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RESEARCH

Probing Behavioural Tagging in Humans: Spatial Memory Reveals Novelty-driven Retroactive Enhancement

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Abstract

Exposure to novelty can enhance memory performance through behavioural tagging, whereby novel experiences strengthen temporally proximate memories. Whilst consistently demonstrated in rodents, human studies have yielded mixed results, possibly due to inadequate novelty manipulations and/or insufficient hippocampal engagement during encoding. Here, we investigated whether exploration of a novel, unpredictable, immersive virtual reality retroactively enhanced spatial memory in humans. Thirty-six participants completed a two-day experiment involving spatial object-location learning in custom mazes, with encoding strength manipulated through repetition, to create initially weak and strong encoding conditions. Following encoding, participants explored either familiar (predictable city) or novel (multi-site outer-space with unpredictable teleportation) virtual environments. Memory was assessed through spatial accuracy metrics and cued recall. We found a retroactive memory enhancement following novel environment exploration, specifically when novelty occurred on Day 2. This enhancement was evident across spatial memory measures and cued recall, but did not interact with encoding strength. Our results demonstrate that retroactive behavioural tagging effects can be elicited in humans using spatial memory tasks paired with immersive novelty experiences, provided participants have appropriate reference points for novelty evaluation. These findings highlight the importance of investigating behavioural tagging using manipulations that emulate those studied in rodents.

Introduction

Exposure to novelty is a key contributor to the enhancement of memory formation, with memories of novel experiences often outlasting those for familiar ones – a crucial mechanism for memory being adaptive and flexible. Novelty not only enhances memory for the novel experience itself, but has also been shown to strengthen weaker memories encoded in temporal proximity to the novel experiences. This phenomenon is known as behavioural tagging, initially identified in rodents, and subsequently documented in humans. However, human findings remain inconsistent, with several studies failing to replicate the enhancement. This variability could be due to the experimental paradigms used in humans, which often may not fully capture the cognitive and neural processes underlying behavioural tagging as measured in rodents. Here, using virtual reality and spatial memory, we investigate behavioural tagging in humans by closely emulating experimental procedures that produce consistent behavioural tagging effects in rodent studies, namely combining spatial memory with a strong novelty manipulation.

Behavioural tagging captures the strengthening of weak memories by temporal proximity to an unrelated but salient (novel) event (Moncada & Viola, 2007), reflecting the behavioural outcomes of the synaptic tag-and-capture process (STC; Frey & Morris, 1997). According to STC, learning initially creates a synaptic tag at activated synapses, marking them for potential strengthening. The tagged

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synapses can then capture plasticity-related proteins that are synthesised in response to a salient event occurring within a critical time window, around 90 min. The capturing of these proteins, triggers changes that transform the initially weak synaptic modifications into stable long-term potentiations. Critically, for the salient event to strengthen the weak one, there must be overlapping neuronal populations (in the hippocampus) activated by both, ensuring that the relevant synapses are tagged and can later capture the available proteins (Nomoto et al., 2016; Redondo & Morris, 2011). The consistent cross-level findings (molecular, cellular, and behavioural) make STC and behavioural tagging a robust framework to study the dynamic interactions between events as they become lasting memories.

In humans, studies investigating behavioural tagging have produced mixed results (Dunsmoor et al., 2022; Lorents et al., 2023). Proactive novelty manipulations, where novel experiences precede memory encoding, have shown more consistent success in demonstrating memory enhancement (Aron et al., 2025; Fenker et al., 2008; Schomaker et al., 2014, 2022; Schomaker & Wittmann, 2021), though some studies using similar paradigms have failed to replicate these effects (Raza et al., 2025). Evidence for retroactive enhancements, where novelty follows memory encoding, is considerably scarcer (Biel & Bunzeck, 2019; McClay & Dunsmoor, 2018; Quent & Henson, 2022), though notable exceptions exist, particularly in developmental populations (Ballarini et al., 2013; Custodio & Justel, 2023). This asymmetry contrasts with rodent studies, which have established that novelty can enhance memory both proactively and retroactively (Ballarini et al., 2009; Frey & Morris, 1998).

Several factors emerge in the literature that might explain the discrepancy between animal and human work. Notably, the use of word-learning as the weak event may contribute to the inconsistent findings. While word paradigms allow manipulation of initial encoding strength, a key theoretical requirement for behavioural tagging, the use of words might not sufficiently engage overlapping neuronal populations in the hippocampus (Kafkas et al., 2024; Kim, 2013) during the salient (novel) experience, as required by STC. Supporting this interpretation, studies that rely on informational overlap have more consistently demonstrated behavioural tagging effects. These include paradigms employing rewarding or aversive stimuli to operationalise salience, which rely on overlap in semantic categories and have demonstrated retroactive enhancements (Dunsmoor et al., 2015; Hennings et al., 2021; Patil et al., 2017). While the information-to-be-remembered is still unrelated to the salient experience in these studies, they more likely capitalise on shared neural processing systems between the initial encoding and the salient event. This putative overlap in neural activation patterns likely fulfils the requirement for STC to operate effectively (Nomoto et al., 2016). Thus, for enhancement of hippocampal-dependent memory by novelty exploration, which also engages the hippocampus during the ‘capture stage’, it might be important to consider tasks that would reliably engage the hippocampus during encoding (‘tagging stage’).

The operationalisation of novelty in human studies represents another critical factor in translating behavioural tagging from rodents to humans. Rodents’ first exposure to novel open-field environments likely involves significant arousal and uncertainty, engaging dopaminergic and noradrenergic neuromodulatory systems, alongside the hippocampus, that support synaptic tag-and-capture processes (Li et al., 2003; Moncada, 2017; Moncada et al., 2015). These same neuromodulatory systems have been implicated in human novelty processing and memory enhancement (Duszkiewicz et al., 2019; Frank & Kafkas, 2021; Kafkas & Montaldi, 2018; Schomaker & Meeter, 2015). However, human studies may often fail to elicit comparable levels of arousal and uncertainty, particularly with between-subjects designs that lack appropriate reference points for meaningful novelty evaluation (Biel & Bunzeck, 2019; Quent & Henson, 2022). Within-subject designs therefore provide inherent comparison opportunities that may be crucial for effective novelty detection and subsequent memory enhancement effects.

Here, we aim to bridge a translational gap in the study of behavioural tagging in rodents and humans, by employing a spatial memory task, paired with a particularly salient novelty manipulation in virtual reality (VR; Fig. 1). This approach capitalises on both experimental familiarisation and environmental novelty and predictability. Spatial memory is a promising candidate as it offers a direct link to rodent studies, heavily relies on the hippocampus (ensuring neuronal overlap between weak and strong events), whilst allowing assessment of conceptually unrelated information. We examined whether exploration of a novel and unpredictable VR environment would retroactively enhance object-location memory, compared to exploration of a familiar, predictable environment. To ensure memory effects are not limited to the spatial domain, we also examine cued-recall of paired associates learned in the maze (but void of spatial information). To explore whether novelty specifically enhances initially-weak memories, we included weak (single exposure) and strong (three interleaved exposures) encoding conditions for spatial memory. We hypothesised that exploration of the novel and unpredictable environment would retroactively enhance memory, and that this would be manifested in the weakly encoded object-location and paired-associated memory performance.

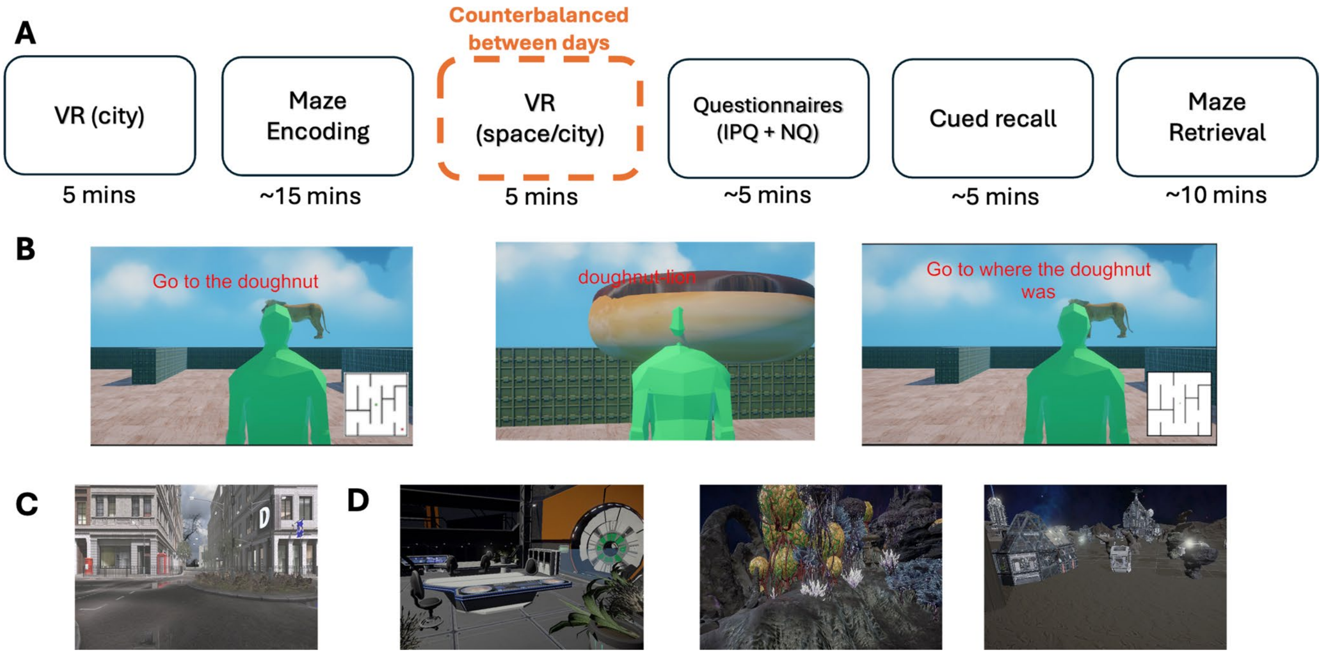

Fig. 1 Task design. **A** Schematic representation of the paradigm. Each day consisted of six phases: VR familiarisation (5 min exploring city environment); maze encoding phase with object-location learning; immersive VR exploration (5 min) which was counterbalanced across participants, half of them explored the novel environment on Day 1 and familiar environment on Day 2, and the other half vice versa; questionnaires on subjective experience of novelty (NQ) and presence (IPQ); cued-recall of the animal-object association; and the final phase, spatial memory retrieval in the maze. **B** Maze task. During maze encoding (left), participants navigated from the centre of custom-built mazes to find target objects (e.g. doughnut), with encoding strength manipulated through repetition (weak: 1 exposure, strong: 3 interleaved exposures). Each maze had a unique build (walls and floors material), as well as object and animal (e.g. lion) pairing, with the animal used as a landmark. To facilitate finding the object, a bird's-eye view map of the maze was presented at the bottom left corner of the screen, marking the starting point in green (static), and object location in red. Upon reaching the object (middle), the animal-object association was presented and participants had 5s to encode it along with the object location within the maze. At retrieval (right). The VR exploration phase involved either **(C)** a familiar, predictable city environment (grid-structured streets with numbered streets and avenues) or **(D)** a novel space environment with three distinct sites (left, space station; middle, alien terrain; right, space camp) with distance-triggered teleportation between locations to make navigating unpredictable

Methods

Participants

The sample size was based on a previous study using a similar approach (Schomaker et al., 2014) reporting a significant effect of novelty exposure on memory ($\eta^2 = 0.16$, $N = 28$), suggesting a sample of 34 participants is sufficient to detect an effect size of $f = 0.25$, with 0.8 power, as calculated in G*Power. To account for potential drop-out, we recruited 40 participants through the University of Manchester's SONA system and posted advertisements. All participants gave written informed consent and received either course credits or monetary compensation for their time. Data from four participants were discarded due to a technical error (one participant), or cybersickness from the VR (three participants). As a result, data from 36 participants (31 female; age range: 18–30 years; M = 22.33, SD = 2.94) is reported. All procedures were approved by the University of Manchester Research Ethics Committee (reference 2025-21340-39537).

Materials

All tasks, except the immersive VR, were performed on a desktop PC (Lenovo ThinkCentre with 24" iiyama monitor). The maze task (encoding and retrieval) was run as a stand-alone executable, built in Unity 2022.3.54f1 using UXF (Brookes et al., 2020) for experimental control of trials. The cued recall task was run using PsychoPy 2024.2.4 (Peirce et al., 2019).

Maze task – In this task, participants were placed in a maze using a third-person view of a green character that they were controlling, and were asked to find a goal object placed in it by navigating through the maze paths until they collided with the object. In addition to the object, each maze also had an external landmark in the form of an animal, which was placed to the north of the maze. Mazes for this experiment were custom-built in Python using Wilson's algorithm as implemented in the *mazelib* package (https://github.com/john-science/mazelib), which employs loop-erased random walks to produce unbiased samples from the uniform distribution of all mazes with no preference for long/short dead-ends or vertical/horizontal corridors. Subsequently, the goal objects were randomly positioned towards the edge of one of the four quadrants, resulting in 256 possible configurations for each maze. There were additional constraints for one of the four object locations, making it more difficult to reach. This object location was not used as a potential goal in the current task, meaning for each maze there were 3 potential object locations. At the end of this procedure we thus created a 50 × 50 pixel images representing the mazes with one object in each quadrant.

The pixel-based maze structure was converted to a 3D environment in Unity by translating pixels floors and walls. The top of the walls were at shoulder height (agent height = 2 virtual meter and wall height = 1.5 virtual meter). To ensure that each maze environment was distinct (i.e. to create unique trials trials), for each maze-object location pairing, we used a unique combination of materials for the floor and walls (e.g. blue tiles for the floor and red bricks for the walls). Therefore, we had 24 unique trial configuration which included a visually distinct maze and a single object embedded within it. These 24 unique trials were presented at encoding on Day 1, and for Day 2, 24 new unique combinations were created (ensuring there is no repetition from Day 1). In each of these trials, a trial-specific extra-maze landmark (a 3D model of an animal) was also included. The 3D models for the objects were sourced from an open database (Peeters, 2018) and the animals were obtained from freely available sources such as CGTrader and Sketchfab. Both were selected based on neutral-valence and nameability following pilot studies (e.g. desk, blazer, bucket; giraffe, lion, monkey). The landmark was always placed to the north of the maze (where the participant was facing at the beginning of each trial, 30 virtual meters away) and at a height above the walls so it is visible from all vantage points (3 virtual meters). To mark the starting point, an arrow pointing at the landmark was placed above the agent (4.5 virtual meters), which was also visible throughout the experiment.

Immersive VR environments – two environments were built in Unity and were run on a Meta Quest 3 headset and VR controllers, paired with an HP Omen 16” gaming laptop (NVIDIA GeForce RTX 4080 GPU). The headset and laptop were either connected via cable, or over a dedicated WiFi 6E network (using a TP-Link Archer AXE75 router), for a stable connection and consistent frame rate. Participants used the controllers to navigate the environment, one for rotation and one for movement. The speed of movement was set of 3 virtual meters per second and the rotation speed was set to Unity’s XR Interaction default of 45 degrees per second. Two environments were used for the familiar and novel condition. The familiar environment was a city environment structured in a grid-manner with numbered streets (1–5) and avenues (A-D) to make navigation more predictable at each junction. The city was designed to look like a typical British town centre, with shops, banks, other typical buildings, and a cloudy skybox. Participants were able to navigate on the road and pavements, but were not able to access the inside of the buildings. Additionally, there were invisible walls at the edges of the city, to prevent participants from walking off the edge. The size of the city environment was 300 by 300 virtual meters, with a total of 20 junctions. The average distance between junctions was 50 virtual meters.

For the novel condition, we used space-themed environment, which was composed of three sites (all three were purchased from the Outer World bundle on the Unity asset store): an indoor space camp (400 by 400 virtual meters), an outdoor space colony with embedded space-related objects (space shuttle, cares, control units; 400 by 400 virtual meters), and a surreal alien terrain environment, embedded with sci-fi, abstract visual features (1000 by 1000 virtual meters). To emulate the junction points from the city environment, participants were automatically teleported from one site to the other after covering 45 virtual meters (see procedure for full details).

Questionnaires – we used the IPQ (Schubert et al., 2001) and devised a novelty questionnaire (NQ) to assess the novelty aspect of the immersive experience (see Supplementary Material) to be able to validate the effectiveness of our manipulation.

Procedure

The experiment took place across two days (Day 1 and Day 2; see Fig. 1 for task design), which were between one and six days apart (median = 1, mean = 1.94, SD = 1.45). The procedure on both days was similar, participants first spent five minutes exploring the city environment ([re]-familiarisation stage). At this point, if they felt uncomfortable or experienced cybersickness, the experiment was terminated. They were then asked to complete a practice phase of the maze task, including both the encoding and retrieval phases (see description below), but were not informed about the cued-recall test. After this practice, participants completed the encoding phase of the maze task. In this part, each trial started with the participant placed in the centre of the maze, facing the animal landmark, and a prompt appeared for three seconds cueing the trial’s goal (e.g. “Go to the chair”). Throughout the encoding phase, a bird’s-eye-view map of the maze was visible in the bottom right corner of the screen, marking the starting location and the object location. The map was included to help participants understand the maze structure and plan a route to the object’s location, following pilot data suggesting it supported more efficient encoding. Participants used the arrow keys to navigate through the maze to get to the object location. Upon reaching the object (by colliding with an invisible sphere enclosing it), another text message appeared stating the animal and object (e.g. “lion – chair”) for five seconds, during which participants could look or move around the object. This was done to ensure sufficiently strong encoding of the location and the association, which participants were instructed to memorise during this time. The maximum duration of a trial 35 s, after which a fixation appeared (3s) prior to the start of the next trial. Following the end of the trial, a fixation cross on a blank screen appeared for three seconds until the next trial started. As behavioural tagging is supposed to affect weak and strong memories differentially, we repeated ten of the objects three times (strong condition) and fourteen of the trials only once during encoding (weak condition). The total number of trials per Day was 44 for the encoding portion of the experiment (10 objects repeated three times + 14 objects repeated once).

Following this encoding part, in the next phase participants explored the immersive virtual reality environment, without any other explicit task. The assignment of the environments to Day 1 and 2 was counterbalanced across participants; half of the participants experienced the novel environment on Day 1 and the familiar environment on Day 2, and the other half vice versa. In this part of the experiment, participants freely explored the environment for five minutes using the Meta Quest controllers. In the space environment, participants were automatically teleported within and between different sites (space colony, indoor space station and alien terrain) after having walked 45 virtual meters. In other words, there were no specific locations to trigger teleportation because was entirely controlled by the distance participant navigated to emulate the distance between junctions in the city environment. Teleportation was introduced as a function of distance covered, as opposed to time spent, to make the teleportation less predictable (the time between each teleportation varied). Teleportation involved a fade-to-black for 1 s, followed by “landing” at a new location (entry port), either within the same site or at a new site. The transition probability was predetermined and there were 8 entry ports in each site.

After completing five minutes of exploration, participants filled in two questionnaires about their immersive experience, the IPQ, and the NQ. This was followed by a surprise cued recall task (surprise on Day 1, but not on Day 2 given previous experience), in which participants were presented with images of the objects they encountered in the maze, and were asked to type in the name of the animal that appeared with them (each animal-object association was unique). This was self-paced, and subsequent scoring was manually verified for typos or misspellings prior to data analysis. Finally, participants completed the maze retrieval task in which they were tested on the 24 unique objects from encoding. On each trial (maximum duration of 30s, participants were placed at the centre of the maze, facing the animal landmark, and were instructed to go to the location where the object was (e.g. “Go to where the chair was”). When they the participant thought they reached the correct spot, they were instructed to press the ‘1’ key on the keyboard (representing the drop position). The object then appeared at its original location for three seconds, as a way of feedback, followed by a fixation cross on a blank screen for three seconds until the next trial. If participant did not press the ‘1’ key within 30s, their last location was recorded and the next trial started (removing these trials for the analyses did not change the results reported below). Participants returned to complete Day 2, which included the same procedure, with new objects and maze materials used in the maze task, and counterbalanced immersive virtual environment.

Statistical analyses

Statistical analyses were performed in JASP (v 0.19; JASP Team, 2024; https://jasp-stats.org/) and in R (R Core Team). Corrections for multiple-comparisons were performed were appropriate using the Holm-Bonferroni correction (referred to as p_{holm}). We devised two spatial memory metrics; first, Euclidean distance between the drop location and the true location of the object (Euclidean Distance = $\sqrt{(Xdrop - Xtrue)^2 + (Zdrop - Ztrue)^2}$). The second was based on the maze quadrant structure (i.e. an object is placed in one of the four quadrants in the maze creation algorithm), allowing us to calculate the proportion of trials in which the object was placed in the right quadrant. Although the two measures are related, they can reveal different processes. Euclidean distance likely reflects allocentric memory for the object location in relation to the landmark or the bird’s-eye map. The quadrant analysis on the other hand, provides a coarser measure of memory (e.g. “the chair was to my right, but I can’t remember how far along the path”). Given how the mazes and object locations were created (see maze task in Materials section above), the quadrant analysis can also reveal memory for the route taken. A participant might remember the object was placed close to a landmark, but this location could be east or west of a given wall (unbeknownst to the participant, creating a quadrant boundary), reached by a different route. In other words, there will be cases where the Euclidean distance will be small, but the quadrant will be wrong (see Fig. 3b, inset ii).

Results

Encoding strength

To test whether the strength manipulation affected participants’ encoding efficiency (as a marker of learning), we examined the time it took participants to reach the target object during encoding, as a function of repetition (weak – one trial, compared to first, second, and third presentation in the strong condition; Fig. 2a). A one-way ANOVA with the four levels yielded a significant effect of repetition (F(3,105) = 19.31, $p < 0.001$, $\eta^2_p = 0.356$. Subsequent post-hoc tests demonstrated that time-to-target was not different between the weak condition and the first and second repetitions of the strong condition (weak – first: mean difference = -0.52, t(35) = -1.362, $p_{holm} = 0.364$; weak – second: mean difference = 0.42, t(35) = 1.77, $p_{holm} = 0.364$), but it did decrease with repetition of strong trials (first – second: mean difference = 0.94, t(35) = 2.64, $p_{holm} = 0.037$; first-third: mean difference = 2.38, t(35) = 7.79, $p_{holm} < 0.001$, second – third: mean difference = 1.45, t(35) = 5.84, $p_{holm} < 0.001$).

Subjective Experience of VR Environments

To assess the participants' experience in the familiar and novel VR environments, we first compared their scores on the IPQ and the newly devised NQ following each environment, using a two-tailed paired-samples t test (Fig. 2B, C). As expected, we found that following the novel environment, participants had higher scores on the NQ (t(35) = 7.64, $p < 0.001$, Cohen's d = 1.27 and marginally on the sum IPQ score t(35) = 1.98, $p = 0.056$, Cohen's d = 0.330. Following previous findings (Schomaker et al., 2014), we also examined the Presence subscale of the IPQ, and found a significant difference between novel and familiar environments t(35) = 2.05, $p = 0.047$, Cohen's d = 0.342, with higher sense of presence reported following exploration of the novel environment. These results confirm the validity of our central novelty manipulation.

Behavioural Tagging Effects on Spatial Memory Performance

We first examined the Euclidean distance between the drop and true locations of the objects in the maze, using a 2 (novelty: novel vs. familiar VR environment) by 2 (encoding strength: weak vs. strong) repeated measures ANOVA (Fig. 3A). As expected, we found a main effect of strength F(1,35) = 66.98, $p < 0.001$, $\eta^2_p = 0.657$, with smaller Euclidean distance (better performance) in the strong encoding condition. There was also a trend towards a main effect of novelty F(1,35) = 2.304, $p = 0.138$, $\eta^2_p = 0.062$ suggesting smaller Euclidean distance following exploration of a novel environment. The interaction was not significant F(1,35) = 0.32, $p = 0.575$, $\eta^2_p = 0.009$. As previous studies found an order effect of the VR environment (Aron et al., 2025; Servais et al., 2024), we conducted a complementary mixed ANOVA (Fig. 3A), with the two repeated measures as above and including the day the novel environment was experienced as a between-subject effect (this was counterbalanced across participants). We found again a main effect of strength (F(1,34) = 64.92, $p < 0.001$, $\eta^2_p = 0.656$), but no interaction between strength and day (F(1,34) = 0.273,

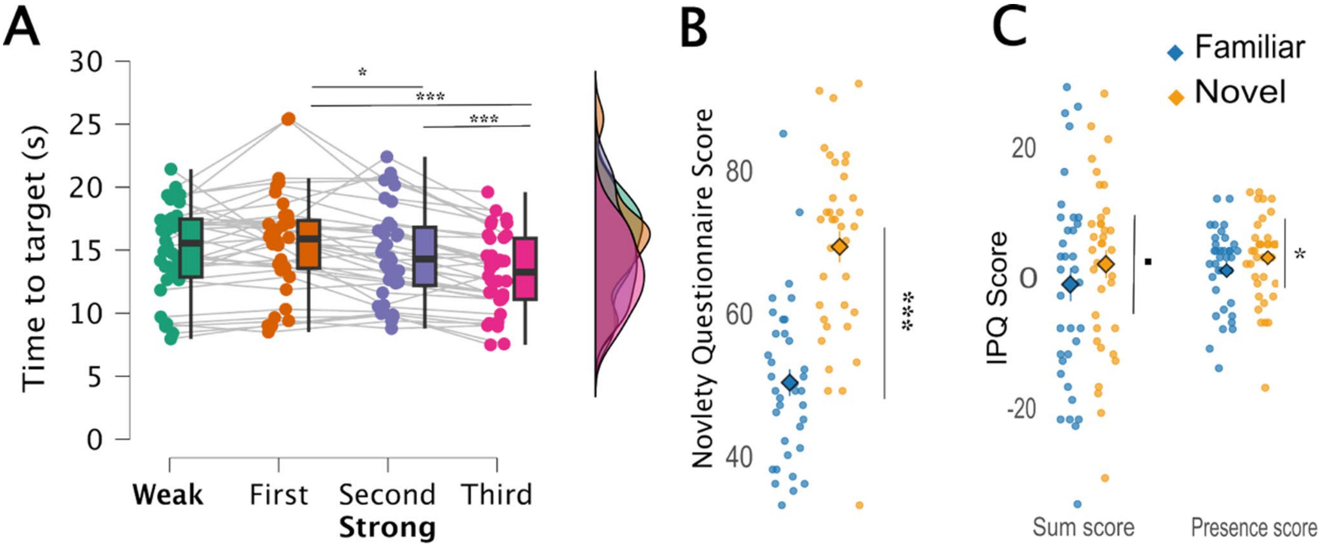

Fig. 2 Encoding strength and questionnaire scores. **A** Time to target during maze encoding as a function of repetition, demonstrating effective encoding strength manipulation. Individual participant data shown as connected points with group means and 95% confidence intervals. Weak condition involved single object exposure, whilst strong condition involved three interleaved repetitions. Time decreased significantly across strong condition repetitions with no difference between weak and first/second presentations. **B** Novelty Questionnaire (NQ) scores following VR exploration, confirming participants experienced the space environment as significantly more novel than the city environment. **C** Igroup Presence Questionnaire (IPQ) scores following familiar versus novel VR environments. Participants reported marginally higher overall (Sum) and significantly higher presence subscale scores following novel environment exploration. Unless otherwise states, error bars represent standard error of the mean (SEM). $^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

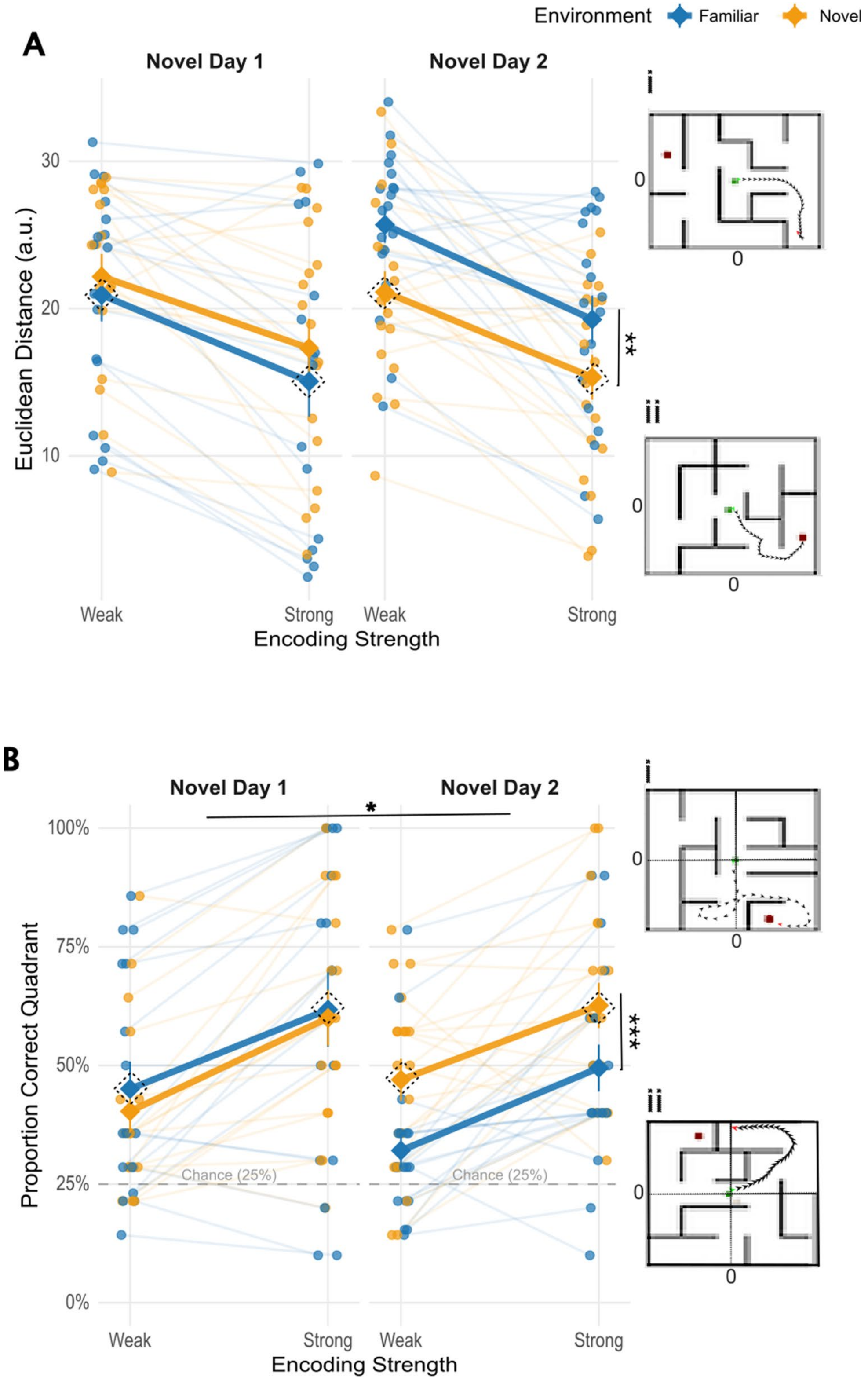

Fig. 3 Spatial memory performance. **A** Euclidean Distance between remembered and actual object locations during spatial memory retrieval. Insets depict example retrieval trials, with the arrows demonstrating the participant's route and the red arrow the participant's remembered location, actual object location represented by a red square (for demonstration purposes; only visible to participants at retrieval after they make a response). (i) an inaccurate placement, corresponding to high Euclidean distance, and (ii) accurate placement corresponding to low Euclidean distance error. Strong encoding trials showed significantly better spatial accuracy than weak trials. A retroactive memory enhancement following novel environment exploration was selective to participants who experienced novelty on Day 2, no differences between conditions were observed participants who explored the novel environment on Day (1) Dashed square around the group mean represent the condition presented on Day (2) **B** Quadrant analysis. Proportion of trials with correct quadrant placement, providing a coarser measure of spatial memory that accounts for maze structure and potential route-based errors. Similar pattern to Euclidean distance with main effect of strength, and significant novelty × day interaction, showing a selective retroactive memory enhancement following novelty when it was presented on Day 2. Insets show example maze configurations illustrating how similar Euclidean distances can yield different quadrant accuracy: (i) correct quadrant placement following an initial wrong navigation choice and (ii) adjacent quadrant error across maze walls

$p = 0.605$, $\eta^2_p = 0.008$). There was again a trend towards a main effect of novelty $F(1,34) = 2.47$, $p = 0.125$, $\eta^2_p = 0.068$, and a significant interaction between novelty and day $F(1,34) = 14.45$, $p < 0.001$, $\eta^2_p = 0.298$. Subsequent post-hoc analyses revealed that when the novel environment was experienced on Day 2, there was a smaller Euclidean distance following exploration of a novel compared to familiar environment (mean difference $= 4.24$, $t = 3.91$, $p_{holm} =$

0.003, Cohen's d = 0.589). All other comparisons were not significant (all p_{holm}'s > 0.294). The interactions between strength and novelty and the three-way interaction with day were not significant. The between-subject main effect of day was not significant F(1,34) = 0.538, $p = 0.468$, $\eta^2_p = 0.016$. Together, these results suggest that the strong encoding trials were associated with better performance compared to weak encoding, as expected, and that this was not modulated by the VR experience. More interestingly, we found a retroactive enhancement of novelty on memory (as indexed by Euclidean distance), but this was selective to those who experienced the novel environment on Day 2.

Euclidean distance provides a highly precise measure of spatial memory accuracy, but as such it may mask a coarser memory representation of the location (e.g. "the chair was to my right"). Furthermore, Euclidean distance does not take into account the structure of maze environment in the context of our task. As such, it more likely reflects allocentric memory for the object location, but not necessarily the route taken during encoding. By design, the objects in our task were placed in one of four maze quadrants, which were separated by walls. Therefore, one might demonstrate the same Euclidean distance between the true and dropped locations, but the drop locations can be either within the same quadrant (taken the correct route), or in an adjacent quadrant, across a wall (took a different route; see Fig. 3B). We can thus quantify memory performance by examining the proportion of correct quadrant placements, enabling assessment of coarser memory representation and/or route-related errors. A 2 × 2 (novelty x strength) repeated measures ANOVA revealed a main effect of strength F(1,35) = 44.75, $p < 0.001$, η^2_p = 0.561, such that strong encoding associated with more accurate quadrant placement compared to weak encoding. There was also a main effect of novelty F(1,35) = 4.35, $p = 0.044$, $\eta^2_p = 0.110$, with a retroactive enhancement of objects studied before exploring a novel environment, compared to a familiar one. The interaction between novelty and strength was not significant F(1,35) = 0.012, $p = 0.914$, $\eta^2_p = 0.0003$.

We also examined the between-subject effect of day on quadrant accuracy using a mixed ANOVA and found similar results; a significant main effect of strength F(1,34) = 43.7, $p < 0.001$, $\eta^2_p = 0.562$, which was not modulated by day F(1,34) = 0.101, $p = 0.753$, $\eta^2_p = 0.003$. A significant main effect of novelty F(1,34) = 4.85, $p = 0.035$, $\eta^2_p = 0.125$ which also interacted with day F(1,34) = 12.41, $p = 0.001$, η^2_p = 0.267. Post-hoc analysis revealed the beneficial effect of novelty on memory in the quadrant analysis was due to the effect when the novel environment was experienced on Day 2 (mean difference = -0.14. t = −4.16, $p_{holm} = 0.001$, Cohen's d = -0.626), all other comparisons were not significant (all p_{holm}'s > 0.463). The interaction between novelty and strength (F(1,34) = 0.019, $p = 0.891$, $\eta^2_p = 0.0005$) and the three-way interaction with day (F(1,34) = 0.297, $p = 0.589$, $\eta^2_p = 0.009$) were not significant. The between-subject main effect of day was not significant F(1,34) = 0.415, $p = 0.524$, $\eta^2_p = 0.012$. Together, these results suggest a retroactive enhancement of novelty on memory that was more pronounced in those who experienced the novel environment on Day 2.

By utilising the maze quadrants, we can also examine the effect of novelty by comparing the navigation time to target during retrieval, given that it was in the right quadrant. A 2 × 2 repeated measures ANOVA revealed a main effect of strength F(1,35) = 10.36, $p = 0.003$, $\eta^2_p = 0.234$, with shorter trial durations for the strong condition. The main effect of novelty F(1,35) = 0.232 $p = 0.633$, $\eta^2_p = 0.007$ and interaction between novelty and strength F(1,35) = 0.108, $p = 0.744$, η^2_p = 0.003, were not significant. In a mixed-ANOVA, including the between-subject day effect, we observed a main effect of strength F(1,34) = 44.33, $p = 0.003$, $\eta^2_p = 0.234$, which was not modulated by day F(1,34) = 0.439, $p = 0.512$, $\eta^2_p = 0.013$. The main effect of novelty was not significant F(1,34) = 0.204, $p = 0.654$, $\eta^2_p = 0.006$, but there was a significant novelty x day interaction F(1,34) = 10.315, $p = 0.003$, $\eta^2_p = 0.238$. Post-hoc tests revealed a significant difference in duration between days following exploration of the familiar environments, with faster responses when the novel environment was experienced on Day 2 versus Day 1; mean difference = -2.93, t = -3.04, $p_{holm} = 0.028$, Cohen's d = -0.877). There was also a trend towards a shorter duration following novel compared to familiar environments, when the novel environment was experienced on day 2 (mean difference = 1.63, t = 2.63, $p_{holm} = 0.065$, Cohen's d.= 0.488). All other comparisons were not significant (all p_{holm}'s > 0.313).

Behavioural Tagging Effects on Cued Recall Performance

Next, we examined whether novelty modulated cued-recall of the paired associates (animal landmark-objects), void of spatial information (Fig. 4). A 2 × 2 repeated measures ANOVA revealed a main effect of strength F(1,35) = 199.01 $p < 0.001$, $\eta^2_p = 0.851$, with strongly encoded trials better recalled than weak ones. The main effect of novelty (F(1,35) = 0.461, $p = 0.502$, $\eta^2_p = 0.013$) and the interaction (F(1,35) = 0.135, $p = 0.716$, $\eta^2_p = 0.004$) were not significant. We proceeded to examine the mixed ANOVA including day as a between-subject effect. There was again a main effect of strength F(1,34) = 193.96, $p < 0.001$, $\eta^2_p = 0.851$, which was not modulated by day F(1,34) = 0.296, $p = 0.590$, $\eta^2_p = 0.009$. The main effect of novelty was not significant F(1,34) = 0.349, $p = 0.558$, $\eta^2_p = 0.01$, but again there was a significant day x novelty interaction F(1,34) = 18.61, $p < 0.001$, $\eta^2_p = 0.354$.

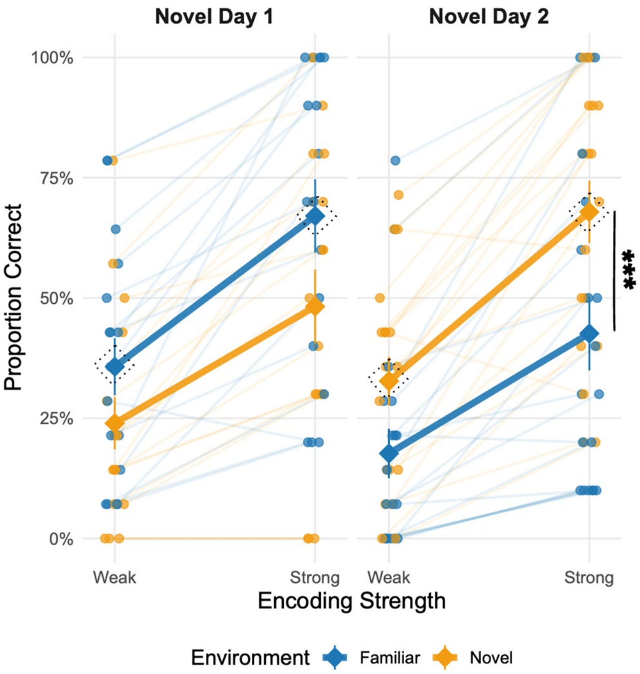

Fig. 4 Cued recall. Proportion of correctly recalled animal-object paired associates during the cued recall task, testing memory for associations devoid of spatial information. Strong encoding trials showed substantially better recall than weak trials across all conditions. In line with the spatial memory results, a retroactive memory enhancement following novel environment exploration was observed selectively when novelty occurred on Day 2. Dashed square around the group mean represent the condition presented on Day 2

Subsequent post-hoc tests of the novelty x day interaction revealed that cued recall was enhanced following exploration of a novel environment compared to a familiar one, when the novel environment was presented on Day 2 (mean difference = -2.02, t = -3.57, p_{holm} = 0.007, Cohen's d = -0.737). There were also trends towards better recall following a familiar environment when it was presented on Day1, compared to on Day 2 (mean difference = 0.212, t = 2.42, p_{holm} = 0.084, Cohen's d = 0.777), and a trend towards better recall on Day1 following familiar compared to novel environments (mean difference = 0.153, t = 2.56, p_{holm} = 0.075, Cohen's d = 0.56). All other tests were not significant (all p_{holm}'s > 0.266). The interaction between novelty and strength was not significant (F(1,33) = 0.047, $p = 0.830$, $\eta^2_p = 0.001$), nor was the 3-way interaction with day (F(1,33) = 1.04, $p = 0.314$, $\eta^2_p = 0.031$). The between-subject main effect of day was also not significant (F(1,33) < 0.001, $p = 0.997$, $\eta^2_p < 0.001$). These results are in line with the spatial memory performance (although the two measures are independent from one another), suggesting that the retroactive effect of novelty is modulated by day, with memory enhancement identified when novelty was experienced on Day 2.

Relationship Between Memory Performance and Subjective Experience of Novelty

We predicted that participants' self-reported experience of novelty and presence would positively predict their novelty-driven retroactive enhancement (see Supplementary Materials for an assessment of relative novelty experience between Day1 and Day2 groups). To investigate this, we extracted the main effect of novelty observed in the quadrant analysis (averaged difference), and correlated it with the difference in IPQ presence and NQ scores for the novel compared to the familiar environment (Fig. 5A). However, the correlation between the novelty-driven memory enhancement and the novelty score was positive at a trend level ($r = 0.264$, $p = 0.12$), whereas there was no correlation between the memory enhancement the IPQ presence score ($r = 0.051$, $p = 0.766$).

We extended our investigation to novelty-driven retroactive enhancement based on Euclidean distance for those who experienced the novel environment on Day 2 (Fig. 5B). As a reminder, negative values indicate better performance following novelty exploration. The correlation between memory enhancement and difference in NQ scores was also not significant (r = -0.064, $p = 0.795$). While there was indeed a negative correlation between memory enhancement and the difference in reported presence, it did not reach statistical significance (r = -0.336, $p = 0.159$). In summary, although the trend-level results are in the expected direction, given the inconsistent findings across memory metrics and questionnaires, these results suggest that the novelty-driven memory enhancement was not dependent on the perceived sense of novelty or presence.

Relationship Between Spatial Memory and Cued Recall

Finally, we examined whether spatial memory performance was related to cued recall, we performed a linear regression, predicting the mean Euclidean distance as a function of mean cued recall performance, novelty, and the interaction between them. Strength was not included as it did not interact with novelty in any of the previous analyses and we wanted to avoid multi-level interactions. We found a main effect of cued recall (ß= -12.98, $\chi^2 = 70.1$, $p < 0.001$), a trend towards a main effect of novelty (ß = 1.00. $\chi^2 = 2.08$, $p = 0.15$), but the interaction between novelty x distance was not significant (ß = -1.24, $\chi_2 = 0.826$, $p = 0.363$). Similar results were obtained when predicting quadrant placement as a function of cued-recall and novelty, with a significant main effect of cued recall (ß= 0.376, $\chi^2 = 56.6$, $p < 0.001$) and a trend towards a main effect of novelty (ß= -0.04, $\chi^2 = 3.17$,

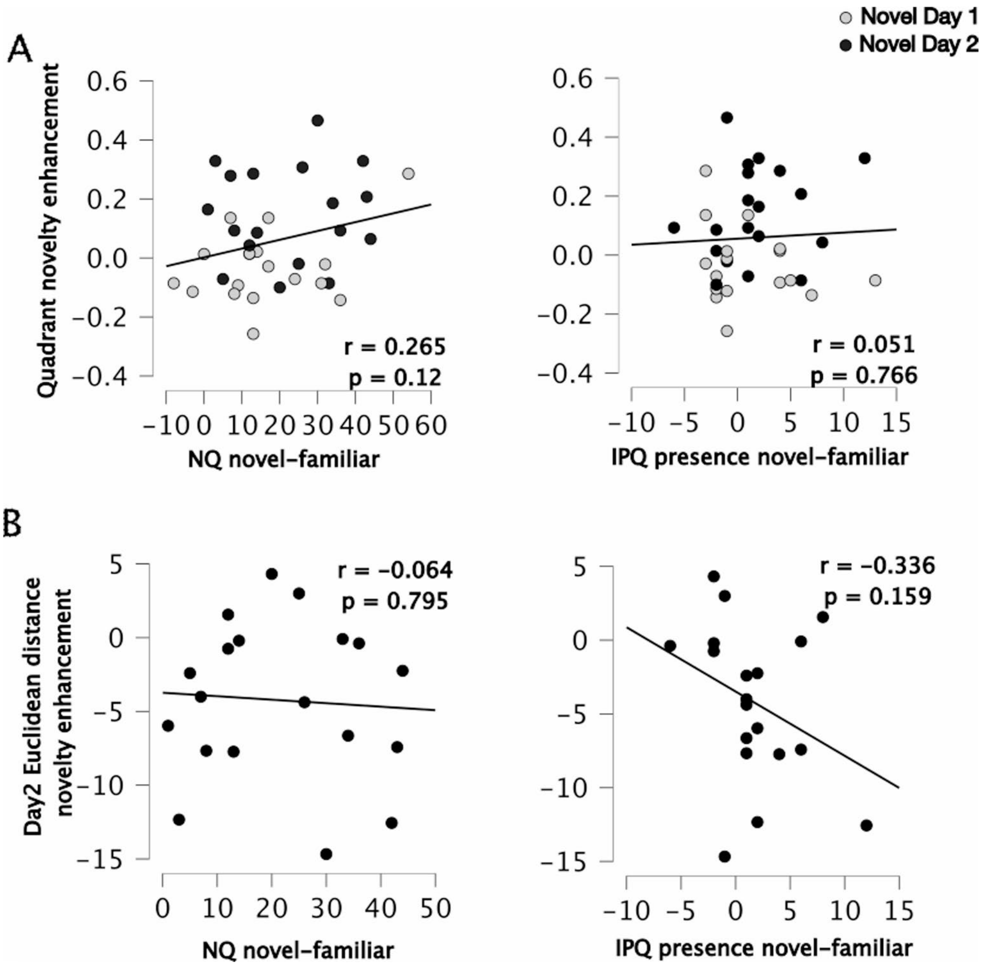

Fig. 5 Correlations between memory enhancement effect and subjective novelty experience. **A** Quadrant-based memory enhancement (proportion correct novel minus familiar conditions) plotted against difference scores for Novelty Questionnaire (NQ; left) and IPQ presence subscale (right) following novel versus familiar environment exploration. **B** Euclidean distance-based memory enhancement for participants who experienced the novel environment on Day 2 only (negative values indicate better performance following novelty) correlated with the same subjective experience difference scores

p=0.075), the interaction did not reach statistical significance (ß= 0.04, χ^2=0.84, p=0.359). As predicted, these results suggest that the spatial memory metrics were related to cued recall (smaller distance/higher proportion of correct quadrant placement, better recall rate) but this relationship was not modulated by novelty.

Discussion

Despite robust and consistent findings in rodents, evidence for behavioural tagging effects in humans remains inconsistent, with few studies demonstrating retroactive memory enhancement. Here, using a spatial memory task combined with immersive VR environments, we found retroactive memory enhancement following exploration of a novel environment, most consistently when the novel environment was experienced on Day 2, but no evidence for a main effect of novelty as predicted. This selective enhancement was observed across spatial memory accuracy (Euclidean distance and quadrant placement) and cued recall, yet did not vary as a function of initial encoding strength as we hypothesised. To assess the feeling of novelty following the VR environment exploration, we devised a novelty questionnaire which confirmed our novel space environment was subjectively experienced as novel, compared to our familiar city environment. Our findings suggest that the effectiveness of novelty manipulations in eliciting behavioural tagging may critically depend on participants having a reference point for evaluating environmental novelty in the context of their overall experience (relative novelty).

Our novelty manipulation encompassed multiple dimensions that may have contributed to its effectiveness in eliciting behavioural tagging effects. Beyond the environmental novelty of the space-themed VR setting, participants experienced contextual unpredictability through surprise teleportation that occurred after covering a specific distance, unbeknownst to them. This combination of novelty dimensions likely contributed to participants' experience of uncertainty, novelty, and arousal, which may more closely emulate the rodent experience in an open field novel environment. Future work could incorporate autonomic measures (e.g. galvanic skin response, pupillometry, electrocardiogram) to capture objective measures of the novelty experience. Subsequently, such environmental novelty may engage the dopaminergic and noradrenergic systems, implicated in processing novel information and supporting behavioural tagging (Duszkiewicz et al., 2019; Frank & Kafkas, 2021; Moncada et al., 2015; Schomaker & Meeter, 2015). The multi-faceted nature of our novel manipulation may help explain why some previous human studies using more limited novelty exposures (e.g. through experimental repetition) have produced inconsistent results. While our group-level questionnaire confirms the novelty manipulation's effectiveness, the weak individual-level correlations between novelty ratings and memory enhancement, as well as the difference in subjective novelty reporting between counterbalancing groups (those who experienced novelty on Day1 vs. Day2), suggest the increased subjective sense of novelty does not have a one-to-one mapping with the subsequent memory enhancement.

Across memory measures, we found a retroactive memory enhancement when the novel environment was experienced on Day 2. This finding is partly in line with our prediction that novelty would retroactively enhance memory, but it highlights the importance of reference points in novelty effects, and may help reconcile inconsistencies in previous human behavioural tagging research. Studies employing within-subject designs with inherent reference points (i.e. participants experience both novel and familiar conditions) have been more successful in demonstrating proactive novelty effects (Aron et al., 2025; Schomaker et al., 2014, 2022), whilst between-subjects approaches have often failed to replicate these findings (Biel & Bunzeck, 2019; Quent & Henson, 2022; Raza et al., 2025). When participants experienced the novel environment on Day 1, they may have lacked sufficient familiarity with the experimental context to establish meaningful comparisons. This could have limited their experience of novelty and subsequent recruitment of the neuromodulatory responses necessary for synaptic tag-and-capture processes (Li et al., 2003; Moncada, 2017), or that the whole experience was novel so the manipulation was less clear-cut. Importantly, we did not observe a main effect of day across our memory measures, indicating that the enhancement was not due to systematic differences between participants, but specifically reflected the interaction between novelty and reference point availability (see Aron et al., 2025 for a similar finding).

The use of spatial memory may have also contributed to the behavioural tagging effects observed. Previous human studies have predominantly employed word-learning paradigms, which, whilst allowing manipulation of encoding strength, may not sufficiently engage overlapping neuronal populations in the hippocampus during encoding (Kafkas et al., 2024; Kim, 2013). Spatial memory tasks inherently engage hippocampal processing during encoding/navigation (Burgess et al., 2002), providing the necessary neural overlap for synaptic tag-and-capture mechanisms when participants subsequently explore novel spatial environments (Nomoto et al., 2016; Redondo & Morris, 2011). However, our findings cannot be attributed solely to the spatial nature of the memory task, as we observed similar retroactive enhancement effects for cued recall of paired associates, void of spatial information. It is important to note the cued recall results are noisier than the spatial memory ones due to the fact that this was a surprise test on Day 1, such that overall performance on Day 2 improved, irrespective of novelty condition (Fig. 4, dashed rectangles; although the between-subject effect of Day was not significant). Together, the cued-recall and spatial memory results suggest that our novelty manipulation was sufficiently salient to enhance multiple types of hippocampal-dependent memories, supporting the broader applicability of behavioural tagging beyond purely spatial domains.

Behavioural tagging findings from rodents predict that strong events, which generate sufficient plasticity-related proteins, should be less dependent on additional protein synthesis triggered by subsequent salient events (Frey & Morris, 1997). Although our encoding strength manipulation effectively modulated overall memory performance, we did not observe the predicted selective enhancement of weaker memories following novelty exploration. This absence of differential enhancement poses a challenge to interpreting our effects as classical behavioural tagging, but several alternative interpretations might explain the lack of interaction with strength. First, the range of encoding strength in our study may not have been sufficiently large, such that even our 'strong' condition produced relatively weak memory traces that remained susceptible to novelty-induced enhancement. An alternative, more speculative, explanation could be found in the differential sensitivity of our spatial memory measures: we observed a significant main effect of novelty for quadrant placement, compared to a trend-level effect for Euclidean distance. Quadrant placement may tap into route-based spatial representations that might be weaker in nature, or more susceptible to consolidation benefits.

Finally, the retroactive nature of the memory enhancement (albeit limited to novelty experienced on Day 2), is theoretically important because such effects likely reflect genuine consolidation mechanisms with well-described neurobiological underpinnings (Frey & Morris, 1997), rather than attentional or motivational factors that could potentially explain proactive novelty effects. However, our study design limits our ability to isolate which specific methodological components were critical for eliciting consistent behavioural tagging effects, including the use of a within-subject design, spatial memory task, and multi-dimensional novelty operationalisation. Future studies should systematically isolate these components to determine whether hippocampal-dependent memory tasks are necessary, which dimensions of novelty manipulation are sufficient, and whether reference point establishment is critical for consistent effects, given that previous studies using different approaches have shown inconsistent results (Biel & Bunzeck, 2019; Quent & Henson, 2022; Raza et al., 2025).

In conclusion, our findings demonstrate that retroactive behavioural tagging effects can be elicited in humans under specific conditions, particularly when novelty experiences occur after participants have established a strong (familiar) reference point. Building on these findings, future work could explore how hippocampal and neuromodulatory systems contribute to the timing-dependent enhancement of memory consolidation. Such research could determine whether the reference point effect reflects distinct neural processes for novelty detection, or differential engagement of synaptic tag-and-capture mechanisms depending on prior contextual familiarity. Understanding these neural underpinnings will be essential for developing reliable cognitive enhancement applications that harness the memory-boosting potential of appropriately timed novel experiences.

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Data Availability The data reported above is publicly available here: https://github.com/frankmemorylab/mazeBT .

Declarations

Ethics approval All procedures were approved by the University of Manchester Research Ethics Committee (reference 2025-21340-39537).

Informed consent All participants gave written informed consent and received either course credits or monetary compensation for their time.

Competing interests The authors declare no competing interests.

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