, p < .001$).

Next, to understand whether this double dissociation in memory style emerged immediately due to the different interfaces (treadmill vs. joystick), or if it developed gradually (reflecting participants' learned

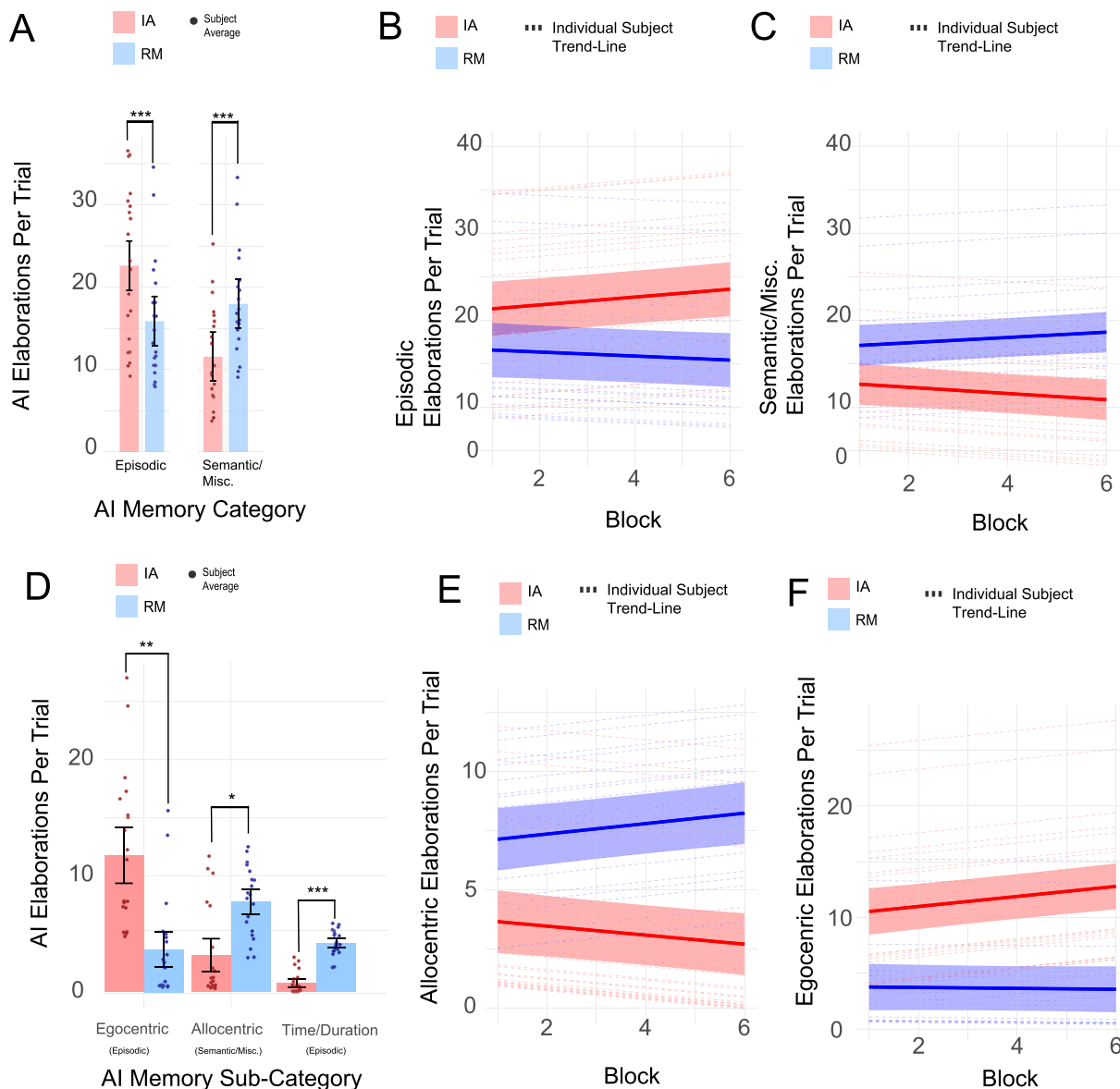


Fig. 2. Differences in memory retrieval strategies as a function of sensory enrichment. (A) Sensory enrichment (IA condition) resulted in a greater number of episodic memory details, while restricted movement (RM condition) yielded an opposing trend of greater semantic/miscellaneous memory details. (B) This double-dissociation was primarily driven by increased egocentric/body-based references in the IA condition, and allocentric spatial and temporal duration-based elaborations in the RM condition. (C–D) Over the course of the task, participants in the IA condition exhibited a progressive increase in the number of episodic details (C), while participants in the RM condition exhibited similarly gradual preference for semantic/miscellaneous elaborations, relative to participants in IA (D). (E–F) This progressive double dissociation in memory style was further characterized by increasing egocentric memory reliance in IA (E) and increasing allocentric references in RM (F).

and differential responses to the conditions), we employed models predicting the sum of episodic or semantic/miscellaneous scores per trial as a function of condition and block (range: 1–6). A mixed-effects regression predicting episodic elaborations per trial as a function of condition and block (range: 1–6) revealed a significant interaction ($F(1,1191) = 6.28, p = .0123$). Simple slopes analysis showed that IA participants showed an increase in episodic cumulative scores over time (Block 6 – Block 1: $+2.26, t(1192) = 2.35, p = .019$), while RM participants showed no corresponding change ($t(1192) = 1.20, p = .231$), as shown in Fig. 2B. A similar model for semantic/miscellaneous elaborations also revealed a condition and block interaction ($F(1,1192.44) = 6.18, p = .013$), though neither group showed a significant within-condition change from Block 1 to 6 (IA: $t(1192) = 1.9, p = .057$; RM: $t(1192) = -1.61, p = .108$). Between-group comparisons, however, showed that RM participants produced significantly more semantic/miscellaneous elaborations beginning in Block 2 ($+4.46$ per trial, $t(48.7) = 2.12, p = .039$) and increasing in magnitude through to Block 6 ($+7.77$ per trial, $t(45.7) = 3.77, p < .001$), as shown in Fig. 2C. Together, these findings suggest that detailed episodic elaborations increased selectively in the IA condition, while semantic/miscellaneous elaborations diverged progressively—decreasing in IA and increasing in RM over blocks of the experiment.

3.2. IA compared to RM differences in verbal elaborations were driven by specific sub-categories related to space and time

We next tested the hypothesis that the IA condition would result in an increased number of verbal elaborations related to space and time. We conducted seven mixed-effects ANOVAs for each subcategory (see Table 2), each model including condition (IA vs. RM) and block (1–6) as fixed effects. As shown in Fig. 2D, significant differences between conditions found in three of the seven subcategories, including allocentric (“north-south-east-west”) elaborations ($F(1,52.76) = 6.42, p_{\text{fdr}} = 0.038$), time/duration (“I walked for a minute”) elaborations ($F(1, 89.90) = 82.70, p_{\text{fdr}} < 0.001$) and egocentric (“I turned right”) elaborations ($F(1,51.09) = 10.89, p_{\text{fdr}} = 0.007$). The IA condition was associated with a greater number of egocentric details per trial ($+6.26, t(51.10) = 3.30, p_{\text{fdr}} = 0.007$). Egocentric statements constituted 48% of all elaborations among participants in IA and only 17 % among participants in RM. In contrast, the RM condition was associated with a greater number of elaborations related to allocentric navigation ($+3.06, t(52.76) = 2.53, p_{\text{fdr}} = 0.038$). Together, these findings suggest that the IA condition enhanced details in episodic elaborations by increasing the number of event-related egocentric references while the RM condition involved more general references to global coordinates (i.e., allocentric). Interestingly, time/duration elaborations were greater in the RM condition ($+3.71, t(89.90) = 9.09, p_{\text{fdr}} < 0.001$), suggesting that reduced sensorimotor feedback, while leading to fewer event-specific details overall, was associated with more detailed recollections related to temporal experience.

We then examined which specific subcategories contributed to progressive changes in verbal elaborations related to episodic or semantic memory (Fig. 2E and F), focusing on condition $\times$ block interactions in models predicting the number of allocentric and time/duration details on a given trial. There was a significant condition $\times$ block interaction for allocentric ($F(1,1192.08) = 10.31, p_{\text{fdr}} = 0.011$), egocentric ($F(1,1191.97) = 6.59, p_{\text{fdr}} = 0.041$) but not time/duration elaborations ($F(1,1194.54) = 1.37, p_{\text{fdr}} = 0.387$). For both the allocentric and egocentric models, post-hoc simple slopes analyses revealed a significant group difference at Block 1, with IA showing greater egocentric recall than RM ($+6.76, t(44.74) = 3.68, p = .002$) and RM showing greater allocentric recall than IA ($+3.47, t(45.58) = 2.98, p = .012$). Notably, the magnitude of these between-group differences increased over trials, as indicated by a stronger effect at Block 6 (Egocentric: $+9.21$ IA > RM, $t(42.88) = 5.07, p < .001$; Allocentric: $+4.80$ RM > IA, $t(43.49) = 4.80, p < .001$), suggesting that the progressive double-

dissociation in memory elaboration (with IA favoring episodic and RM favoring semantic/miscellaneous) may be driven by a similar gradual divergence in participants’ recall preference for egocentric (in IA) vs. allocentric (in RM) details.

3.3. The IA condition resulted in shorter paths but otherwise did not affect the objective accuracy of spatiotemporal memory

We next examined objective space and time variables to determine how they were affected by immersion and greater sensorimotor input by focusing on temporal accuracy (temporal order score, temporal error ratio, and Temporal CV), navigational efficiency (excess path), and spatial memory (absolute pointing error during the JRD). We modeled trial-level mixed-effects models with condition as a fixed effect for all variables except CV, which was analyzed using a t -test since it is computed as a single value per participant. Excess path differed by condition ($F(1,37.32) = 8.60, p_{\text{fdr}} = 0.023$), with excess path (in meters) significantly lower in Immersive-Ambulatory compared to Restricted-Movement (-21.02 m, SE = 6.28, $t(33.54) = -3.35, p_{\text{fdr}} = 0.010$), suggesting that participants took shorter paths overall in the Immersive-Ambulatory condition (Fig. 3). All other objective dependent measures did not differ between conditions (based on FDR correction): temporal error ratio ($F(1,37.98) = 0.112, p_{\text{fdr}} = 0.739$), temporal order score ($F(1,38.36) = 4.49, p_{\text{fdr}} = 0.08$), temporal coefficient of variance ($t(34) = 1.089, p_{\text{fdr}} = 0.284$), and JRD pointing error ($F(1,37.38) = 0.717, p_{\text{fdr}} = 0.537$). Among these measures, temporal order scores were observed to be near-ceiling (see table S1 in Supplemental Materials), which may have influenced the null result for this particular variable. The lack of a difference for JRD pointing error persisted when we excluded chance performing participants ($F(1,12.93) = p_{\text{fdr}} = 0.005$), based on Huffman and Ekstrom (2019b). To further examine potential relationships between subjective memory quality, as captured by the verbal subcategories adapted from the AI, and the measures of spatiotemporal accuracy, we conducted a series of bivariate correlations between each subjective and objective measure at the participant level (averaging scores across trials for each participant). After correcting multiple comparisons, no correlations remained significant, except for a negative relationship between egocentric elaborations and temporal order score ($r = -0.52, p = .004$, Fig. 3B). Post-hoc analysis revealed that the negative association between egocentric elaborations and temporal order score was limited to the IA condition (see Fig. S1 in Supplemental Materials).

3.4. Both individual differences and condition contribute to variability in episodic elaborations

To better understand the nature of the complex verbal elaborations provided by participants, we performed a principal component analysis (PCA). For each subject, we computed the average tally of scores per trial in each of the adapted Autobiographical Interview (AI) subcategories, resulting in an 8-dimensional feature vector per participant (time/duration, place, egocentric, visual, emotion, semantic, allocentric, and general-event). Tally averages were mean-centered and scaled (z-scored) prior to analysis, with the resulting 40 subjects $\times$ 8 feature matrix being submitted to PCA for dimensionality reduction. The first two principal components were selected for further investigation as they cumulatively accounted for a substantial proportion (>50 %) of the total variance. We found that the first principal component (PC1) explained 38.5 % of the variance, primarily reflecting individual variability in memory style. The second principal component (PC2) accounted for 24.1 % of the variance and was more closely aligned with the distinction between the IA and RM conditions.

We then applied k-means clustering to participants’ episodic recall data (Fig. 4A) to better understand PC2. To do so, we visualized a three-cluster solution as this was lowest number of clusters that revealed segregation in PC2, demonstrating a difference in memory style

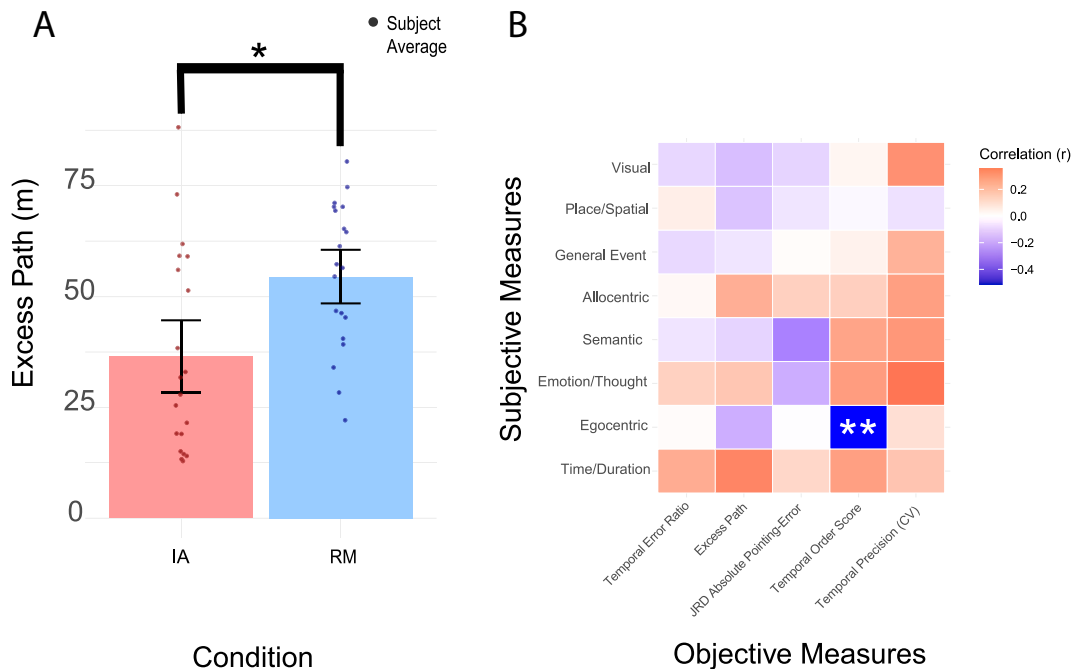


Fig. 3. Differences in objective performance measures by condition and their relationships with subjective memory dimensions. (A) Among objective navigation metrics, only excess path, a measure of navigational efficiency, showed a significant difference between conditions, with participants in the IA condition exhibiting more direct paths compared to those in the RM condition. (B) Across both conditions, there were no significant correlations between subjective episodic memory dimensions and objective performance metrics (with one exception between egocentric elaborations and temporal order score, see supplemental).

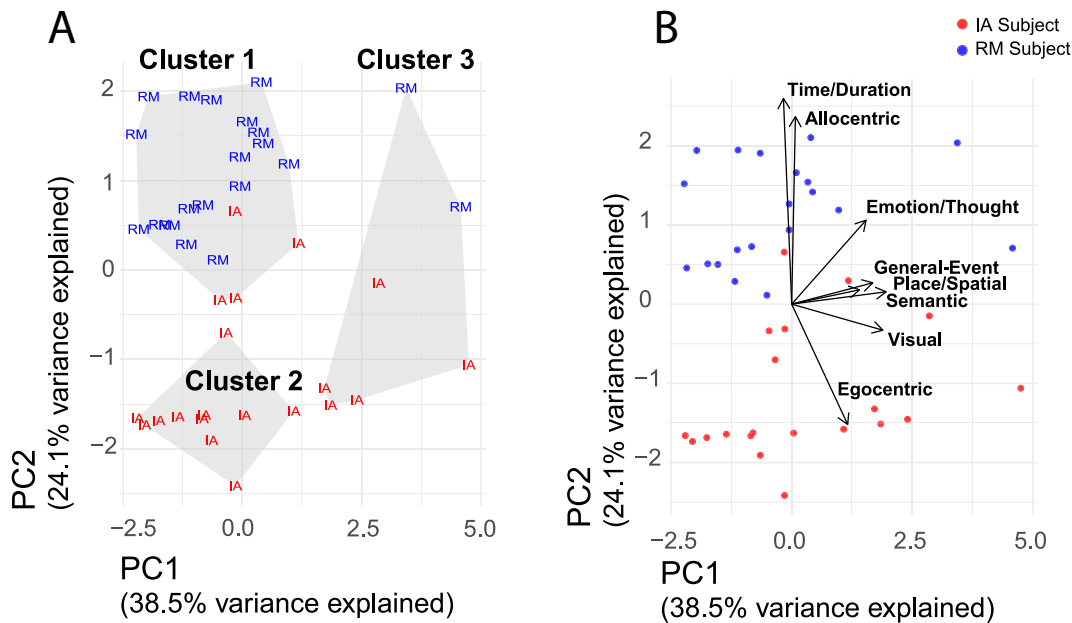


Fig. 4. Principal Component Analysis of latent variables in participants' memory recall styles. (A) Cluster analysis using K-means ($K = 3$) revealed that PC2 effectively differentiates participants by condition, with Cluster 1 and Cluster 2 largely segregating IA and RM participants. (B) The PCA biplot further examines the variables that load onto PC1 and PC2, showing that egocentric/body-based details load negatively onto PC2 whereas allocentric and temporal duration details load positively onto PC2. Meanwhile, visual, emotional, and place-related elaborations contribute more strongly to PC1.

depending on participants' condition. Notably, as shown in Fig. 4a, the k-means analysis revealed that two clusters (1 & 2) were non-overlapping within PC2, collectively captured 33/40 participants and segregated participants by condition with 88 % accuracy overall (cluster 1 featured 18/22 RM, cluster 2 featured 11/11 IA, while cluster 3 was undiagnostic with 5 IA and 2 RM). Owing to its displacement along PC1 from Clusters 2 and 3, Cluster 3 may capture a divergent memory style unrelated to the experimental manipulation.

To better understand the relationship between memory components and the experimental conditions, we examined the loadings of each subcategory of the AI onto PC1 and PC2 (see Table S2 in supplemental for all values). This allowed us to determine which subcategories were more associated with individual differences in recall style (PC1) compared to those that may have been influenced by the between-groups manipulation (PC2). The PCA biplot (Fig. 4b) provides a visual representation of these loadings. For PC1, we observed moderate

positive loadings for two categories within semantic/miscellaneous: semantic details (0.49) and emotion/thought references (0.39), suggesting that participants scoring high on PC1 tended to provide more generalized and emotionally elaborative recall. PC1 also showed moderate loading for several categories relevant to the broader episodic category, including visual details (0.49), place (0.34), and general event recall (0.42).

PC2 explained 24.1 % variance and was more aligned with experimental condition differences, with the strongest positive loadings found for Time/Duration (0.65) and Allocentric details (0.59). The PCA biplot (Fig. 4B) confirms that greater emphasis on temporal duration and external spatial references was characteristic of the RM condition. Conversely, egocentric details loaded negatively (-0.38), suggesting that elaborations about egocentric details were more prevalent in the IA condition. Notably, semantic, visual, and place-based elaborations showed weak or negligible loadings on PC2, further supporting that these memory elaborations reflected individual differences rather than experimental condition. PC2, which showed separation by condition, supports our earlier findings that sensory immersion (walking on a treadmill with a head-mounted display) enhances egocentric elaborations but, conversely, less immersion results in greater elaborations focused on allocentric cues and temporal durations and sequences.

Our earlier results suggested no statistically meaningful relationship between participant verbal elaborations measured with the AI and objective measures of space and time. To follow-up on those analyses, we conducted an additional PCA incorporating all objective and subjective measures. This PCA failed to yield a clear separation between conditions, and the variance explained by the first two dimensions fell below 50 %. This suggests weak and inconsistent correlations between measures of objective navigation and verbal elaborations, supporting our earlier mixed-effect regression results, which also showed a lack of a consistent relationship (Fig. 3B).

4. Discussion

Our findings suggest that naturalistic body and head movements during navigation enhance episodic memory richness, as participants in the IA condition provided progressively more highly-rated event-specific verbal elaborations than those in the RM condition. The immersive condition most strongly enhanced egocentric elaborations (“the park is on my right”), suggesting that body-based sensory inputs, such as vestibular, somatosensory, and proprioceptive feedback, were an important determinant of episodic richness. Although RM participants also made egocentric references, they were less frequent. Given that the IA condition increased the number of verbal elaborations specifically related to egocentric body turns, these findings are consistent with episodic memory involving input and integration through specific sensory channels, such as those related to somatosensory, proprioceptive, and interoceptive input (Rubin, 2006; Rubin & Umanath, 2015).

Interestingly, episodic richness in the IA condition was not associated with increased accuracy in objective measures of spatiotemporal reproduction. The only significant difference in objective measures was reduced excess path in the IA condition, possibly reflecting the greater physical effort required for treadmill walking. No correlations between objective measures of space and time and subjective measures of episodic or semantic details were significant, with one exception: IA participants who reported more egocentric details (e.g., related to turning) were less likely to sequence landmarks correctly. Although we do not have a ready explanation for this correlation, it could possibly relate to a greater focus on interoceptive information rather than external features of the environment in the IA condition. It is also possible that we were underpowered to detect meaningful correlations between objective and subjective variables, although this would also imply that these effect sizes were necessarily smaller. The lack of a correlation between any objective measures of space and time and episodic richness would support the idea that sensory-driven richness of

episodic memory may not directly correspond to accurate spatiotemporal memory, at least based on the measures commonly used in the fields of spatial navigation and time perception (Ekstrom & Hill, 2023; Fan et al., 2023; Iriye & St Jacques, 2021; Kensinger & Schacter, 2006; Palombo, Te, Checknita, & Madan, 2021). Instead, our results suggest that episodic memories are connected primarily to verbal elaborations and do not have a clear parallel with information learned as part of navigation (i.e., judgments of relative direction and excess path) or judgments of supra-second time perception (temporal error ratio and CV).

Surprisingly, increases in episodic richness also did not show a clear correspondence with the development of elaborations relating to spatiotemporal knowledge. While we found that allocentric and time duration verbal elaborations were different between conditions, these were greater in the RM condition. With regard to allocentric elaborations, one explanation is that attention was allocated away from body movements and toward external features of the environment (see also, Zhong & Kozhevnikov, 2016). The finding that temporal elaborations were higher in the RM condition was more surprising, as time is often thought to be fundamental to episodic memory. While there are several possible explanations, two appear most reasonable. One could be that participants in the RM condition relied to a greater extent on scripts (i.e., temporal scaffolds) and less on detail-rich sensory experience. Another possible explanation is that “time” with regard to episodic memory refers primarily to “temporal order,” with a previous study suggesting a significant relationship between the accuracy of spontaneously recalled events (i.e., a visit to a museum) and temporal order (Diamond, Abdi, & Levine, 2020). Although we did not find a correlation between episodic richness and temporal order in our study, our measure of temporal order focused on correct landmark orderings, and it is possible that these were less salient aspects of the experience than details of a paintings seen in a museum. Furthermore, we investigated memory of a recent experience, and it is possible that naturalistic movement may confer a benefit to the time-dependent reorganization (i.e., consolidation) of spatiotemporal memory during a multiday delay (as was observed in Diamond et al., 2020).

The principal components analysis (PCA) showed that variance in participants’ verbal elaborations was explained, in part, by experimental condition, with k-means derived clusters segregating participants along PC2 with 88% accuracy. However, individual differences in memory style accounted for a greater share of variance, as reflected by PC1, which loaded strongly on emotion, visual, and place-related memory elaborations. Our findings seem to have captured natural variability in the population, revealing a broad distribution of memory styles. Past studies reported individual differences in episodic memory style (Fan et al., 2021; Petrican, Palombo, Sheldon, & Levine, 2020) and evidence that individuals vary in their preference for more egocentric or allocentric navigation strategies (Committeri et al., 2020). In our paradigm, variance in egocentric and allocentric details were primarily related to the manipulation, loading onto PC2, whereas variance in other categories (e.g. ‘visual’ within the episodic category) were more influenced by individual differences in narrative style, loading onto PC1. Results from this data-driven approach align with those of mixed-effects models, with both suggesting that exposure to the treadmill during navigation increases participants’ preference for egocentric as opposed to allocentric details during memory recall.

Our findings reported here, coupled with some of the past studies mentioned above, help to resolve factors necessary for enriching episodic memory. Although previous studies demonstrated naturalistic contexts resulting in more vivid memory (Diamond et al., 2020; Gauthier et al., 2020), there has been less thorough investigation into precisely which factors of naturalistic enrichment enhance memory. Here, we showed that greater access to proprioceptive input (in the IA condition) benefited episodic richness. These findings provide an important link between immersive sensory experiences and episodic memory, which could be seen as supporting the view that a core component of episodic

memory is sensory experience, perhaps via sensory “channels” (Rolls & Wirth, 2018; Rubin, 2006; Rubin & Umanath, 2015). Another important implication of our findings is that episodic richness is not strongly dependent on parallel increases in either objective or subjective reports of space and time. These findings are inconsistent with the hypothesis that spatiotemporal details accompany rich episodic memory, or with models that assume a strong correspondence between episodic memory and navigation (Bellmund et al., 2018; Buzsáki & Moser, 2013; Chandra et al., 2025; Eichenbaum, 2017; Ekstrom & Ranganath, 2018; Hassabis & Maguire, 2007). Instead, our findings are more consistent with models that argue for episodic memory arising broadly from sensory channels and integration with internal narratives, neither of which is necessarily dependent on space nor time (Kensinger & Schacter, 2006; Rubin, 2006; Rubin & Umanath, 2015; Schacter et al., 2011).

It is possible that we did not find significant correlations between objective measurements of space and time and subjective measurements of episodic memories because the experiences participants had while navigating were inherently “free form.” In other words, participants were free to navigate any route between two landmarks and could focus on whatever details they deemed necessary when navigating, verbally elaborating, or performing the JRD and temporal interval reproduction tasks. In previous studies, navigation has been constrained via a tour or video clips (Diamond et al., 2020; Lehn et al., 2009), and it is possible that the ordered nature of these experienced induced more of a dependence on serial order memory. It is also possible that if we had instructed participants to pay more attention to certain details, such as the location of landmarks, there would have been significant correlations between episodic memory and spatial-related objective variables. The null finding for one particular correlation (temporal order score) may have also been limited by variance issues. Furthermore, due to the lack of a neural component in this paradigm, we did not have means of directly investigating neural evidence of spatiotemporal encoding. In spite of these caveats, the unconstrained nature of our experiment likely more closely resembles our everyday experience and therefore could be seen as better reflecting naturalistic forms of episodic memory. Additionally, inter-rater reliability for some verbal categories (particularly allocentric details) was low. This may have been influenced by our scoring procedure, which combined counts and graded ratings of verbal detail, thereby introducing an additional source of grader-specific variability that would have been minimized if counts alone were used. Finally, while sample size is a limitation in our study, we note that we collected objective and subjective reports in the same participants. We also note that our between-subject manipulation of immersion did have a significant impact on the richness of episodic memory.

CRedit authorship contribution statement

Sameer Sabharwal-Siddiqi: Visualization, Investigation, Formal analysis, Data curation, Writing – original draft. **Andrew S. McAvan:** Software, Investigation. **Eva M. Robinson:** Supervision, Project administration, Funding acquisition, Conceptualization. **Michael Starrett:** Investigation, Conceptualization. **Joshua D. Garren:** Investigation. **Jingyi Zheng:** Supervision, Project administration, Funding acquisition, Conceptualization, Writing – review & editing. **Eve A. Isham:** Methodology. **Arne D. Ekstrom:** Supervision, Project administration, Funding acquisition, Conceptualization. **Matthew D. Grilli:** Writing – review & editing.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cognition.2025.106358>.

Data availability

All study materials (primary data, and analyses scripts are publicly available at https://osf.io/spjqv/?view_only=b9a65598b12c4437afd77b4e45318242).

Naturalistic movements enrich episodic memories but not their spatiotemporal structure (Original data) (OSF)

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