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Author for correspondence:
Judit Fiedler
e-mail: fiedlerjudit@gmail.com

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When moving in a sphere, gender gaps may disappear

Judit Fiedler and Alessandro Treves

Cognitive Neuroscience, SISSA, Trieste, Italy

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Sex differences in spatial cognition often show males outperforming females, especially in familiar, landmark-rich environments. This study examined whether such differences persist when subjects encounter a novel spatial paradigm. We designed a sparse, spherical virtual reality space lacking traditional landmarks and orientation cues. In such a non-Euclidean and unusual space, recall performance shows a surprising bimodal distribution, and males and females exhibit similar performance with no clear preference for a particular strategy. Moving to more familiar environments, we observed a shift from bimodal to trimodal to roughly normal distributions, which may reflect the increased spatial plausibility of the environment making available a multiplicity of cues. Still, this does not translate into an overall improvement in performance. Differences in familiarity were also associated with sex differences. Already in the spherical environment, but rich in traditional landmarks, males exhibit a significant strategy preference, while in a flat (Euclidean) setting, they outperform females in sequential recall. These results indicate that when males and females experience an equally novel spatial paradigm, sex differences tend to vanish, suggesting that the male advantage in spatial cognition may require environmental familiarity and the activation of culturally honed schemata.

1. Introduction

Navigation towards a goal in an unknown non-trivial environment involves the encoding, storage and replay of a sequence of spatial locations [1]. Spatial sequential working memory is limited in both capacity and duration [2–4]. Research across human and non-human animals consistently shows that performance in spatial memory tasks can vary by sex, with males typically outperforming females in both small-scale (e.g. mental rotation [5–7]) and large-scale (e.g. navigation) spatial abilities [8,9]. In addition to performance differences, males and females often differ in their spatial strategies. Males tend to use a ‘survey’ or ‘allocentric’ strategy, forming a map-like, global representation of the environment, relying on Euclidean metrics such as distances and direction. Females are reported to prefer to use a 'route' or 'egocentric' strategy, connecting landmarks through sequences of decision points from the observer's perspective [10–14]. This aligns with neuroimaging findings that show that in large-scale navigation tasks, males exhibit greater activation in the hippocampus, a region associated with allocentric encoding, while females show more activation in the prefrontal cortex, suggesting a reliance on egocentric encoding [15–18].

There have been numerous theories attempting to explain this gender gap. The sex-specific hypothesis suggests that the male advantage in spatial abilities is an evolutionary adaptation, rooted in historically larger home ranges [19]. However, evidence indicates that sex differences in spatial behaviour typically emerge during childhood, soon after children begin to segregate and start participating in their gender-specific adult activities [20,21]. In most non-industrialized societies, girls tend to stay in their homes close to their mothers, assisting in caregiving and household chores, while boys take part in activities farther from home, such as fishing or hunting [22,23]. This pattern holds even in industrialized societies, where boys tend to enjoy greater spatial freedom than girls, whose mobility is often restricted due to safety concerns. For example, Webley [24] found that boys at age 8–9 had larger home ranges and drew more accurate and detailed cognitive maps than girls. However, when the same children were taken to a new, limited area to explore, this sex difference disappeared. Similarly, other studies have reported no sex differences in performance on both large-scale and small-scale spatial skills when range sizes are matched [25–29]. These findings suggest that sex-related differences in spatial cognition may reflect environmental experience and not necessarily be due to innate male superiority, e.g. as a product of evolution.

Virtual-reality-based tasks provide an opportunity to construct spatial paradigms that are unusual in the real world [30]. Leveraging this advantage, we aimed to design a minimally complex yet unfamiliar environment that provides novel spatial experience to both males and females. Specifically, we created a sparse spherical space that lacks qualitative spatial information, such as traditional landmarks and orientation cues. Research on non-Euclidean spaces suggests that even in spherical environments, human participants exhibit a Euclidean bias in navigation [31–33], while distortions in spatial representation are observed, including in rodent grid cells [34,35], highlighting the novelty of such unfamiliar settings. We then changed the environment by adding different familiar cues across the conditions. We hypothesized that these manipulations would lead to progressive increases in perceived familiarity/plausibility and that such changes would be reflected in sex-dependent trends in spatial memory performance.

The three experiments were conducted at different times and are integrated to address this question. Experiment 1 served as the starting point, representing the most unusual setting, where we investigated sex differences in either performance or strategy preference and found none. Experiment 2 then introduced traditional landmarks within the spherical environment, allowing us to examine whether previously reported sex-specific strategy preferences begin to emerge. Experiment 3 employed a flat Euclidean environment, representing the most familiar spatial structure, to explore whether performance patterns and strategy use diverge more clearly between sexes as environmental familiarity increases.

In a broader sense, the present work adopts an exploratory approach aimed at understanding how spatial behaviour in non-standard environments can be interpreted through cognitive maps and examining how varying degrees of familiarity influence memory performance and navigational strategies.

2. Experiment 1—spherical, sparse environment

2.1. Methods

2.1.1. Participants

Sample size was estimated *a priori* using the *pwr.anova.test* function from the *pwr* package. With n = 96 (48 per level, sex-balanced), the design had approximately 80% power to detect an effect of f = 0.29 (medium by conventional benchmarks [36]). For the full 2 × 2 × 2 between-subjects design (8 cells; n = 12 per cell), power for interaction effects of f = 0.35 was about 66%. We acknowledge that reported sex/gender differences in navigation tasks are often smaller than this [9], and thus the present study may not have been optimally powered for such effects. The chosen sample size represented a balance between adequate sensitivity and the practical constraints of exploratory work and feasible recruitment.

Participants were recruited via Prolific using pre-screening filters for biological sex. Additional criteria included age 18–40, ≥95% approval rate and worldwide recruitment. Sex was also asked within the task, revealing a small number of mismatches with gender identity. These participants were excluded. The final sample included 96 healthy adults (48 females, mean age = 25.66 ± 7.25 years), all with normal or corrected-to-normal vision, and no history of neurological or psychiatric disorders. They provided informed consent prior to participation and received monetary reward for their involvement. The study was approved by the Ethics Committee of the International School for Advanced Studies (SISSA), ensuring compliance with ethical standards.

2.1.2. Material

Participants navigated a spherical environment with minimal spatial cues, hereafter referred to as the *Spherical Sparse* condition.

Uniform spaces were created by projecting Platonic solids onto a sphere—specifically a cube in one variant and a dodecahedron in another—as navigable spaces within the sphere. Each face of these solids was assigned a distinct colour (figure 1). A dot texture was added to surfaces solely to enhance depth perception. Because Platonic solids are constructed from identical regular polygons, this symmetrical design provides environments where each coloured plane serves as an integration of space and landmark, reducing qualitative differences and eliminating any fixed orientation cues. One can therefore navigate by understanding the relative positions of the coloured tiles.

The navigable spherical space had a diameter of approximately 6.5 Unity units (1 Unity unit corresponding to 1 m). Movement speed was fixed across conditions, corresponding to approximately 1 Unity unit per second.

Spatial learning and sequential working memory capacities were tested by manipulating the number of objects (identical small white spheres, or 'balls') whose location participants were required to retain in memory (up to eight objects) and by using environments of differing complexity (cube versus dodecahedron). These balls always appeared at the vertices of the Platonic solid, defined by the junctions of three coloured faces. This required participants to rely on memorizing combinations of colours and their spatial relations.

Movements were also of two different types. In the '3D movement' variant, participants navigated inside the sphere by floating freely in all directions and rotating along all axes, similar to movement in zero-gravity space. In the 'terrestrial movement' variant, participants navigated along the inner surface of the sphere, mimicking terrestrial movement akin to walking on the ground.

By varying both the environmental symmetry—using either a cube or a dodecahedron as the internal structure—and the type of navigation ('3D movement' or 'terrestrial movement'), we created four distinct variants where we aimed to investigate how these factors influence spatial learning and memory in environments lacking traditional landmarks and orientation cues.

To facilitate learning through the initial orientation process, participants were instantiated in the centre of the sphere, facing a randomized direction.

2.1.3. Unity technical specifications

The virtual environments were developed in Unity (v. 2019.4.16f1, Unity Technologies), using C#. Builds were exported in the WebGL format to allow online participation via Prolific. Participant data were saved locally during the session in JSON format and automatically uploaded to a secure server at the end of the experiment. The environment was rendered using Unity's Universal Render Pipeline (URP) in high-quality mode (60 Hz refresh rate) to ensure consistent visual fidelity across systems. The task was tested across multiple browsers, and Chrome and Firefox were recommended to participants, whereas Safari and Internet Explorer were not supported. Minimum system requirements corresponded to Unity WebGL defaults (desktop or laptop computer with ≥2 GB RAM, GPU supporting WebGL 2.0 and broadband internet connection). Data quality assurance included pilot testing across machines and browsers, and excluding incomplete data uploads. Attrition due to technical issues was minimal, with two datasets lost in Experiment 1, one in Experiment 2 and two in Experiment 3 due to upload failure.

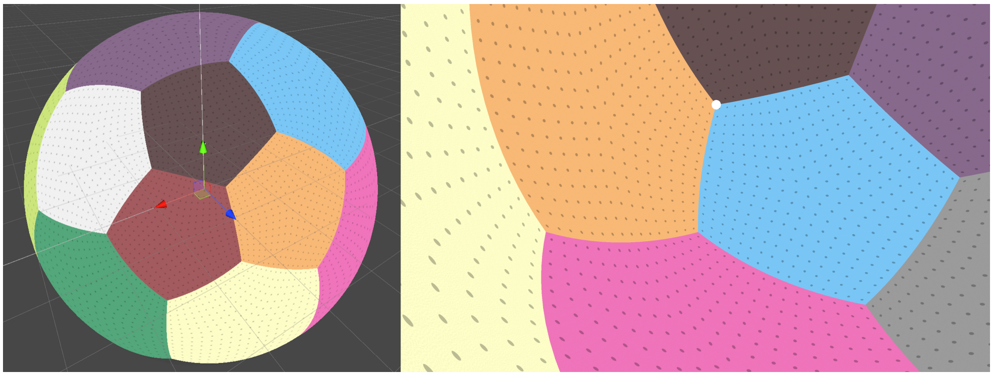

Figure 1. External view (left) and internal/game view (right), of the spherical (dodecahedron) environment.

2.1.4. Procedure

Participants experienced the environment from a first-person perspective. In the 'terrestrial movement' variants, participants navigated by using a standard keyboard: the W, A, S, D keys controlled the direction of movement, and the arrow keys controlled direction of gaze. In the '3D movement' variants, Q and E keys enabled roll rotation, allowing participants to navigate freely in three dimensions.

Participants were then asked to locate and memorize the positions of white spheres ('balls') that appeared within the virtual environment. To collect a ball, participants had to walk into it. The ball then disappeared, and the next one appeared at a different location. They appeared sequentially, each positioned at a vertex of the Platonic solid, i.e. where three coloured regions meet on the spherical surface. In the cubic variants, the six different colours resulted in eight possible location points (vertices), while in the dodecahedron variants, the 12 colours resulted in 20. The number of balls participants were required to locate and memorize increased by one in each subsequent trial, starting with one in the first trial. There was a total of eight trials, resulting in 36 location points to memorize across all trials. This incremental increase in memory load tested participants' spatial learning and working memory capacities.

After locating the ball(s) in the current trial, a 6 s delay followed, and participants were then asked to recall and navigate to the locations in the correct order. At each location, they were instructed to press the 'Enter' key to record their response before proceeding to the next. Recording was only possible when participants were within one of the predefined, invisible target areas, implemented as spherical regions centred on the vertices (radius approx. 40% of the edge length). Accuracy was based on whether participants responded within the correct target area.

Participants were instructed to perform the task as accurately as possible. The task was self-paced, and participants could take as much time as needed to navigate and memorize the locations. Across the eight trials, the total encoding phase lasted on average 10.72 min (s.d. = 8.93, median = 9.15) and the total recall phase 9.07 min (s.d. = 4.49, median = 8.34). These durations exclude the retention period.

At the end of the experiment, participants were asked to describe the strategies they used to memorize the location points. Similar strategy reports were collected in all three experiments and are analysed comparatively in §§2.2, 3.2 and 4.2.

Before the main task, participants completed three self-paced practice trials with one, two and three balls, respectively, to familiarize themselves with navigation and ball collection. No performance criterion was imposed, and data from these trials were not included in the analyses.

2.1.5. Data analysis

Statistical analyses were performed in R (v. 4.3.1; R Core Team, 2023), using RStudio as an interface.

To better understand participant behaviour in this novel task, the distributions of total correctly recalled location points (sequential recall scores) were analysed across variants. A point was awarded for each correctly recalled location in the correct serial position, with a maximum total score of 36 across the eight trials. To formally assess whether the distributions deviated from unimodality, we conducted tests of multimodality. Specifically, we applied Hartigan's Dip Test [37], a conservative test of unimodality, using the *diptest* package, and the excess mass test [38] using the *multimode* package.

Due to violations of normality and the bimodal distribution of sequential recall, a standard ANOVA was deemed inappropriate. Instead, to examine the effects of sex, environment and movement type on sequential recall performance, a permutation-based factorial ANOVA was conducted using the *aovp* function from the *lmPerm* package. A total of 1000 permutations were performed to assess the significance of main effects and interactions.

Complementary Bayesian ANOVAs were conducted using the *BayesFactor* package with default JZS priors, and top-down model comparisons (full versus reduced models) were used to obtain Bayes factors (BF_{01}), to quantify evidence for the absence of each effect. The analyses were run with 100 000 iterations to ensure stable Bayes factor estimates (Monte Carlo error < 10%)

2.2. Results

2.2.1. Sequential recall distributions

The Dip Test provided marginal evidence against unimodality ($D = 0.052$, $p = 0.050$), suggesting that the data contain at least two modes, whereas the excess mass test strongly rejected unimodality ($p = 0.008$). Similarly, when analysed separately by sex, while Hartigan's Dip Test did not indicate significant deviations from unimodality in either males or females, the more sensitive excess mass test showed evidence for multimodality in both groups (males: $p < 0.05$; females: $p < 0.05$).

Figure 2 illustrates the distribution of sequential recall scores across variants, revealing a consistent bimodal pattern where participants clustered at either higher or lower recall scores, with no participant performing at the median level. This bimodal distribution may reflect the novelty of the spatial task and indicates variability in approaches, present across both males and females.

2.2.2. No effects of environment, movement and sex on sequential recall

A permutation-based three-way ANOVA revealed no significant main effects of sex, $F_{1,88} = 0.06$, $p = 0.803$; environment, $F_{1,88} = 1.00$, $p = 0.320$; or movement type, $F_{1,88} = 0.01$, $p = 0.946$. Likewise, no significant interactions were found for sex × environment, $F_{1,88} = 0.27$, $p = 0.602$; sex × movement type, $F_{1,88} = 0.35$, $p = 0.556$; environment × movement type, $F_{1,88} = 2.05$, $p = 0.155$; or the three-way interaction, $F_{1,88} = 1.19$, $p = 0.278$ (figure 3).

Complementary Bayesian analyses provided moderate evidence for the absence of main effects of sex ($BF_{01} \approx 4.63$), environment ($BF_{01} \approx 3.06$) and movement type ($BF_{01} \approx 4.33$), as well as the sex × environment ($BF_{01} \approx 3.13$) and sex × movement ($BF_{01} \approx 2.90$) interactions. Evidence regarding the environment × movement interaction ($BF_{01} \approx 1.56$) and the three-way interaction ($BF_{01} \approx 1.76$) was anecdotal.

Self-reported strategies will be analysed in a later section, alongside with Experiment 2.

3. Experiment 2—spherical environment, with traditional landmarks

3.1. Methods

3.1.1. Participants

Sixty-eight participants (34 females) were recruited through Prolific (mean age = 27.07 ± 4.69 years). Participant eligibility, consent procedures and ethical approval were identical to those of Experiment 1. Combined with Experiment 1, the full sample provided approximately 80% power to detect an effect of $f = 0.26$ ($\alpha = 0.05$), corresponding to a medium effect in a 2 × 2 between-subjects design, as determined using the *pwr.anova.test* function from the *pwr* package in R. This experiment drew on a participant pool from a larger project, which accounts for the unequal sample sizes across experiments.

3.1.2. Material

Building upon Experiment 1 (*Spherical Sparse* condition), Experiment 2 introduced traditional landmarks within the environment, creating what will now be referred to as the *Spherical Landmark* condition. Since environment and movement types did not significantly influence participant performance in the *Spherical Sparse* condition, in this experiment only the combination of the

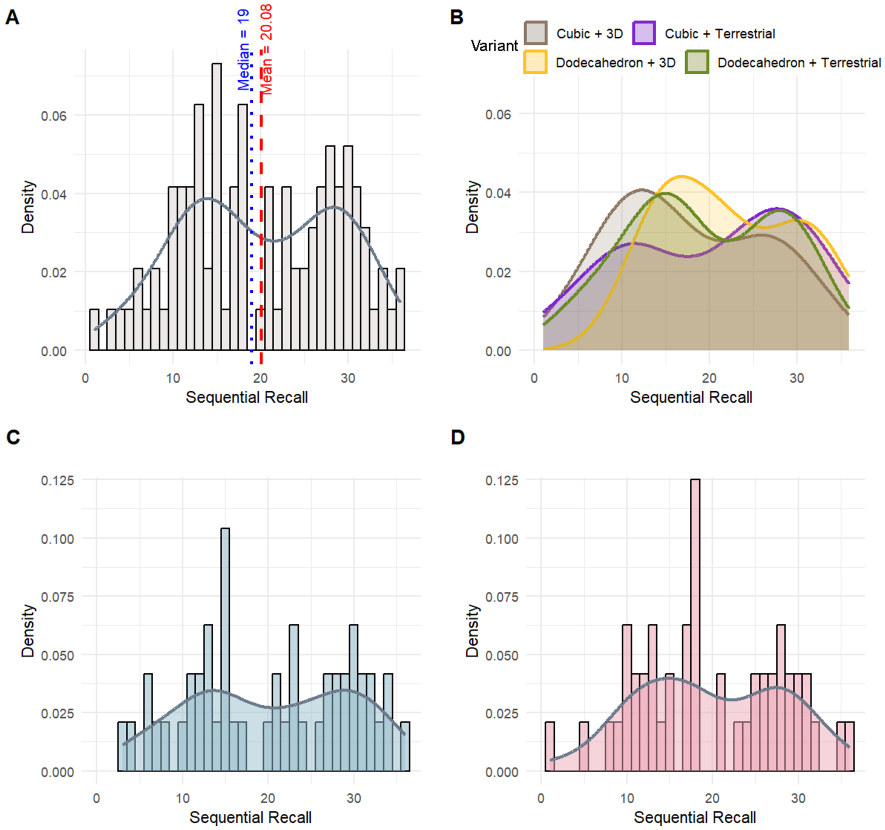

Figure 2. (A) Sequential recall score distribution across all participants, (B) smoothed distributions across variants and (C) among males and (D) females. In these and similar panels, the continuous curves, serving merely as guides to the eye, represent kernel density estimates of the data, obtained using a Gaussian kernel with an automatically determined bandwidth in RStudio.

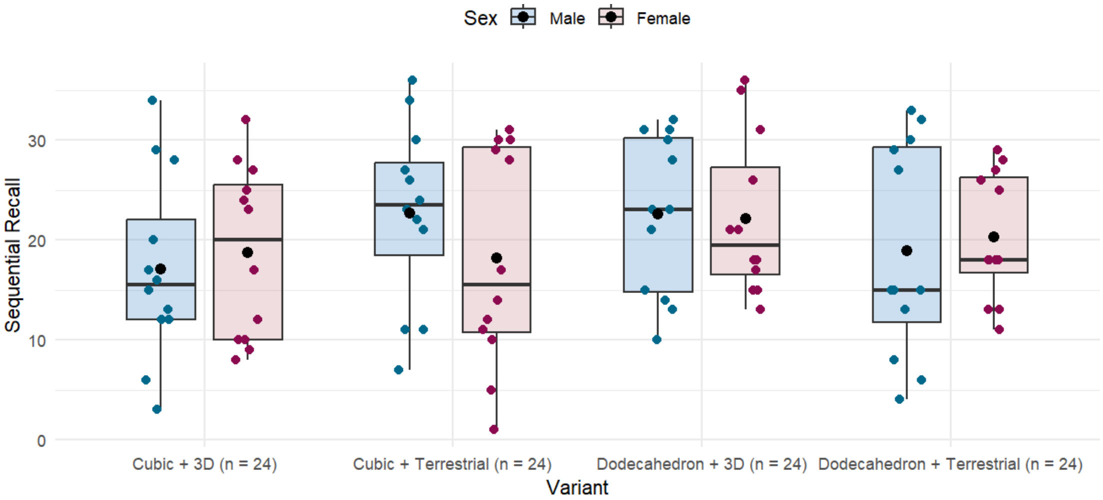

Figure 3. Sequential recall score by variant and sex. Groups were sex-balanced in all variants. We found no significant differences between the experimental variants. In this and similar figures, the bold line marks the median while the black dot shows the mean; the boxes represent the interquartile range (25th to 75th percentiles), and the whiskers extend to the minimum and maximum values within 1.5 times the interquartile range.

dodecahedron environment with 3D movement was used. Eighteen landmarks were placed along some of the edges of the faces and three landmarks on each face (figure 4). To maintain engagement and encourage steady task progression in the online setting, given the high variability in completion times observed in Experiment 1, we added a 40 s time constraint per ball (in both the encoding and recall phases) and provided corrective feedback (CORRECT/FALSE) after each recorded location.

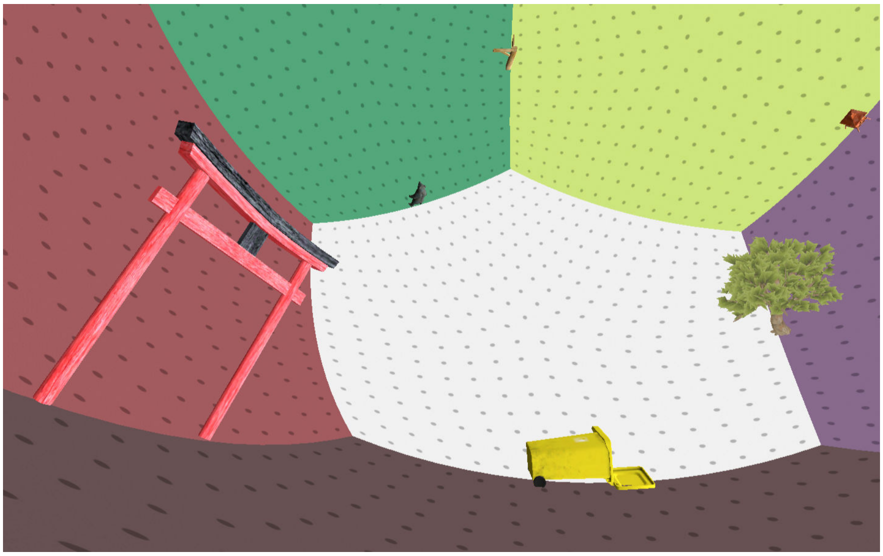

Figure 4. Game view of the *Spherical Landmark* condition. The landmarks were placed on the centre of the edges.

3.1.3. Procedure

The procedure was identical to that of Experiment 1, except that a time constraint and corrective feedback were introduced. Across the eight trials, the total encoding phase lasted on average 10.92 min (s.d. = 3.48, median = 9.73), and the total recall phase 10.07 min (s.d. = 3.37, median = 9.41), excluding the retention period.

3.1.4. Strategy assessment

After completing the task, participants were asked to describe the strategy they used to memorize the ball locations in an open-ended text response. This procedure was identical to that used in Experiment 1. Strategy prompts are provided in electronic supplementary material, S1.

Strategy categories were derived in a data-driven manner based on recurring patterns in participants' free-text descriptions in Experiment 1, as the task was exploratory in nature and lacked conventional spatial cues. Responses from Experiment 2 further confirmed these categories, with the inclusion of a landmark-based strategy.

Strategy reports were coded by a single researcher using predefined criteria. Coding was performed based on the free-text responses, independent of participant data (such as sex or experimental condition). Inter-rater reliability was not assessed.

3.1.5. Data analysis

The excess mass test was used to assess modality of sequential recall distributions.

The distribution of sequential recall scores was examined to characterize participant behaviour in this somewhat more familiar environment with added traditional landmarks. To further investigate the effects of condition and sex, sequential recall scores from the *Spherical Sparse* condition (Experiment 1) and the *Spherical Landmark* condition (Experiment 2) were compared. Due to violations of normality and unequal group sizes, a permutation-based ANOVA was conducted by fitting a linear model and computing the F-statistic across 1000 permutations, in which the predictor labels (*Spherical Sparse* versus *Spherical Landmark* and male versus female) were randomly shuffled while keeping the sequential recall scores fixed.

In addition to the permutation-based ANOVA, a complementary Bayesian ANOVA was conducted using the *BayesFactor* package with default JZS priors, providing Bayes factors (BF_{01}), to quantify evidence for or against each effect.

Self-reported strategies were categorized into four distinct strategy preferences. Separate chi-square tests of independence were conducted to examine whether a basic dichotomic strategy preference (spatial versus non-spatial) differed by sex within each condition. Given the binary nature of such basic strategy variable and the relatively small sample sizes, Yates' continuity correction was applied to each test.

3.2. Results

3.2.1. Sequential recall distributions

Although the excess mass test did not reject unimodality ($p = 0.080$), visual inspection of the distribution of sequential recall scores across participants revealed a multimodal pattern. Compared with the *Spherical Sparse* condition, the recall distribution in the *Spherical Landmark* condition showed a peak emerging around the centre, indicating that the addition of landmarks influenced the distribution of participant recall performance. Notably, this distribution appears closer to normality, with the appearance of a cluster of participants performing at 'intermediate' levels, between those who 'get it' and those who basically do not 'get it'. Note that, separating the score distributions of the two sexes, the intermediate cluster appears to be largely contributed by male participants (figure 5C,D).

3.2.2. No significant effects of condition and sex on sequential recall

The permutation-based ANOVA revealed no significant effect of the combination of condition (Sparse versus Landmark) and sex (male versus female) on (average) sequential recall performance (figure 6). A permutation test with 1000 iterations yielded a p-value of 0.891. Regression coefficients showed slight variation of recall scores across conditions. The full regression coefficients are reported in electronic supplementary material, table S1.

Complementary Bayesian analyses indicated moderate evidence for the absence of a sex effect ($\mathrm{BF}_{01} \approx 5.59$), moderate evidence for the absence of a condition effect ($\mathrm{BF}_{01} \approx 4.81$) and moderate evidence for the absence of a sex × condition interaction ($\mathrm{BF}_{01} \approx 4.45$).

3.2.3. Strategy preference—qualitative analysis

Self-reported strategy preferences were now categorically analysed, together with those from Experiment 1, based on classification criteria, reported in electronic supplementary material, S1. In the *Spherical Sparse* condition, three distinct basic strategy preferences were identified:

1. *Colour rehearsal*: mentally repeating or otherwise referencing colour combinations, using either full colour names or abbreviated forms (e.g. 'red–white–green', 'r–w–g').
2. *Associations*: associating colour combinations with familiar concepts or assigning meanings (e.g. 'Italian flag', 'lighter-toned colours versus darker-toned colours').
3. *Spatial*: using spatial cues such as turns, angles or distances (e.g. 'I tried to memorize my starting point and which path I followed').

To minimize bias and eliminate overlap, these categories were collapsed into two binary groups: *spatial* versus *non-spatial* strategies. Participants who relied on strategy 3 were categorized as spatial strategy users, otherwise they were categorized as non-spatial strategy users.

In the *Spherical Landmark* condition, an additional basic strategy category emerged:

4. *Landmark*: using traditional landmarks as reference points (e.g. 'I have used sometimes colours, sometimes the little objects').

Since traditional landmarks were placed at the centre of the edges of the coloured faces and not in immediate proximity to the white balls, relying on them inherently required, unlike cue-navigation in the Morris water maze [39], some spatial reasoning. Therefore, the *Landmark* strategy was classified as part of the *Spatial* strategy category in the collapsed analysis.

Figure 7 presents the proportions of spatial and non-spatial strategy users by sex and by condition. Chi-square tests showed no significant association between sex and strategy preference in the Sparse condition ($\chi^2(1) = 0.39$, $p = 0.535$). However, in the Landmark condition, a significant association was found ($\chi^2(1) = 4.20$, $p = 0.040$). Interestingly, this significant difference in strategy preference did not translate into a significant difference in sequential recall performance.

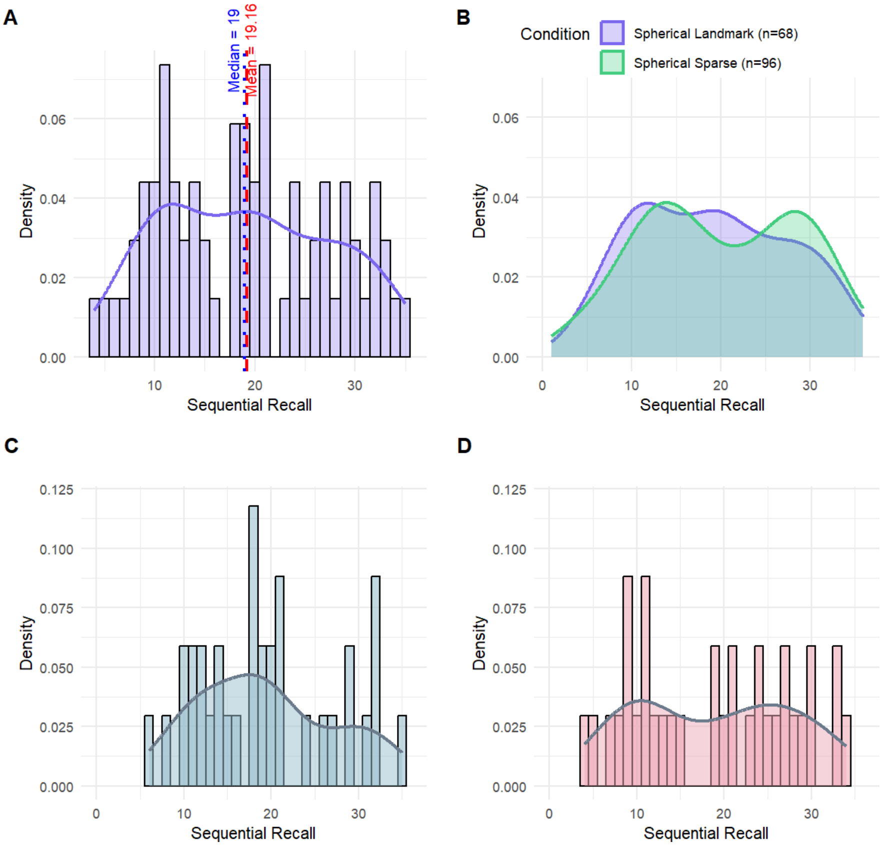

Figure 5. (A) Sequential recall score distribution across participants in the *Spherical Landmark* condition, (B) smoothed distributions in the *Spherical Sparse* and *Spherical Landmark* conditions and (C) among males and (D) females in the *Spherical Landmark* condition.

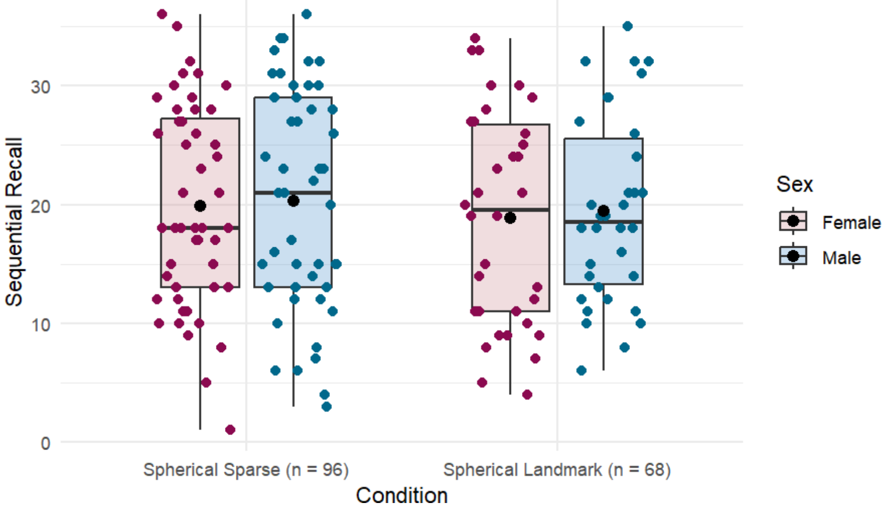

Figure 6. Sequential recall score by condition and sex in Experiment 1 versus Experiment 2. Groups were sex-balanced. The model could not identify a difference between the two sexes in either of the two conditions.

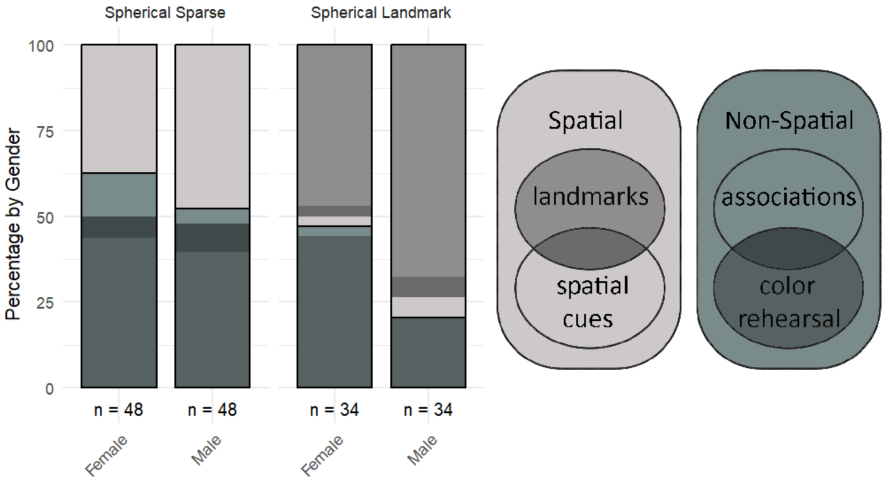

Figure 7. Spatial and non-spatial strategy preferences by condition and sex. Grey represents spatial strategies, green represents non-spatial strategies. The darkest shade within each colour indicates overlapping use of multiple sub-strategies within that category.

4. Experiment 3—flat, sparse environment

4.1. Methods

4.1.1. Participants

Sixty-eight participants (34 females, mean age = 28.22 ± 5.7 years) were recruited through Prolific. Participant eligibility, consent procedures and ethical approval were identical to those of Experiment 1. Combined across all three experiments (n = 232), the full sample provides 80% power (α = 0.05, f = 0.22) to detect medium effects in a 2 × 3 between-subjects design, as determined using the *pwr.anova.test* function from the *pwr* package in R. This experiment drew on a participant pool from a larger project, which accounts for the unequal sample sizes across experiments.

4.1.2. Material

Experiment 3 introduced a Euclidean environment, that is, the flat version of the spherical, sparse environment, which will now be referred to as the *Flat Sparse* condition. The 17 coloured hexagon tiles composed 20 vertices (figure 8), making it identical to the number of possible ball location points in the dodecahedron. The navigable surface was approximately 7 × 8 Unity units. The size was chosen to optimize overall visibility of the coloured tiles and to make the environment visually and perceptually comparable with the spherical setup. Based on this surface size, the movement speed (approx. 0.6 Unity units per second) was then selected to maintain perceptual comparability.

4.1.3. Procedure

The procedure was identical to that of Experiment 1, except that, following the sequential recall task, participants not only provided free verbal descriptions of their strategies, but also indicated them by selecting from predefined categories. Across the eight trials, the total encoding phase lasted on average 8.21 min (s.d. = 5.31, median = 6.21) and the total recall phase 7.65 min (s.d. = 5.35, median = 6.02), excluding the retention period.

4.1.4. Strategy assessment

Participants first provided a free-text description of their strategy and were subsequently asked to select from a set of predefined strategy categories (see electronic supplementary material, S1). Participants were not informed of these categories prior to providing the free-text report. Final strategy labels were assigned primarily based on the free-text responses, with the categorical selections used to support classification where applicable. The procedure of strategy coding was otherwise identical to Experiments 1 and 2.

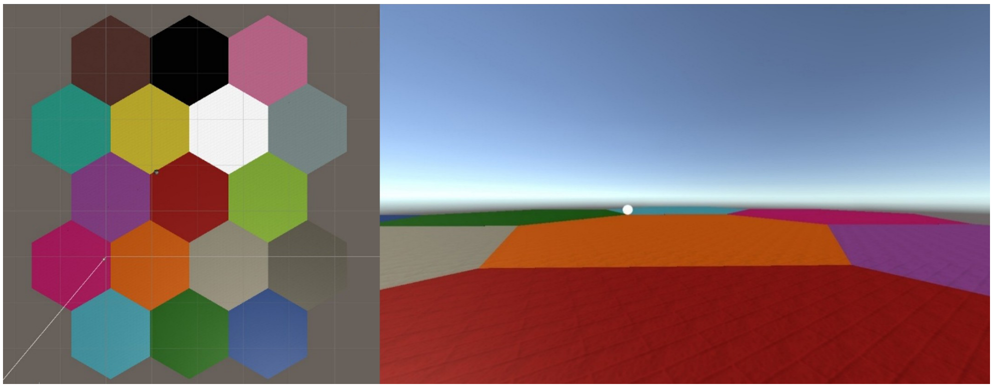

Figure 8. Map view (left) and game view (right), of the *Flat Sparse* condition.

4.1.5. Data analysis

The distribution of sequential recall scores was examined to understand participant behaviour in such a flat environment of increased (Euclidean) familiarity/plausibility.

To further investigate the effects of condition and sex, sequential recall scores from the *Spherical Sparse* condition (Experiment 1), *Spherical Landmark* condition (Experiment 2) and *Flat Sparse* condition (Experiment 3) were analysed together. Due to violations of normality and unequal group sizes, a permutation-based ANOVA was conducted by fitting a linear model and computing the F-statistic across 1000 permutations, in which the predictor labels (*Spherical Sparse* versus *Spherical Landmark* versus *Flat Sparse* and male versus female) were randomly shuffled while keeping the sequential recall scores fixed.

A complementary Bayesian ANOVA was conducted using the *BayesFactor* package with default JZS priors, providing Bayes factors (BF_{01}), to quantify evidence for the absence of each effect.

Since the *Flat Sparse* condition data approximately followed a normal distribution, an independent-samples t-test was conducted to further examine the difference in sequential recall scores between males and females in this condition. Given the nominally significant result, a complementary Bayesian independent-samples t-test with default JZS priors was conducted, and a Bayes factor (BF_{10}) was used to quantify the strength of evidence for a sex difference.

A chi-square test of independence with Yates' continuity correction was conducted to examine whether strategy preference (spatial versus non-spatial) differed by sex.

A linear regression model was conducted to examine associations between sequential recall performance, condition (*Spherical Sparse* → *Spherical Landmark* → *Flat Sparse*, ordered by increasing environmental familiarity) and sex (male versus female), among those who employed a spatial strategy. A separate analysis was conducted for participants who used a non-spatial strategy.

To assess navigational efficiency, the mean encoding and recall times and total encoding and recall path lengths were analysed within each condition. These measures were log-transformed to reduce skewness and analysed separately by condition, as they were not directly comparable across environments.

Linear regression models examined associations between sequential recall and encoding or recall efficiency (both times and paths), including sex and interaction terms. In addition, sex differences in times and path lengths were tested within each condition using independent-samples t-tests or Wilcoxon tests as appropriate, with Holm–Bonferroni corrections applied for multiple comparisons.

4.2. Results

4.2.1. Sequential recall distributions

The distribution of sequential recall scores across participants followed a roughly normal distribution (figure 9). Compared with the *Spherical Sparse* and *Spherical Landmark* conditions, this distribution reflected a more continuous and nuanced range of recall performance. This may suggest that Euclidean spatial structure alone, rather than traditional landmarks, offers a more familiar and effective spatial reference framework.

4.2.2. Effects of condition and sex on sequential recall

The permutation-based ANOVA revealed no significant effect of the combination of condition and sex on average sequential recall performance (figure 10). A permutation test with 1000 iterations yielded a *p*-value of 0.428.

While complementary Bayesian analyses indicated strong evidence for the absence of a condition effect ($BF_{01} \approx 14.44$), and moderate evidence for the absence of a sex × condition interaction ($BF_{01} \approx 5.51$), only anecdotal evidence supported the absence of a sex effect ($BF_{01} \approx 2.86$).

By contrast, an independent samples *t*-test revealed a nominally significant difference in sequential recall between sexes in the *Flat Sparse* condition, with males outperforming females $t_{(66)} = 2.08$, $p = 0.041$, 95% CI [0.17, 8.07]. However, a Bayesian *t*-test provided only anecdotal evidence for a sex difference ($BF_{10} \approx 1.5$).

4.2.3. Strategy preference

A chi-square test showed no significant association between sex and strategy preference ($\chi^2(1) = 0.24$, $p = 0.624$). Participants in this condition showed similar sex-specific strategy preferences to participants in the *Spherical Sparse* condition. Figure 11 illustrates the proportions of spatial versus non-spatial strategy users by sex and by condition.

4.2.4. Effect of spatial versus non-spatial strategy on sequential recall

The linear regression model revealed no significant main effect of condition ($\beta = -3.18$, $p = 0.124$), indicating that sequential recall scores did not vary systematically as a function of condition when averaging across sex. However, a significant linear condition × sex interaction ($\beta = 6.34$, $p = 0.024$) was observed, suggesting that the association between condition and performance differed by sex. Specifically, the regression coefficients suggested that, among spatial strategy users, males showed an increasingly positive association between performance and more plausible conditions compared with less plausible ones. Female spatial strategy users did not exhibit the same pattern; instead, performance in the Euclidean condition tended to be lower relative to the two non-Euclidean conditions. *Post hoc* pairwise comparisons indicated a significant sex difference in the *Flat Sparse* condition ($p = 0.035$), with males outperforming females. No significant sex differences were found in the *Spherical Sparse* ($p = 0.310$) or *Spherical Landmark* ($p = 0.958$) conditions.

The linear regression model conducted for participants who employed a non-spatial strategy did not reveal any significant main effects or interactions (all $p > 0.05$). The overall model was not significant, $F_{(5,\ 112)} = 1.30$, $p = 0.268$. Although figure 12 suggests a notable difference in sequential recall performance among males in the *Spherical Landmark* condition, the disproportionately small sample size ($n = 7$) makes this trend less reliable and may have skewed the results.

4.2.5. Navigational efficiency

In the *Spherical Sparse* and *Flat Sparse* conditions, longer encoding and recall times were associated with higher sequential recall (all encoding $p \leq 0.022$; all recall $p \leq 0.003$), with no sex × time interactions. In the *Spherical Landmark* condition, encoding and recall times did not reliably predict performance; however, direct comparisons revealed that males were faster than females during both encoding and recall (Holm-corrected $p < 0.05$). By contrast, no sex differences in encoding or recall times were observed in either sparse condition.

In the *Spherical Sparse* and *Spherical Landmark* conditions, neither encoding nor recall path length reliably predicted sequential recall, and no sex × path interactions were observed. In the *Flat Sparse* condition, shorter recall paths were associated with higher sequential recall ($p = 0.018$), whereas encoding path length was not predictive, and no sex × path interactions were observed. Direct comparisons revealed a sex difference in recall path length only in the Landmark condition (Holm-corrected $p = 0.0025$), with no sex differences in path length in the sparse conditions.

5. Discussion

The experiments reported here are part of a wider programme intended to assess to what extent spatial behaviour in non-standard environments can be understood in terms of cognitive maps. In

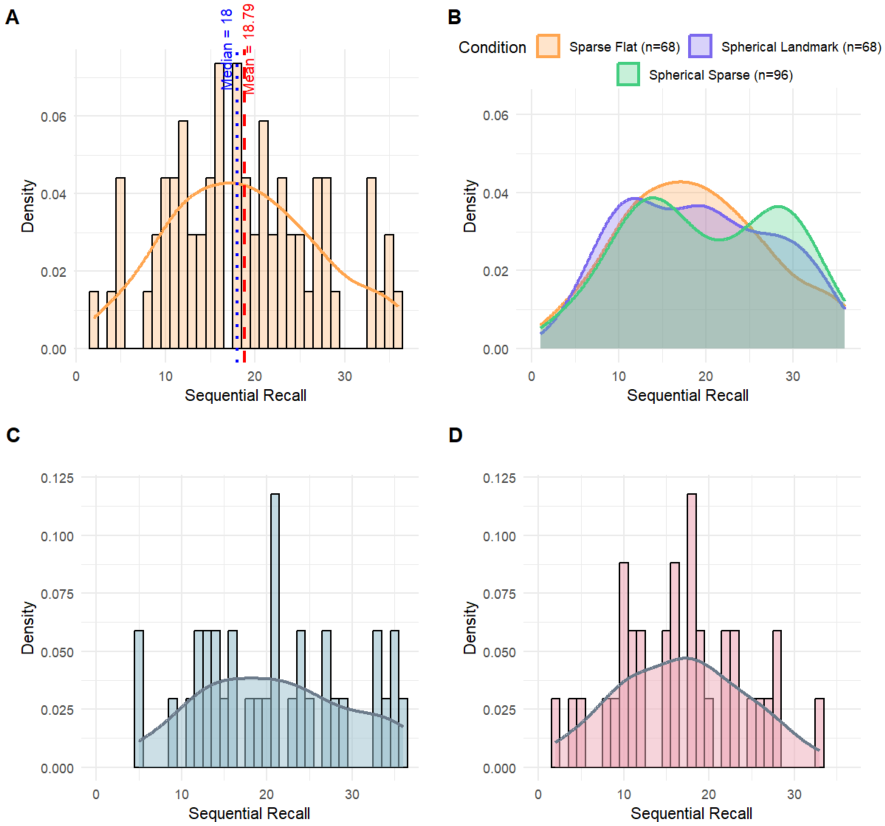

Figure 9. (A) Sequential recall score distributions across participants in the *Flat Sparse* condition and (B) in the *Spherical Sparse*, *Spherical Landmark* and *Flat Sparse* conditions, and (C) among males and (D) females in the *Flat Sparse* condition.

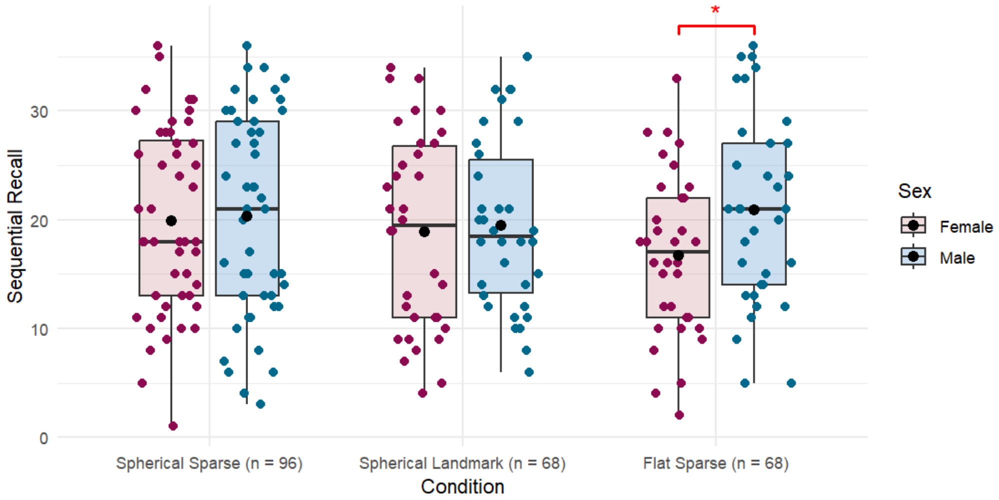

Figure 10. Sequential recall score by condition and sex. The bold line marks the median and the black dot shows the mean. Groups were sex-balanced in all conditions.

the present case, we have striven to maintain as much as possible the same structure of the spatial memory task across conditions, aiming for comparable performance. Still, we expected differences (between conditions, as well as between sexes) to appear primarily in *average* performance scores. It was surprising to observe such a modulation of the score *distribution*.

The novel spatial structure in the *Spherical Sparse* condition may have led to the bimodal distribution, as participants either adapted effectively to the task or struggled to develop a strategy. This behavioural pattern was consistent across variants of this condition and between sexes, indicating that in highly unfamiliar environments, individual differences in navigation ability are increased. The difference between the bimodal distribution in the *Spherical Sparse* condition and the somewhat

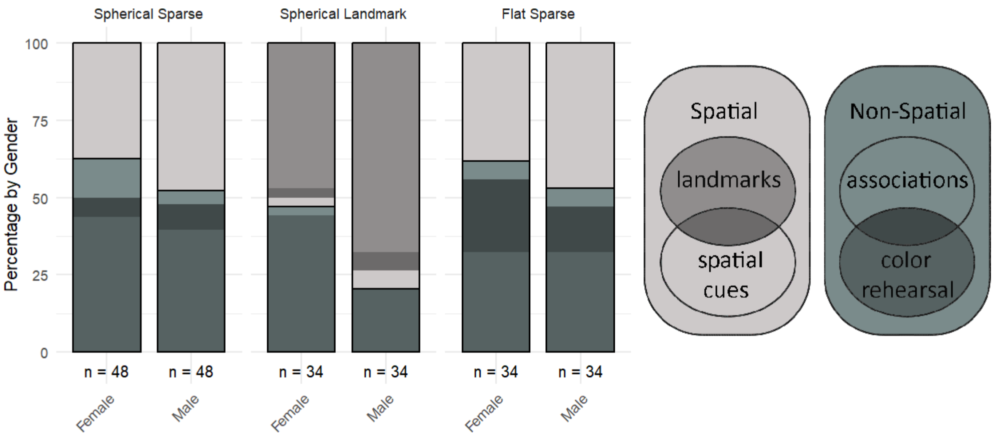

Figure 11. Spatial and non-spatial strategy preferences by condition and sex.

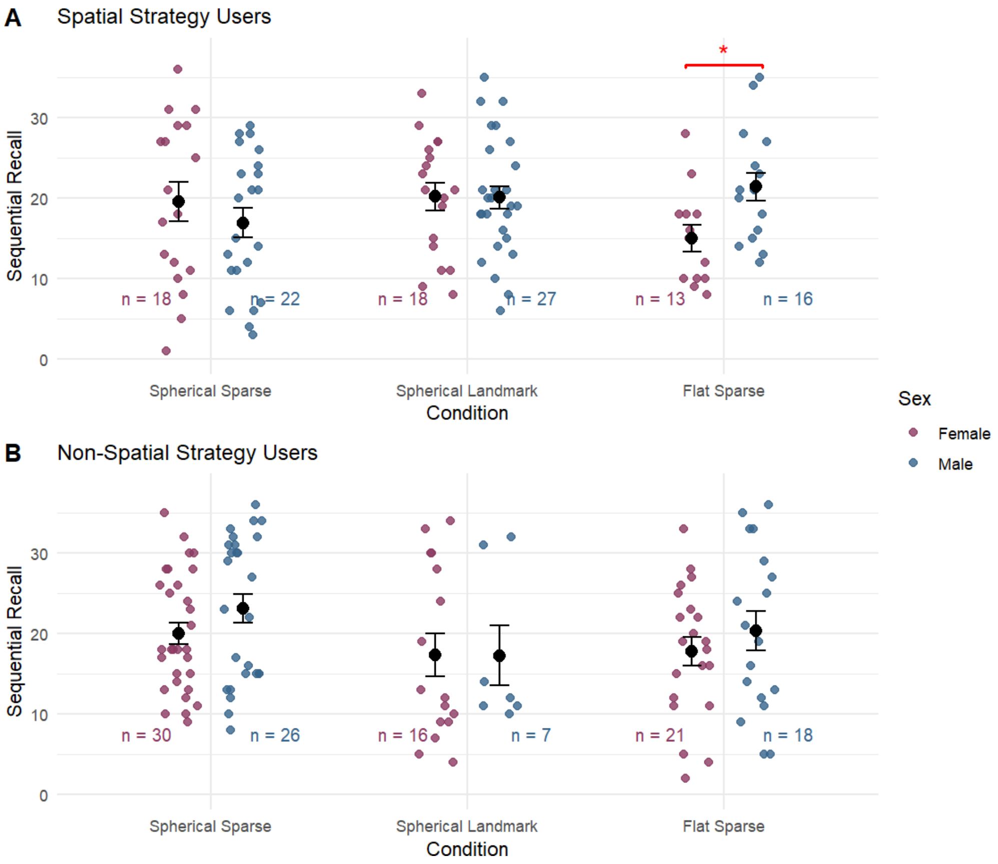

Figure 12. Effect of (A) spatial strategy and (B) non-spatial strategy, on sequential recall by condition and by sex.

more normal-like distribution in the *Spherical Landmark* condition suggests that the introduction of familiar spatial cues (traditional landmarks) already influenced recall behaviour, particularly by males, and then that the move to a standard Euclidean environment led to the use of familiar routines, by both sexes. While in the less plausible *Spherical Sparse* environment participant performance patterns were polarized, the addition of traditional landmarks in the *Spherical Landmark* condition may have provided some familiar elements of a reference frame, that enabled the use of a more varied set of cues for recall, reflected in the more continuous distribution of recall scores. The contrast between the multimodal distributions in both spherical conditions and the roughly normal distribution in the *Flat Sparse* condition may suggest that Euclidean space, even without traditional landmarks, tends to elicit complex recall processes with multiple contributions, none of them dominant, leading to quasi-normal distributions. It also suggests that spatial structure contributed more than landmarks to perceived environmental plausibility and led to more use of standard spatial memory schemata. Thus, the observed differences in performance distribution, ranging from bimodal to trimodal to normal, may reflect varying degrees of perceived plausibility in the task environments. It should be noted, though, that there were no significant differences in average performance, to accompany such differing degrees of spatial plausibility.

If one abstracts away from sex differences, this pattern might mirror a shift from a hippocampus-dependent 'episodic' recollection of a spherical map to a prevailingly neocortical familiarity-based mode of managing navigation towards the ball locations. According to the 'remember/know' paradigm in memory studies, recollection of specific events tends to produce categorical, all-or-none responses supported by the hippocampus, while familiarity with some features of the available cues, analysed in neocortical regions such as the perirhinal cortex, leads to more graded responses [40]. The critical notion is that failure to recollect would yield completely random responses, for example in famous face recognition studies, while the activation of neocortical schemata can generate partially correct ones [41]. In our spatial memory task, the reasoning could be, with more familiar and plausible environments participants may quickly adapt spatial memory schemata, or routines [42], which work to some extent, resulting in more continuous distributions of sequential recall scores. In the more unfamiliar environment of the *Spherical Sparse* condition, such schemata might be inapplicable, which might explain the polarized performance. This may not be in contrast with findings from Ciaramelli *et al.* [43], who showed that egocentric navigation and the re-experiencing of spatial memories depend on posterior parietal cortex function, suggesting that familiarity-based processes may involve neocortical regions more specifically, but see Rugg & Vilberg [44].

When taking into account the observed sex differences, however, this simple reasoning does not seem to coalesce into a consistent dichotomic perspective. In mice, a male advantage in an incidental memory task was explicitly related to increased hippocampal activation and could be reversed by deactivating the hippocampus [45]. By extrapolation across species, tasks and time scales, one could expect the all-or-none recollection of the spherical configuration of the environment, perhaps of a spherical cognitive map, to be hippocampus-dependent [46], and to be more effective in males. Such an extrapolation glosses over a complex phenomenology [16,47].

Notably, in our experiments the typical male advantage was not observed in the non-Euclidean environments, as males and females showed similar sequential recall scores in the *Spherical Sparse* and the *Spherical Landmark* conditions. The male advantage emerged in the most familiar environment, in the *Flat Sparse* condition. This may suggest that males are benefiting from Euclidean structure as they tend to rely more on coordinate-based spatial processing [10,48].

The change in spatial structure also evoked a sex difference in strategy preference. In the *Spherical Landmark* condition, only males showed a significant preference for a spatial strategy, particularly in landmark use. Males' higher reliance on the traditional landmarks does not contradict the literature. In this spatial paradigm, the colour combinations also serve as landmarks. However, unlike the traditional landmarks that are not in the proximity of the target object and therefore require spatial cues, the colour combinations only provide visual feature cues. The distinction between the spatial and non-spatial landmarks therefore suggests that the male preference for traditional landmarks may be a reliance on spatial relations, rather than on feature cues. By contrast, the female preference for landmark use reported in the literature may stem from a reliance on visual features. This interpretation is consistent with the findings of Jones & Healy [13], who observed that females prefer to rely on object visual cues, while males use both visual and spatial cues.

Interestingly, strategy preferences in Experiment 3 closely resembled those in Experiment 1, despite differences in spatial structure (non-Euclidean versus Euclidean). In both cases, where no traditional landmarks were available, males and females showed no significant differences in strategy selection, using spatial and non-spatial strategies at similar frequencies. However, among participants who employed a spatial strategy, male performance tended to be higher in the environment with greater spatial familiarity. Females did not show the same trend, suggesting that increased familiarity may be more strongly associated with better performance in males, specifically among spatial strategy users. This may reflect enhanced processing in a number of cortical areas, where higher activation has been observed in males [49]. In contrast, females appear to benefit more from non-spatial strategies, i.e. utilizing visual feature cues.

Together, these findings suggest that sex differences in spatial memory are not fixed but context dependent. When the environment is unfamiliar, the gender gap may diminish. In more structured and plausible environments, gendered strategy preferences are more pronounced, and performance differences tend to favour males, particularly those using spatial strategies. It remains to be seen, possibly in a future imaging study, whether the bimodal performance distribution observed in the

Spherical Sparse condition reflects an all-or-none recollection operation taking place in the hippocampus or in specific cortical regions or, perhaps, in a global workspace.

6. Limitations

Several methodological considerations should be noted when interpreting the present findings. First, the overall strength of evidence for sex-related effects was limited, with Bayesian analyses indicating weak or moderate support for some patterns. Accordingly, the present study should be regarded as exploratory, aimed at identifying potential trends and associations rather than establishing conclusive sex differences. Larger samples will be required in future work to robustly distinguish evidence of absence from evidence for sex-related effects. Second, prior experience with video games or virtual environments was not assessed. Such experience, particularly with action or 3D video games, has been shown to influence spatial performance and may differ between sexes [50]. Future studies should assess and control for this factor to disentangle task-specific effects from prior familiarity with virtual navigation. Third, task constraints differed across experiments. Experiments 1 and 3 were fully self-paced, whereas Experiment 2 imposed a 40 s time limit per ball and provided corrective feedback. Although these changes were introduced to reduce variability in completion times and maintain engagement, differences in timing and feedback may have altered task demands or strategy use and should be considered when comparing results across experiments. Fourth, strategy reports were coded by a single researcher, and inter-rater reliability was not assessed, and this should be considered when interpreting strategy-related findings. Finally, although prior neurobiological work is discussed to contextualize the findings, no biological variables were measured in the present study. Cultural, experiential and socially learnt factors may therefore also contribute to the observed sex-dependent associations. Future work combining behavioural paradigms with background measures or neuroimaging will be necessary to clarify these contributions.

7. Conclusion

Taken together, the present findings suggest that environmental familiarity affects sequential recall of spatial locations and is associated with sex-related differences. In the most unfamiliar, non-Euclidean environment, performance was bimodal and similar across sexes, with no dominant strategy. In the landmark-rich condition, still non-Euclidean, males favoured spatial strategies significantly and showed a more continuous performance distribution. In the Euclidean environment, performance followed roughly a normal distribution, for both sexes, and males outperformed females. These results suggest that sex differences in spatial memory are not fixed but vary depending on environmental familiarity and plausibility, especially in settings that resemble real-world spatial structures.

Ethics. The study was approved by the Ethics Committee of the International School for Advanced Studies (SISSA) and was conducted according to the Declaration of Helsinki (1964) and its later amendments.

Data accessibility. All data, analysis scripts and materials supporting this study are publicly available at the Open Science Framework [51].

Electronic supplementary material is available online [52].

Declaration of AI use. Artificial intelligence was used for some assistance with coding syntax. All analyses and interpretations were performed by the authors.

Authors' contributions. J.F.: conceptualization, data curation, formal analysis, investigation, methodology, software, visualization, writing—original draft; A.T.: conceptualization, formal analysis, methodology, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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