Journal of Memory and Language 141 (2025) 104587

Contents lists available at ScienceDirect

Journal of Memory and Language

journal homepage: www.elsevier.com/locate/jml

Flexible utilization of spatial representation formats in working Memory: Evidence from both small-scale and large-scale environments

Wei Chen [a], Wenwen Li [a], Yushang Huang [b], Xiaowei Ding [a,*]

[a] *Department of Psychology, Sun Yat-sen University, Guangzhou, China*
[b] *School of Education Science, Zhoukou Normal University, Zhoukou, China*

ARTICLE INFO

Keywords:
Spatial representation
Working memory
Polar coordinates
Cartesian coordinates
VR

ABSTRACT

Extensive studies have examined spatial representations in working memory (WM). However, their format and consistency across laboratory and large-scale environments remain less understood. Drawing insights from perception research, we proposed two hypotheses regarding the formats: polar coordinates and Cartesian coordinates, and examined these hypotheses in both small-scale and large-scale environments by error correlation analysis. Participants memorized target locations and reproduced them on a computer screen or navigated to corresponding locations in a virtual reality environment. The results revealed that participants defaulted to using polar coordinates to represent space in both environments, rather than Cartesian coordinates. Moreover, the spatial representation format proved flexible. In laboratory settings with grid-like memory contexts, participants tended to adopt Cartesian representations, with the encoding phase playing a more crucial role than the response phase. In large-scale environments, an indirect response type prompted participants to adopt Cartesian representations. Overall, our study underscores the prevalence and flexibility of polar representations for space in WM.

Introduction

The retention of spatial information serves as a crucial component of working memory (WM), as demonstrated by influential works (Baddeley, 1992; Baddeley & Hitch, 1974; Logie, 1986; Mishkin & Ungerleider, 1982). Its impact extends to diverse domains of human cognition, including mathematical abilities (Caviola et al., 2020; Holmes et al., 2008), social cognition (Parkinson & Wheatley, 2013), and navigation (Blacker et al., 2017; Maguire et al., 1997; Weisberg & Newcombe, 2016). Consequently, WM representations of spatial information have intrigued vast investigations, encompassing topics such as the role of space in feature binding within WM (e.g., Heuer & Rolfs, 2021; Pertzov & Husain, 2014; Schneegans & Bays, 2017), neural correlates associated with spatial representations in WM (e.g., Alekseichuk et al., 2016; Foster et al., 2017; Tamura et al., 2017), and factors influencing WM of spatial information (e.g., Brady & Tenenbaum, 2013; Huang, 2023; Langlois et al., 2021). However, few studies have addressed a fundamental question: What is the format of spatial representations in WM, which governs how these representations are manipulated and utilized (but see Huttenlocher et al., 1991; Yousif et al., 2024). While these studies have provided preliminary evidence that spatial information is represented in polar coordinates within WM, it remains unclear whether this format is constant or flexible. Moreover, these studies have primarily focused on laboratory settings. Given the importance of WM spatial representations in real-life tasks such as navigation, and the potential differences in cognitive mechanisms between laboratory and real-world tasks (Taylor-Phillips et al., 2024), it is necessary to explore their format in large-scale environments. To bridge these gaps, our study aims to investigate the WM format of spatial representations across both small-scale and large-scale environments.

While various mathematical representations exist for spatial information, our study specifically focuses on two common formats: Cartesian coordinates (x, y) and polar coordinates (angle, radius). A Cartesian reference frame represents spatial locations via orthogonal x and y dimensions, providing an allocentric encoding of spatial relationship (Klatzky, 1998). In contrast, a polar reference frame encodes space based on a radial distance from a central origin point and an angular direction. This format naturally captures the egocentric spatial relationships experienced from a first-person perspective, with the observer's current position serving as the reference origin (Klatzky, 1998). Recent research has highlighted the discernibility of these two formats through an analysis of the correlation of reproduction errors in the two

* Corresponding author at: Department of Psychology, Sun Yat-sen University, Guangzhou, China.
E-mail address: dingxw3@mail.sysu.edu.cn (X. Ding).

https://doi.org/10.1016/j.jml.2024.104587
Received 16 April 2024; Received in revised form 10 September 2024; Accepted 29 November 2024
Available online 2 December 2024
0749-596X/

dimensions within the same coordinate system (Yousif & Keil, 2021; Yousif et al., 2024). The underlying rationale stems from the orthogonality of dimensions within both coordinate systems. Specifically, the noise sources for each underlying coordinate dimension are assumed to be uncorrelated. Thus, if observers employ a certain coordinate system to represent space, then unsigned errors in the two dimensions within that system should be independent or unrelated. For polar representations, this analytical approach makes further assumptions that unsigned errors on the x and y axes will exhibit a significant correlation concurrently. In contrast, the pattern of polar correlations predicted by Cartesian representations depends on specific task details (Yousif et al., 2024). Thus, polar representations predict both correlated Cartesian errors and uncorrelated polar errors, whereas Cartesian representations predict only uncorrelated Cartesian errors. These assumptions are well-supported by simulation analyses from previous research (Yousif & Keil, 2021; Yousif et al., 2024), which confirm the validity of this approach. A similar analytical approach has also been applied to differentiate whether WM stores items as a bound unit or independent features (Bays et al., 2011). Remarkably, employing this error correlation analysis, researchers have discovered that spatial information defaults to being represented in polar coordinates within WM (Yousif et al., 2024). Additional evidence supporting the utilization of polar coordinates includes findings from animal studies, where desert ants were revealed to navigate home by continuously updating their homing direction and distance (Sommer & Wehner, 2005; Wittlinger et al., 2006).

Beyond these studies, an unresolved question is whether the representation of polar coordinates in WM is invariant or operates in a flexible way. Existing evidence seems to support the latter. For instance, in perception, Yousif and Keil (2021) found that participants' mislocalizations were more consistent with the use of Cartesian coordinates under grid-like contexts, rather than polar coordinates. Furthermore, different spatial formats have been identified for representing different types of information or fulfilling different task demands (Hudson & Landy, 2012; Park et al., 2020; Peer et al., 2021; Yousif et al., 2024). In large-scale navigation tasks, task settings have also been revealed to influence the format of spatial representations (He & Brown, 2019; Peer et al., 2024). Additionally, researchers have proposed flexible or hybrid models that integrate the advantageous characteristics of both Euclidean and topological models for representing space (Chown et al., 1995; Kuipers, 2000; Mallot & Basten, 2009; Trullier et al., 1997). These findings collectively imply the flexible use of different spatial formats in WM. To directly examine the flexibility of spatial representations in WM, the current study implemented distinct memory contexts. We examined whether the formats of spatial information varied across these contexts by employing error correlation analysis. Crucially, we independently manipulated contexts during encoding and retrieval stages to determine the critical stage that governs the utilization of divergent representation formats.

Moreover, considering the practical implications of spatial information in WM, particularly in navigation, arises the question of how such information is represented in large-scale real-world environments. While much spatial WM research has been confined to laboratory settings, where encoding and retrieval occur within a limited area on a computer screen, real-world navigation often involves transitions across different scales. For instance, in a typical navigation task, individuals must first memorize spatial locations on a small-scale 2D map and then locate the target within a larger-scale real-world setting. It remains uncertain whether spatial information retains its representation as polar coordinates during this process. Relevant to this issue, massive studies have examined the structure of spatial knowledge in long-term memory used for navigation in large-scale spatial systems. Nevertheless, ongoing debates persist, with various proposals being put forward. One such proposal is the Euclidean cognitive map, which is akin to Cartesian coordinates (Jacobs et al., 2013; Maidenbaum et al., 2018; O'Keefe & Nadel, 1978; Siegel & White, 1975). Another proposal is the theory of a network-like cognitive graph, which emphasizes angle and distance information, resembling polar coordinates (Kuipers, 1978; Warren, 2019; Warren et al., 2017). To investigate whether spatial information encoded in a small-scale environment automatically translates into polar coordinates for navigation in a larger-scale environment, the current study employs virtual reality (VR) technology to simulate navigation environment. Through the error correlation analysis, we directly examine the representation formats of space in large-scale WM. Additionally, this study examines the flexibility of representation formats. For that in the large-scale VR environment, participants are unable to accurately perceive the full scope of the terrain context, and the grid appears distorted from the participant's first-person perspective, we did not examine the influence of context. Instead, we drew inspirations from prior research (Yousif et al., 2024), which found that the format of presented information (direct vs. indirect) influenced the representation format adopted in motor WM. Specifically, we examined how the response type (direct vs. indirect) modulated the format of spatial representations by manipulating participants to reproduce the spatial locations freely or indirectly within the large-scale scenario.

Taken together, to investigate the WM format of spatial representations in small and large environments, we conducted a series of experiments. Participants were tasked with reproducing target locations presented either on a computer screen (small-scale, Experiments 1, 2, 3A, and 3B) or within a VR environment (large-scale, Experiments 4A and 4B) after memorizing these locations on a 2D display. Experiment 1 investigated the default format of spatial representations in small-scale WM by manipulating memory contexts as blank. While in Experiment 2, we examined the flexibility of spatial representations by manipulating memory contexts as grid-like. Furthermore, we independently manipulated memory contexts during encoding (Experiment 3A) and response phases (Experiment 3B) to determine the critical stages that govern the utilization of divergent representation formats. Experiment 4 utilized a VR environment to simulate navigation tasks in large-scale real-world settings. By manipulating participants' navigation methods to either freely (Experiment 4A) or indirectly (Experiment 4B) reach the target location, we investigated the potential flexibility of representation formats in large-scale spatial memory tasks.

Data availability

All data have been made publicly available via Open Science Framework and can be accessed at https://osf.io/ubkym/.

Experiment 1: The default format of spatial representation in small-scale WM

Experiment 1 employed blank memory contexts (Fig. 1A) to investigate how spatial information is represented in WM by default. Our aim was to determine whether participants' patterns of errors were more consistent with polar or Cartesian coordinates.

Methods

Participants. Twenty volunteers (11 males and 9 females, aged 18–24) from Sun Yat-sen University participated in this experiment for payment. All participants were all right-handed and reported normal or corrected-to-normal visual acuity. The sample size was determined *a priori* based on PANGEA (Westfall, 2016). Based on similar designs from prior studies (Yousif & Keil, 2021; the polar correlation vs. the Cartesian correlation in Experiment 1a; Cohen's $d = 1.62$), we anticipated an effect size (Cohen's d) of 1.62 for paired t-tests in our experimental setup. To achieve at least 95 % power for the effect of paired t-tests at a significance level of 0.05, a suggested sample size of 16 was calculated. We recruited twenty participants for Experiment 1 to ensure robust statistical power.

Before participation, all individuals provided signed informed consent. The study received approval from the Research Ethics Board of Sun

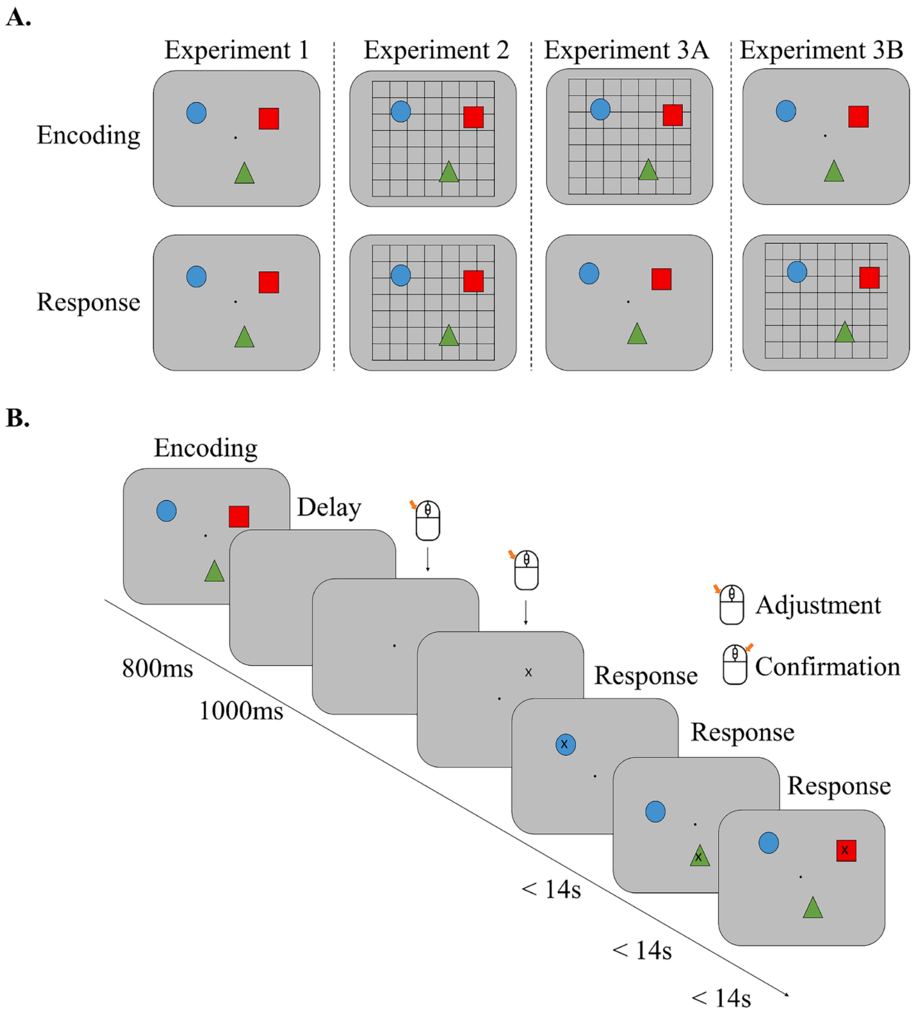

Fig. 1. *Experimental conditions and procedures in Experiments 1-3B.* **A.** Memory context manipulation: Experiment 1 employed blank memory contexts during both encoding and response phases, while Experiment 2 utilized grid-like contexts in both phases. Experiment 3A exclusively introduced grid-like contexts during the encoding phase, whereas Experiment 3B introduced them solely during the response phase. **B.** Experimental task description: Participants were required to remember the positions of three shapes first. After a 1000 ms blank interval, the fixation reappeared. Participants should click the left mouse button twice, and then reproduce the positions of the three shapes serially through mouse.

Yat-sen University and was conducted in accordance with the approved guidelines.

Stimuli and apparatus. The experiment was programmed in Python with the PsychoPy libraries (Peirce et al., 2019). The experimental stimuli were presented on a 27-inch LCD monitor (resolution: 2560 × 1440, refresh rate: 60 Hz) against a grey background (RGB: 128, 128, 128). Participants' viewing distance from the screen was approximately 57 cm.

The memory stimuli consisted of three shapes – a red square, a blue circle, and a green triangle, each with a radius of 0.36°. For each trial, the positions of these three shapes were randomly selected within a range of 4.48° horizontally and 4.48° vertically relative to the center of the screen. Besides, a constraint was imposed that the distance between any two shapes should be more than 1.25°.

Procedure and Experimental design. The experimental procedure was depicted in Fig. 1B. After a 500 ms fixation period, a memory display featuring three shapes appeared for 800 ms. Participants were instructed to memorize the positions of these three shapes. Following a 1000 ms blank interval, the fixation reappeared, prompting participants to click the left mouse button to make the mouse cursor (x) visible. Subsequently, participants should click the left mouse button again, causing one randomly chosen shape to appear at the mouse location. Their task was to place the shape to its corresponding position in the memory display by clicking the left mouse button. This process can be repeated multiple times until the right mouse button was clicked, indicating a locked response. Participants then proceeded to click the left mouse button again to make another memory shape visible and reproduce its position in the same manner. The trial ended after all three shapes have been responded to. Each response must be completed within 14 s. Otherwise, this trial was skipped, and a warning message was displayed, urging participants to respond more quickly in the later responses. Skipped trials would be randomly interleaved into subsequent trials.

Each participant completed 192 trials, distributed randomly across six blocks. Before formal trials, participants underwent 10–15 practice trials to familiarize themselves with the procedure. The entire task took approximately 50 min.

Data analysis. The first, second and last responses were analyzed separately. Responses with reproduction errors (calculated as Euclidean distance between the target and reported position) exceeding +/- 3 standard deviations (SD) from the participant's mean error were excluded from subsequent analyses. We mainly focused on the correlation between the absolute errors in the constitutive dimensions within each coordinate system. Consequently, correlations were calculated between the absolute errors in the x and y dimensions, as well as between the absolute errors in the angle and distance dimensions, for each participant. These two correlation values were then respectively compared to 0 using one-sample t-tests. Additionally, a paired t-test was conducted to compare the two correlation values.

Results & discussion

1.6 % of responses were removed due to reproduction errors exceeding +/- 3 standard deviations (SD) from the mean error of each participant.

First responses: Analysis of the first responses revealed a significant correlation solely between the absolute errors in the x and y dimensions (r = 0.16; $t(19) = 5.19$, $p < .001$, Cohen's $d = 1.16$, 95 % CI for the mean = [0.094, 0.222]). In contrast, the correlation between the absolute errors in the angle and distance dimensions was insignificant (r = 0.03; $t(19) = 1.36$, $p = .189$, Cohen's $d = 0.30$, 95 % CI for the mean = [-0.018, 0.083]). Notably, a significant discrepancy emerged between these correlation values (r = 0.13; $t(19) = 5.02$, $p < .001$, Cohen's $d = 1.12$, 95 % CI for the mean = [0.073, 0.178]).

Second and Third responses: In both second and third responses, significant correlations were observed for Cartesian errors (Second: r = 0.29, $t(19) = 7.72$, $p < .001$, Cohen's $d = 1.73$, 95 % CI for the mean = [0.214, 0.373]; Third: r = 0.26, $t(19) = 7.11$, $p < .001$, Cohen's $d = 1.59$, 95 % CI for the mean = [0.181, 0.333]). Polar errors also exhibited significant correlations (Second: r = 0.11, $t(19) = 3.60$, $p = .002$, Cohen's $d = 0.81$, 95 % CI for the mean = [0.045, 0.170]; Third: r = 0.07, $t(19) = 2.43$, $p = .025$, Cohen's $d = 0.54$, 95 % CI for the mean = [0.010, 0.129]), which were significantly smaller than those in Cartesian dimensions (Second: r = 0.19, $t(19) = -7.82$, $p < .001$, Cohen's $d = -1.75$, 95 % CI for the mean difference = [-0.236, −0.136]; Third: r = 0.19, $t(19) = -6.18$, $p < .001$, Cohen's $d = -1.38$, 95 % CI for the mean difference = [-0.252, −0.124]) (see Fig. 2).

These results indicate that, particularly in the first responses, participants spontaneously adopted polar coordinates to represent spatial information, consistent with previous findings (Yousif et al., 2024). However, in the case of the last two responses, we still observed small correlations in polar dimensions. This could be attributed to the inconsistent anchoring behavior exhibited by certain participants when reproducing the positions of the second and third targets. They may have employed the first responses as the anchor points in some trials, deviating from the expected anchoring at the center point. Consequently, the polar errors calculated based on the center point were highly correlated for these participants, who were likely to be the outliers shown in Fig. 2. Nonetheless, the larger Cartesian correlations persistently support the advantageous role of polar representations in WM under default conditions.

Experiment 2: The flexibility of spatial representation formats in small-scale WM

Experiment 1 replicated previous findings that in tasks with minimal intervening spatial structure, participants' error patterns aligned more with the use of polar coordinate representations. However, the critical question remained: Is spatial format fixed, or does it adapt based on the provided spatial layout and reference frame. To address this, in Experiment 2, we drew inspirations from the manipulation employed in the prior research (Yousif & Keil, 2021). Specifically, we structured the memory context as a grid-like environment (Fig. 1A) that strongly implied a Cartesian system, aiming to determine whether spatial representations in WM would remain in polar coordinates under such a context.

Methods

Another group of twenty volunteers (7 males and 13 females, aged 18–24) from Sun Yat-sen University participated in Experiment 2. The sample size determination followed a similar approach to that of Experiment 1. The whole task took approximately 50 min.

The procedures in Experiment 2 closely paralleled those in Experiment 1, with a few key distinctions. Specifically, the memory contexts during both the encoding and response phases were configured in a grid pattern, contrasting Experiment 1′s utilization of blank memory contexts.

Results & discussion

2.7 % of responses were removed due to reproduction errors exceeding +/- 3 standard deviations (SD) from the mean error of each participant. Across all responses, only the correlations in polar dimensions exhibited significance (First: 0.20, $t(19) = 11.15$, $p < .001$, Cohen's $d = 2.49$, 95 % CI for the mean = [0.165, 0.242]; Second: 0.15, $t(19) = 6.62$, $p < .001$, Cohen's $d = 1.48$, 95 % CI for the mean = [0.104, 0.200]; Third: 0.14, $t(19) = 5.47$, $p < .001$, Cohen's $d = 1.22$, 95 % CI for the mean = [0.088, 0.198]). In contrast, the correlations in Cartesian dimensions were not statistically significant (First: 0.03, $t(19) = 1.82$, $p = .085$, Cohen's $d = 0.41$, 95 % CI for the mean = [-0.005, 0.070]; Second: 0.04, $t(19) = 1.96$, $p = .065$, Cohen's $d = 0.44$, 95 % CI for the

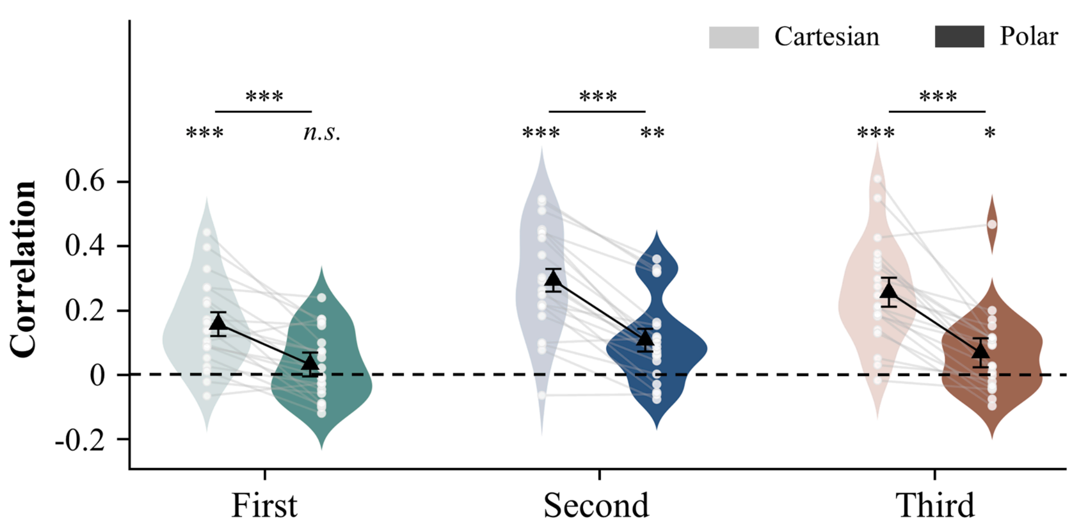

Fig. 2. *The results in Experiment 1.* The correlation values were separately calculated for each response (first, second, and third) and coordinate system (Cartesian and polar). The black triangles represented group mean, while error bars indicating the within-subject 95 % confidence intervals. The smaller white dots represented the results of each participant. '*' represented the significance of the data comparing to zero or paired t-tests. *n.s.* > .05, *p < 0.05, **p < 0.005, ***p < .001.

mean = [-0.003, 0.090]; Third: 0.04, $t(19) = 1.88$, $p = .076$, Cohen's $d = 0.42$, 95 % CI for the mean = [-0.005, 0.092]). The correlation values in Cartesian dimensions were consistently and significantly smaller compared to those observed in polar dimensions (First: −0.17, $t(19) = -8.00$, $p < .001$, Cohen's $d = 1.79$, 95 % CI for the mean difference = [-0.216, −0.126]; Second: −0.11, $t(19) = -3.04$, $p = .007$, Cohen's $d = 0.68$, 95 % CI for the mean = [-0.183, −0.034]; Third: −0.10, $t(19) = -2.67$, $p = .015$, Cohen's $d = 0.60$, 95 % CI for the mean = [-0.178, −0.022]) (Fig. 3).

These findings provide evidence that participants tend to adopt a Cartesian representation format in grid-like contexts, suggesting a flexibility in their capacity to utilize distinct spatial representation formats contingent upon the characteristics of the memory context.

Experiment 3: The decisive stage of transitions in spatial representation format within small-scale WM

The results of Experiment 2 revealed the flexible nature of spatial representations in WM. In Experiment 3, we aimed to pinpoint the critical stage that determines whether participants adopt a polar or Cartesian representation. To do this, Experiment 3 consisted of two sub-experiments. In Experiment 3A, only the encoding phase featured a grid pattern in the memory background, while in Experiment 3B, this pattern was introduced solely during the response phase.

Methods

Two separate groups of twenty new volunteers from Sun Yat-sen University participated in Experiment 3A (10 males and 10 females, aged 18–24) and Experiment 3B (8 males and 12 females, aged 18–23) respectively. The sample size determination followed a similar approach to that of Experiment 1.

The experimental procedures were similar to Experiment 1, except for that the memory contexts during either the encoding or response phases were configured in a grid pattern. Each task took approximately 50 min.

Results & discussion

Experiment 3A: 1.6 % of responses were removed due to reproduction errors exceeding +/- 3 standard deviations (SD) from the mean error of each participant. Both Cartesian errors and polar errors exhibited reliable correlations (Cartesian: First: 0.11, $t(19) = 3.50$, $p = .002$, Cohen's $d = 0.78$, 95 % CI for the mean = [0.044, 0.176]; Second: 0.15, $t(19) = 4.97$, $p < .001$, Cohen's $d = 1.11$, 95 % CI for the mean = [0.084, 0.207]; Third: 0.17, $t(19) = 6.43$, $p < .001$, Cohen's $d = 1.44$, 95 % CI for the mean = [0.113, 0.223]); Polar: First: 0.08, $t(19) = 2.91$, $p = .009$, Cohen's $d = 0.65$, 95 % CI for the mean = [0.022, 0.136]; Second: 0.10, $t(19) = 5.38$, $p < .001$, Cohen's $d = 1.20$, 95 % CI for the mean = [0.063, 0.143]; Third: 0.07, $t(19) = 2.62$, $p = .017$, Cohen's $d = 0.59$, 95 % CI for the mean = [0.013, 0.121]). In contrast to the results in Experiment 1, the two correlations did not differ from each other significantly in the first two responses (First: 0.03, $t(19) = 0.95$, $p = .355$, Cohen's $d = 0.21$, 95 % CI for the mean difference = [-0.037, 0.099]; Second: 0.04, $t(19) = 1.43$, $p = .168$, Cohen's $d = 0.32$, 95 % CI for the mean difference = [-0.019, 0.104]; Third: 0.10, $t(19) = 3.36$, $p = .003$, Cohen's $d = 0.75$, 95 % CI for the mean difference = [0.038, 0.164]) (Fig. 4).

The results indicate that the introduction of a grid-like context during the encoding phase may potentially induce a change in the spatial representation format adopted by participants, even though these results neither align with the predictions of the Cartesian representations nor the predictions of the polar representations.

A cross-experiment analysis between Experiments 1 and 3A: To further confirm the effects of solely introducing grid-like memory contexts during the encoding phase, we selected the first responses as a typical example and conducted a cross-experiment analysis comparing Experiments 1 and 3A. The results revealed a significant interaction between memory context and coordinate system (Interaction: $F(1, 38) = 5.28$, $p = .027$, $\eta_p^2 = 0.12$; Context: $F(1, 38) < 0.001$, $p = .991$, $\eta_p^2 < 0.001$; Coordinate system: $F(1, 38) = 14.46$, $p < .001$, $\eta_p^2 = 0.28$), indicating a degree of change in the representation format.

Experiment 3B: 1.4 % of responses were removed due to reproduction errors exceeding +/- 3 standard deviations (SD) from the mean error of each participant. Similar to the results in Experiment 1, across all responses, only Cartesian correlations exhibited significance (Cartesian: First: 0.16, $t(19) = 4.50$, $p < .001$, Cohen's $d = 1.01$, 95 % CI for the mean = [0.084, 0.231]; Second: 0.19, $t(19) = 5.66$, $p < .001$, Cohen's $d = 1.27$, 95 % CI for the mean = [0.121, 0.264]; Third: 0.18, $t(19) = 5.41$, $p < .001$, Cohen's $d = 1.21$, 95 % CI for the mean = [0.109, 0.247]); Polar: First: −0.02, $t(19) = -0.78$, $p = .448$, Cohen's $d = 0.17$, 95 % CI for the mean = [-0.062, 0.028]; Second: 0.03, $t(19) = 1.30$, $p = .208$, Cohen's $d = 0.29$, 95 % CI for the mean = [-0.030, 0.084]; Third: 0.02, $t(19) = 1.01$, $p = .323$, Cohen's $d = 0.23$, 95 % CI for the mean = [-0.026, 0.074]). And the Cartesian correlations were significantly larger than polar correlations (First: 0.18, $t(19) = 5.26$, $p < .001$, Cohen's $d = 1.18$, 95 % CI for the mean difference = [0.105, 0.244]; Second: 0.16, $t(19) = 4.82$, $p < .001$, Cohen's $d = 1.08$, 95 % CI for the mean difference =

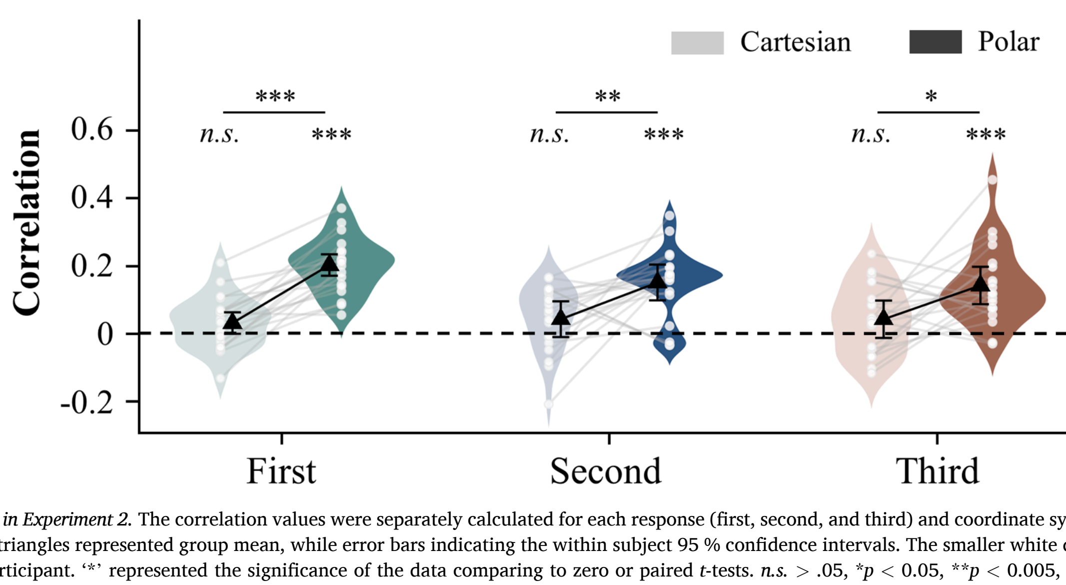

Fig. 3. *The results in Experiment 2.* The correlation values were separately calculated for each response (first, second, and third) and coordinate system (Cartesian and polar). The black triangles represented group mean, while error bars indicating the within subject 95 % confidence intervals. The smaller white dots represented the results of each participant. '*' represented the significance of the data comparing to zero or paired *t*-tests. *n.s.* > .05, *$p < 0.05$, **$p < 0.005$, ***$p < .001$.

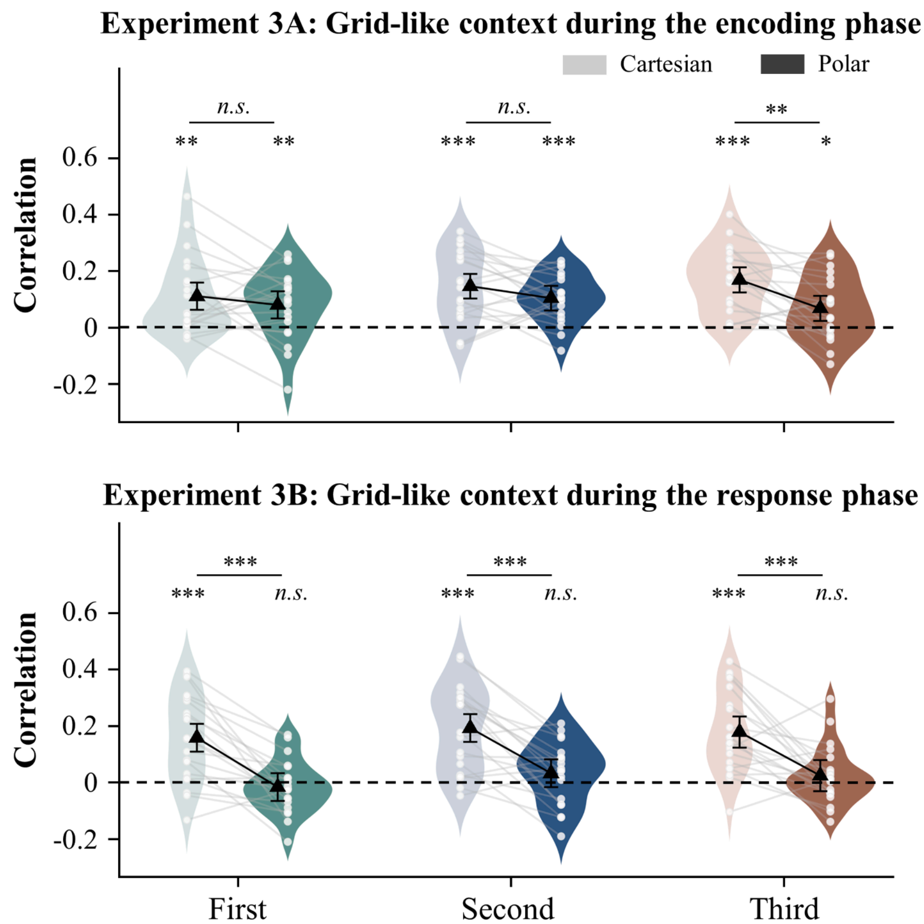

Fig. 4. *The results in Experiment 3A and 3B.* The correlation values were separately calculated for each response (first, second, and third) and coordinate system (Cartesian and polar). The black triangles represented group mean, while error bars indicating the within subject 95 % confidence intervals. The smaller white dots represented the results of each participant. '*' represented the significance of the data comparing to zero or paired *t*-tests. *n.s.* > .05, *p < 0.05, **p < 0.005, ***p < .001.

[0.091, 0.230]; Third: 0.15, $t(19) = 4.14$, $p < .001$, Cohen's $d = 0.93$, 95 % CI for the mean difference = [0.076, 0.232]) (Fig. 4). These results demonstrate that space is still represented in polar coordinates when only the memory context during the response phase is configured as a grid pattern.

A cross-experiment analysis between Experiments 1 and 3B: Similarly, to further confirm the effects of solely introducing grid-like memory contexts during the response phase, we selected the first responses as a typical example and conducted a cross-experiment analysis comparing Experiments 1 and 3B. The results revealed an insignificant interaction between memory context and coordinate system (Interaction: $F(1, 38) = 1.40$, $p = .243$, $\eta_p^2 = 0.04$; Context: $F(1, 38) = 0.52$, $p = .475$, $\eta_p^2 = 0.013$; Coordinate system: $F(1, 38) = 52.05$, $p < .001$, $\eta_p^2 = 0.58$), indicating no change in the representation format.

Combined with the results in previous two sub-experiments, Experiment 3 illustrates the constrained flexibility of spatial representations in WM. Specifically, the dominance of a Cartesian coordinate system for representing spatial information is only observed when both the encoding and response phases are configured as a grid-like memory context. Notably, the encoding phase appears to play a more crucial role in determining the spatial representation format, whereas the response phase seems to have little influence on the representation format.

Experiment 4: The flexibility of spatial representations in large-scale WM

Experiments 1-3B were conducted in laboratory settings to investigate the representation format of spatial information in small-scale WM. In Experiment 4, we employed virtual reality (VR) technology to further examine how space was represented in large-scale WM. Results from previous experiments suggested that the use of polar coordinates was context-dependent. In grid-like environments that suggested a more Cartesian structure, error patterns aligned with Cartesian coordinates. Therefore, in the current experiment, we also examined the flexibility of spatial representation format in large-scale WM. To address this, participants were required to complete a spatial localization task similar to Experiment 1, but in a VR environment. Given the distortion of grid structure experienced from a first-person perspective within the VR environment, we subsequently employed an alternative manipulation approach. Drawing inspirations from Yousif et al. (2024), we examined the influence of two distinct response types in separate sub-experiments. In Experiment 4A, participants were asked to directly navigate to the target location during the response phase. In Experiment 4B, participants were required to navigate horizontally and then vertically (or vice versa) to the target location during the response phase.

Methods

Participants. Two separate groups of twenty new volunteers from Sun Yat-sen University participated in Experiment 4A (10 males and 10 females, aged 18–24) and Experiment 4B (8 males and 12 females, aged 18–23) respectively. All participants were right-handed and reported normal or corrected-to-normal visual acuity. The sample size was determined in the similar manner as Experiment 1.

Before participation, all individuals provided signed informed consent. The study received approval from the Research Ethics Board of Sun Yat-sen University and was conducted in accordance with the approved guidelines.

Stimuli and apparatus. The experiment was implemented using Unity software (Peirce et al., 2019). Participants were positioned at a stationary location and equipped with a joystick and an HTC Vive head-mounted display. SteamVR was utilized to enable the access and

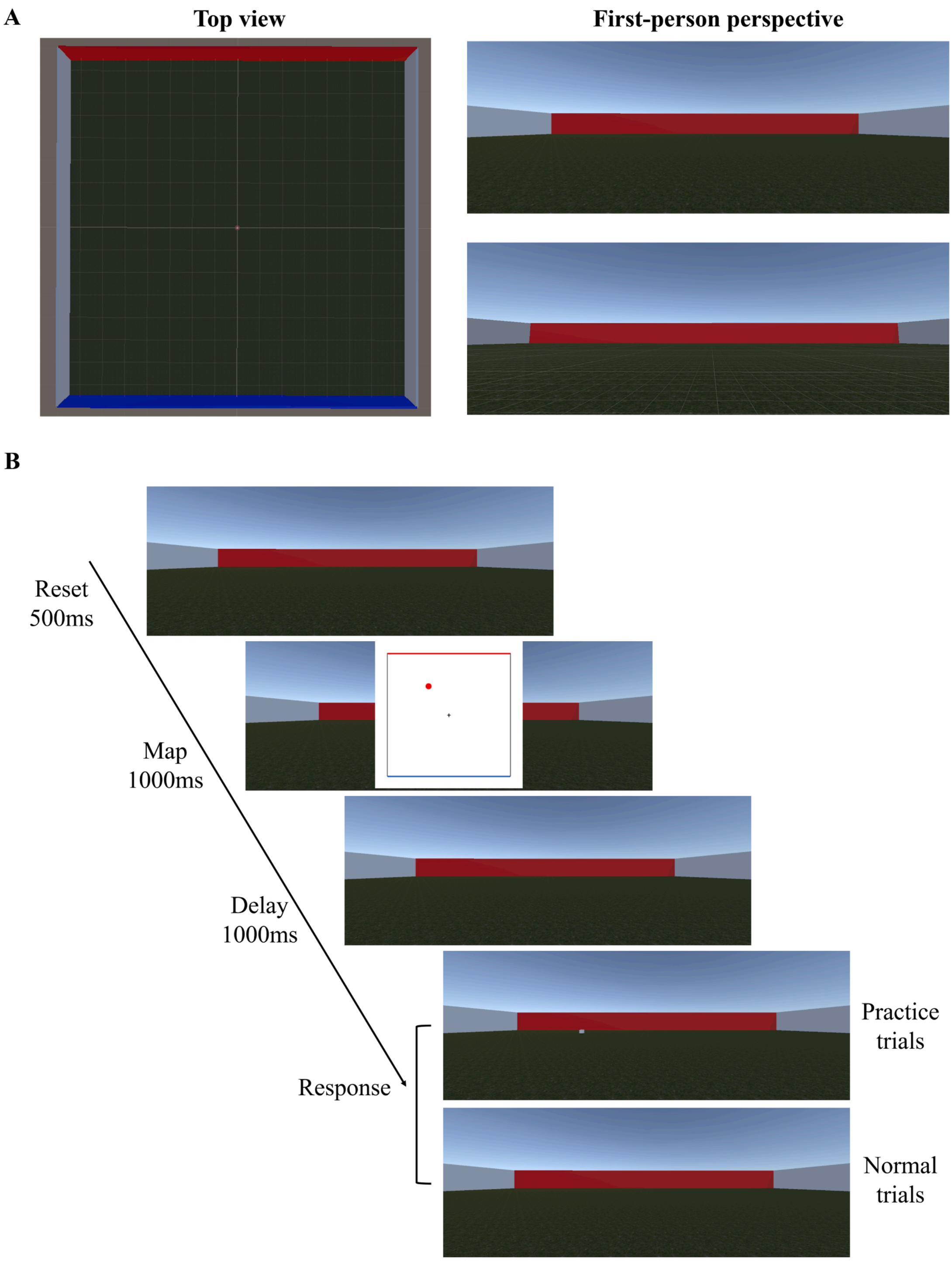

Fig. 5. *Experimental conditions and procedures in Experiment 4.* **A.** VR environment: Experiment 4 utilized a square area as the VR environment, enclosed by four walls. The north wall was colored red, while the south wall was colored blue. The left panel illustrated the top view of the VR environment, and the right panel depicted the first-person perspective from the reset position within the VR environment. The top image in the right panel showed the absence of a grid-like pattern, while the bottom one showed the VR environment configured with a grid pattern. **B.** Experimental task description: Participants were first reset to the center of the VR environment. Subsequently, they were presented with a map and were required to memorize the position of the red target on this map. After a 1000 ms blank interval, participants should manipulate a joystick to move to the corresponding location of the target within the current VR environment. During practice trials, a while cube would appear at the correct target position to aid navigation, while no cube would be present during the normal trials. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

interaction with virtual reality contents.

The VR environment employed in Experiment 4 consisted of a square area enclosed by four walls (150 m × 150 m). In order to facilitate the differentiation of directions, the north wall was colored red, while the south wall was colored blue. And the center of the VR environment was marked as a red circle. Notably, in Experiment 4B, the terrain within the VR environment was gridded to assist participants in indirectly navigating to the target locations (Fig. 5A). Target locations in each trial were randomly generated within a range of 11.25 m to 63.75 m horizontally and vertically from the central point.

Experimental design and procedure. The experimental procedure is depicted in Fig. 5B. Prior to the start of each trial, participants' positions were reset to the center of the current environment, corresponding to the location of the central cross on the map, and their orientations were reset to face northward. In each trial, a square map composed of a central cross and a red circle as the memory target was presented for 1000 ms. Participants were instructed to memorize the position of the target. After a blank interval of 1000 ms, participants were required to manipulate a joystick to move to the corresponding location of the target within the current VR environment. The distinction between Experiments 4A and 4B lay in the participants' movement constraints: in Experiment 4A, participants had unrestricted movement, whereas in Experiment 4B, the terrain within the VR environment was gridded, and participants were directed to navigate along the grid lines. The entire trajectories of participants in each trial were recorded.

Each participant completed a total of 192 trials, distributed randomly across four blocks. Before formal trials, participants underwent 10–15 practice trials to familiarize themselves with the procedure. During these practice trials, a white cube would appear at the correct target position in the VR environment during the response phase, serving as a navigation aid—an element absent in the subsequent normal trials. On average, each task session lasted approximately 60 min.

Data analysis. To unify the unit of distance between the map and the VR environment, we first normalized the distances by dividing them by the corresponding maximum possible values in each respective context (map size/2 or terrain size/2). Other analyses followed the same procedures as those employed in previous experiments.

Results & discussion

Experiment 4A: 1.6 % of responses were removed due to reproduction errors exceeding +/- 3 standard deviations (SD) from the mean error of each participant or RT exceeding 15 s. By examining the entire trajectories of participants, we found that all participants navigated to the target position directly in all trials. Only Cartesian correlations were significant (0.15; $t(19) = 5.00$, $p < .001$, Cohen's $d = 1.12$, 95 % CI for the mean = [0.090, 0.219]). In contrast, polar correlations were not significant (−0.01; $t(19) = -0.38$, $p = .705$, Cohen's $d = -0.09$, 95 % CI for the mean = [-0.061, 0.042]), which were smaller than Cartesian correlations (−0.16, $t(19) = -3.77$, $p = .001$, Cohen's $d = -0.84$, 95 % CI for the mean difference = [-0.254, −0.073]) (Fig. 6).

These results demonstrate that, consistent with laboratory findings, spatial information in large-scale environment is also represented in polar coordinates by default within WM.

Experiment 4B: 3.9 % of responses were removed due to reproduction errors exceeding +/- 3 standard deviations (SD) from the mean error of each participant or RT exceeding 15 s. The entire trajectories of participants showed that as requested, participants indeed navigated to the target position indirectly. Both Cartesian correlations and polar correlations were insignificant (Cartesian: 0.02, $t(19) = 0.84$, $p = .409$, Cohen's $d = 0.19$, 95 % CI for the mean = [-0.032, 0.075]; Polar: −0.01, $t(19) = -0.31$, $p = .759$, Cohen's $d = 0.07$, 95 % CI for the mean = [-0.036, 0.027]). And these two correlations were not significantly different (0.03, $t(19) = 0.91$, $p = .375$, Cohen's $d = 0.20$, 95 % CI for the mean difference = [-0.034, 0.087]). This pattern deviated from the predictions of both hypothesized representation formats. However, previous research (Yousif et al., 2024) demonstrated that the pattern of results generated by polar representation was highly robust, with correlated Cartesian errors and uncorrelated polar errors. Conversely, the pattern of results produced by Cartesian representations depended on specific task details. Actually, the results in Experiment 4B were consistent with the simulation analysis of Cartesian representations using the actual noise estimated from Experiment 4B. Specifically, this analysis revealed insignificant correlations for both coordinate systems (see supplementary results). However, caution should be taken when interpreting these results. Nevertheless, we can at least conclude that the manner of response affected the representation format of spatial information in large-scale WM.

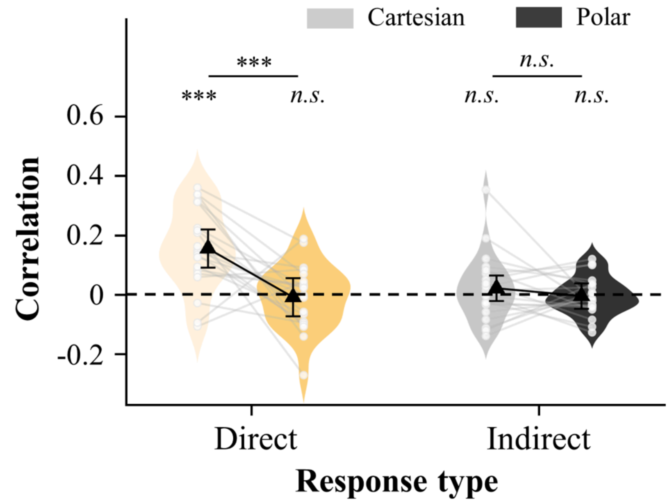

Fig. 6. *The results in Experiment 4.* The correlation values were separately calculated for each response type (direct and indirect) and coordinate system (Cartesian and polar). The black triangles represented group mean, while error bars indicating the within subject 95 % confidence intervals. The smaller white dots represented the results of each participant. '*' represented the significance of the data comparing to zero or paired *t*-tests. *n.s.* > .05, ***$p < .001$.

A cross-experiment analysis between Experiments 4A and 4B: To further verify the flexibility of spatial information formats in large-scale WM, we conducted a cross-experiment comparison between Experiments 4A and 4B. The results revealed a significant interaction between response type and coordinate system (Interaction: $F(1, 38) = 6.93$, $p = .012$, $\eta_p^2 = 0.15$; Response type: $F(1, 38) = 7.59$, $p = .009$, $\eta_p^2 = 0.17$; Coordinate system: $F(1, 38) = 13.26$, $p < .001$, $\eta_p^2 = 0.26$), indicating the presence of flexible utilization of spatial representation formats which is dependent on the response type (Fig. 6).

In summary, the results in Experiment 4 indicate that akin to small-scale WM, space is also represented in polar coordinate system in large-scale WM by default, despite involving transitions of spatial information across different scales in WM. Moreover, the representation formats of space in large-scale WM are flexible as well, which are notably influenced by the specific response requirements.

Discussion

By utilizing error correlation analysis, the current study uncovered the WM format of spatial representations within both small and large environments. In Experiments 1–3, participants were tasked with reproducing previously memorized locations of three targets. The results in Experiment 1 aligned with prior research (Yousif et al., 2024), affirming that participants spontaneously employed polar coordinates to represent space within WM in small-scale environments. These findings also validated the error correlation analysis. Consistent with previous research (Yousif & Keil, 2021), Experiment 2 revealed the utilization of a

Cartesian representation format in grid-like contexts, indicating the flexible nature of spatial representations within WM. Furthermore, when introducing a grid pattern solely in the encoding phase (Experiment 3A), the results did not align with predictions of either Cartesian or polar representations. Conversely, when grid-like contexts were introduced solely during the response phase (Experiment 3B), spatial representation remained predominantly in polar coordinates. These results demonstrated that the changes in representation format were driven by the combined influence of context modifications during both the encoding phase and the response phase. Specifically, changes to the context during the encoding phase alone elicit moderate modifications to the format of spatial representations. In contrast, changes solely to the response phase context have minimal impact on altering the representation format.

In Experiment 4, participants initially memorized the target's position on a map, and then navigate to the corresponding target position in a VR environment. In unconstrained situations, polar representations were employed by default (Experiment 4A). Conversely, when participants were constrained to navigate indirectly to the target position, they adopted Cartesian coordinates to represent space (Experiment 4B). Overall, these findings provide compelling evidence supporting the prevalence of polar representations in WM for spatial information across both small and large environments. Moreover, these polar representations exhibit considerable flexibility. Specifically, in laboratory settings where both the encoding and response phases incorporate grid-like memory backgrounds, or in large-scale environments where participants are required to indirectly reproduce locations, Cartesian representations are employed.

Although numerous studies have explored WM representations, little research has specifically addressed how spatial information is represented in WM. Typically, current investigations either conflate spatial information with other visual stimuli or emphasize its unique role in representing other features. In the classic debate over whether WM stores independent or hierarchical representations, locations are treated similarly to other features. Traditional theories assume that items are stored independently in WM (Adam et al., 2017; Luck & Vogel, 1997; Zhang & Luck, 2008). However, recent evidence challenges this notion. For example, Brady and Alvarez (2011) found that participants' memory for the size of a circle was biased toward the average size of circles of the same color. This led to the hierarchical encoding model, which posits that WM operates on multi-tiered displays that integrate objects and ensembles (Brady & Alvarez, 2011; Brady & Alvarez, 2015; Utochkin & Brady, 2020). Since then, numerous studies have provided support for the hierarchical representation theory by adopting various features like orientation and color (Oh et al., 2019; Son & Chong, 2023; Son et al., 2020). Similarly, researchers have also utilized locations as experimental material solely to furnish additional evidence for this theory (Brady & Tenenbaum, 2013; Lew & Vul, 2015).

In the ongoing debate about the basic unit of WM, spatial information has been suggested to play a crucial role in representing other features. The object-based theory posits that WM stores features as integrated objects, with non-spatial features automatically binding to specific locations (Balaban & Luria, 2017; Kondo & Saiki, 2012; Luck & Vogel, 1997). However, some findings challenge this theory. For instance, some studies have reported a modest decline in accuracy when additional features are included (Oberauer & Eichenberger, 2013; Hardman & Cowan, 2015). This has led to an alternative theory suggesting that features are the basic units of WM. In this framework, locations seem to hold a unique status as well. Researchers employing surprise tests have found that recall accuracy for non-spatial features drops to chance levels when they are task-irrelevant (Chen & Wyble, 2016; Wyble et al., 2019). In contrast, task-irrelevant locations can still be robustly recalled (Chen & Wyble, 2015; Foster et al., 2017). The recently proposed Boolean map theory further emphasizes the critical role of spatial information, positing that WM represents spatial occupancy as Boolean maps and all features within a single map can be simultaneously processed (Huang, 2020).

In sum, our study enriches the theoretical understanding of WM by focusing on the specific representation format of spatial information. This contributes to a better understanding of how spatial information is encoded and represented, thereby advancing theoretical models of WM. Additionally, our research aids in creating training programs to improve spatial information processing skills (e.g., navigation, map usage) and provides a foundation for optimizing spatial information representation in fields such as VR and human–computer interaction.

Our study contributes to the understanding of spatial information representation within WM compared to Yousif et al. (2024) in two key ways. Firstly, building upon their work, our study further explored the flexibility of spatial representation formats and elucidated the determining stages that governed the utilization of divergent representation formats. This deepens our understanding of the inherent nature of spatial representation formats in WM. Specifically, how spatial information is represented depends on task demands and which format is more conducive to task completion within the given situation or task. Secondly, our study extended beyond a laboratory computer setting to a large-scale VR environment to investigate this issue, given the practical significance of spatial representations. The results revealed that despite involving transitions of spatial information across different scales, the default representation remained in polar coordinates, while also demonstrating flexible utilizations depending on task demands.

Besides, these findings are in line with previous studies on mislocalizations, suggesting the prevalence of polar representations in cognitive processes involving spatial information. For instance, Yousif et al. (2020) demonstrated distinct sensitivities to deviations in the angle dimension across different regions when participants judged whether the positions of two dots within separate shapes were matched. Conversely, no region-specific sensitivities were observed in the distance dimension. These findings imply independent perceptual judgments of spatial location within the polar coordinate system, highlighting the utilization of polar representations in spatial perception. Similarly, evidence for polar representations emerged in large-scale spatial navigation tasks (Chrastil & Warren, 2014; Ericson & Warren, 2020; Warren, 2019). Additionally, studies on motor actions have identified a reliance on polar coordinates as well (Flanders et al., 1992; Gordon et al., 1994). In contrast to previous studies, our work quantitatively demonstrated polar representations of space within WM in both small and large contexts by analyzing error correlations across different dimensions. Moreover, we presented an alternative hypothesis of polar representations, specifically Cartesian representations, and conducted a comparison between the two through this error correlation analysis. Collectively, these findings suggest the general applicability of polar coordinates in various spatial information processes domains.

Moreover, our study advances the understanding of how we represent spatial information within WM in the context of natural behavior. Recently, with the increasing emphasis on ecological validity in experiments, VR has been widely adopted to investigate visual search and spatial navigation (e.g., Draschkow & Võ, 2016; Helbing et al., 2020; Igloi et al., 2010; Kit et al., 2014; Warren et al., 2017). However, the use of VR in studying WM has been limited (but see Draschkow et al., 2021; Draschkow et al., 2022). In this study, we utilized VR technology to simulate a real-life task that requires the utilization of WM spatial representations. The results showed that in this immersive WM task, spatial information is still represented in polar coordinates and is influenced by the response type. Our study combines methodological rigor and ecological validity, revealing the consistency of spatial WM representation formats between real-life and laboratory environments, as well as the flexibility of cognitive systems in real-world settings. These findings provide valuable insights for future endeavors aiming to incorporate ecological elements into laboratory-based research.

Finally, the current study has several limitations, which holds implications for future research. The first one regards the analytical approach employed, which only considered two simple opposing hypotheses – Cartesian representation and polar representation. However, these two hypotheses may not be mutually exclusive. As suggested by Yousif (2022), spatial information may be simultaneously represented in multiple formats. Certain results obtained in this study that did not align with the predictions of either Cartesian or polar coordinates also implied this possibility. For example, in Experiment 1, significant correlations were observed in both Cartesian and polar dimensions during the second and third responses. To explore this aspect further, future research could leverage more sensitive analysis methods or task paradigms capable of investigating spatial information representation in more complex scenarios.

Secondly, although our study revealed the flexibility of spatial representation formats in WM, it focused solely on the effects of memory context and response type. It remains unclear whether other factors influence the conversion of representation formats and what fundamentally determines these transitions. Additionally, in large-scale environments, we observed that direct or indirect navigation to target locations influenced the representation format of spatial information. However, real-life situations often involve non-linear paths with multiple turns. Further research is needed to examine if these findings hold true in such cases.

Lastly, in light of previous research, the universality of polar representations in various spatial information processes is suggested. However, the neural basis of this trait remains unclear. Numerous studies have already identified neural cells that represent spatial information, such as place cells that are sensitive to specific locations (Moser et al., 2008; O'Keefe & Dostrovsky, 1971), head-direction cells that represent an organism's heading direction (Taube, 1998), and grid cells (Hafting et al., 2005; Kraus et al., 2015) that represent multiple structured locations. Future research could explore which neural activities of these cells determine the use of polar representation.

Author notes

All data have been made publicly available via Open Science Framework and can be accessed at https://osf.io/ubkym/.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT 3.5 in order to improve readability and language. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRediT authorship contribution statement

Wei Chen: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wenwen Li:** Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yushang Huang:** Software, Methodology, Conceptualization. **Xiaowei Ding:** Writing – review & editing, Visualization, Supervision, Software, Resources, Project administration, Methodology, Funding acquisition, Formal analysis.

Funding

This work was supported by the National Natural Science Foundation of China (32271103), Natural Science Foundation of Guangdong Province (2023A1515011762), Guangzhou Science and Technology Plan Project—Leading Elite Program (2024A04J3301), and the Fundamental Research Funds for the Central Universities, Major Project Cultivation and Emerging Interdisciplinary Cultivation Plan (24wkjc02) awarded to author Xiaowei Ding.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jml.2024.104587.

Data availability

The data that has been used is confidential.

References

Adam, K. C., Vogel, E. K., & Awh, E. (2017). Clear evidence for item limits in visual working memory. *Cognitive Psychology, 97*, 79–97.
Alekseichuk, I., Turi, Z., Amador de Lara, G., Antal, A., & Paulus, W. (2016). Spatial Working Memory in Humans Depends on Theta and High Gamma Synchronization in the Prefrontal Cortex. *Current Biology, 26*(12), 1513–1521.
Baddeley A. D. Hitch G. (1974). Working memory. Bower G. The psychology of learning and motivation. New York: Academic Press Vol. VIII, 47-89.
Baddeley, A. (1992). Working memory. *Science, 255*(5044), 556–559.
Balaban, H., & Luria, R. (2017). Neural and Behavioral Evidence for an Online Resetting Process in Visual Working Memory. *Journal of Neuroscience, 37*(5), 1225–1239.
Bays, P. M., Wu, E. Y., & Husain, M. (2011). Storage and binding of object features in visual working memory. *Neuropsychologia, 49*, 1622–1631.
Blacker, K. J., Weisberg, S. M., Newcombe, N. S., & Courtney, S. M. (2017). Keeping track of where we are: Spatial working memory in navigation. *Visual Cognition, 25*(7–8), 691–702.
Brady, T. F., & Alvarez, G. A. (2011). Hierarchical encoding in visual working memory: Ensemble statistics bias memory for individual items. *Psychological Science, 22*(3), 384–392.
Brady, T. F., & Alvarez, G. A. (2015). Contextual effects in visual working memory reveal hierarchically structured memory representations. *Journal of Vision, 15(15): 6*, 1–24.
Brady, T. F., & Tenenbaum, J. B. (2013). A probabilistic model of visual working memory: Incorporating higher order regularities into working memory capacity estimates. *Psychological Review, 120*(1), 85–109.
Caviola, S., Colling, L. J., Mammarella, I. C., & Szűcs, D. (2020). Predictors of mathematics in primary school: Magnitude comparison, verbal and spatial working memory measures. *Developmental Science, 23*(6), Article e12957.
Chen, H., & Wyble, B. (2015). The location but not the attributes of visual cues are automatically encoded into working memory. *Vision Research, 107*, 76–85.
Chen, H., & Wyble, B. (2016). Attribute amnesia reflects a lack of memory consolidation for attended information. *Journal of Experimental Psychology: Human Perception and Performance, 42*(2), 225–234.
Chown, E., Kaplan, S., & Kortenkamp, D. (1995). Prototypes, location, and associative networks (PLAN): Towards a unified theory of cognitive mapping. *Cognitive Science, 19*(1), 1–51.
Chrastil, E. R., & Warren, W. H. (2014). From cognitive maps to cognitive graphs. *PloS One, 9*(11), Article e112544.
Draschkow, D., & Võ, M.-L.-H. (2016). Of "what" and "where" in a natural search task: Active object handling supports object location memory beyond the object's identity. *Attention, Perception, & Psychophysics, 78*(6), 1574–1584.
Draschkow, D., Kallmayer, M., & Nobre, A. C. (2021). When Natural Behavior Engages Working Memory. *Current Biology, 31*(4), 869–874.e5.
Draschkow, D., Nobre, A. C., & van Ede, F. (2022). Multiple spatial frames for immersive working memory. *Nature Human Behaviour, 6*(4), 536–544.
Ericson, J. D., & Warren, W. H. (2020). Probing the invariant structure of spatial knowledge: Support for the cognitive graph hypothesis. *Cognition, 200*, Article 104276.
Flanders, M., Tillery, S. I. H., & Soechting, J. F. (1992). Early stages in a sensorimotor transformation. *Behavioral and Brain Sciences, 15*, 309–320.
Foster, J. J., Bsales, E. M., Jaffe, R. J., & Awh, E. (2017). Alpha-Band Activity Reveals Spontaneous Representations of Spatial Position in Visual Working Memory. *Current Biology, 27*(20), 3216–3223.e6.
Gordon, J., Ghilardi, M. F., Cooper, S. E., & Ghez, C. (1994). Accuracy of planar reaching movements. *Experimental Brain Research, 99*, 112–130.
Hafting, T., Fyhn, M., Molden, S., Moser, M. B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature, 436*(7052), 801–806.
Hardman, K. O., & Cowan, N. (2015). Remembering complex objects in visual working memory: Do capacity limits restrict objects or features? *Journal of Experimental Psychology: Learning, Memory, and Cognition, 41*(2), 325–347.
He, Q., & Brown, T. I. (2019). Environmental Barriers Disrupt Grid-like Representations in Humans during Navigation. *Current Biology, 29*(16), 2718–2722.e3.
Helbing, J., Draschkow, D., & Võ, M.-L.-H. (2020). Search superiority: Goal-directed attentional allocation creates more reliable incidental identity and location memory than explicit encoding in naturalistic virtual environments. *Cognition, 196*, Article 104147.

Heuer, A., & Rolfs, M. (2021). Incidental encoding of visual information in temporal reference frames in working memory. *Cognition, 207*, Article 104526.
Holmes, J., Adams, J. W., & Hamilton, C. J. (2008). The relationship between visuospatial sketchpad capacity and children's mathematical skills. *European Journal of Cognitive Psychology, 20*(2), 272–289.
Huang, L. (2023). A quasi-comprehensive exploration of the mechanisms of spatial working memory. *Nature Human Behaviour, 7*(5), 729–739.
Huang, L. (2020). Unit of visual working memory: A Boolean map provides a better account than an object does. *Journal of Experimental Psychology: General, 149*(1), 1–30.
Hudson, T. E., & Landy, M. S. (2012). Motor learning reveals the existence of multiple codes for movement planning. *Journal of Neurophysiology, 108*, 2708–2716.
Huttenlocher, J., Hedges, L. V., & Duncan, S. (1991). Categories and particulars: Prototype effects in estimating spatial location. *Psychological Review, 98*(3), 352–376.
Igloi, K., Doeller, C. F., Berthoz, A., Rondi-Reig, L., & Burgess, N. (2010). Lateralized human hippocampal activity predicts navigation based on sequence or place memory. *Proceedings of the National Academy of Sciences, 107*(32), 14466–14471.
Jacobs, J., Weidemann, C. T., Miller, J. F., Solway, A., Burke, J. F., Wei, X.-X., Suthana, N., Sperling, M. R., Sharan, A. D., Fried, I., & Kahana, M. J. (2013). Direct recordings of grid-like neuronal activity in human spatial navigation. *Nature Neuroscience, 16*(9), 1188–1190.
Kit, D., Katz, L., Sullivan, B., Snyder, K., Ballard, D., & Hayhoe, M. (2014). Eye movements, visual search and scene memory, in an immersive virtual environment. *PloS One, 9*(4), Article e94362.
Klatzky, R. L. (1998). Allocentric and egocentric spatial representations: Definitions, distinctions, and interconnections. In Spatial cognition (Vol. 1404, pp. 1-17). Springer, Berlin, Heidelberg.
Kondo, A., & Saiki, J. (2012). Feature-Specific Encoding Flexibility in Visual Working Memory. *PLoS ONE, 7*(12), Article e50962.
Kraus, B. J., Brandon, M. P., Robinson, R. J., Connerney, M. A., Hasselmo, M. E., & Eichenbaum, H. (2015). During Running in Place, Grid Cells Integrate Elapsed Time and Distance Run. *Neuron, 88*(3), 578–589.
Kuipers, B. (1978). Modeling spatial knowledge. *Cognitive Science, 2*, 129–153.
Kuipers, B. (2000). The spatial semantic hierarchy. *Artificial Intelligence, 119*, 191–233.
Langlois, T. A., Jacoby, N., Suchow, J. W., & Griffiths, T. L. (2021). Serial reproduction reveals the geometry of visuospatial representations. *Proceedings of the National Academy of Sciences, 118*(13), Article e2012938118.
Lew, T. F., & Vul, E. (2015). Ensemble clustering in visual working memory biases location memories and reduces the Weber noise of relative positions. *Journal of Vision, 15(4): 10*, 1–14.
Logie, R. H. (1986). Visuo-Spatial Processing in Working Memory. *The Quarterly Journal of Experimental Psychology Section A, 38*(2), 229–247.
Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*(6657), 279–281.
Maguire, E. A., Frackowiak, R. S., & Frith, C. D. (1997). Recalling routes around London: Activation of the right hippocampus in taxi drivers. *Journal of Neuroscience, 17*(18), 7103–7110.
Maidenbaum, S., Miller, J., Stein, J. M., & Jacobs, J. (2018). Grid-like hexadirectional modulation of human entorhinal theta oscillations. *Proceedings of the National Academy of Sciences, 115*(42), 10798–10803.
Mallot, H. A., & Basten, K. (2009). Embodied spatial cognition: Biological and artificial systems. *Image and Vision Computing, 27*(11), 1658–1670.
Mishkin, M., & Ungerleider, L. G. (1982). Contribution of striate inputs to the visuospatial functions of parieto-preoccipital cortex in monkeys. *Behavioural Brain Research, 6*(1), 57–77.
Moser, E. I., Kropff, E., & Moser, M. B. (2008). Place cells, grid cells, and the brain's spatial representation system. *Annual Review of Neuroscience, 31*, 69–89.
O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map. Preliminary evidence from unit activity in the freely-moving rat. *Brain Research, 34*, 171–175.
O'Keefe, J., & Nadel, L. E. (1978). *The hippocampus as a cognitive map*. Oxford: Clarendon Press.
Oberauer, K., & Eichenberger, S. (2013). Visual working memory declines when more features must be remembered for each object. *Memory & Cognition, 41*(8), 1212–1227.
Oh, B. I., Kim, Y. J., & Kang, M. S. (2019). Ensemble representations reveal distinct neural coding of visual working memory. *Nature Communications, 10*(1), 5665.
Park, S. A., Miller, D. S., Nili, H., Ranganath, C., & Boorman, E. D. (2020). Map Making: Constructing, Combining, and Inferring on Abstract Cognitive Maps. *Neuron, 107*(6), 1226–1238.e8.
Parkinson, C., & Wheatley, T. (2013). Old cortex, new contexts: Re-purposing spatial perception for social cognition. *Frontiers in Human Neuroscience, 7*, Article 645.
Peer, M., Brunec, I. K., Newcombe, N. S., & Epstein, R. A. (2021). Structuring knowledge with cognitive maps and cognitive graphs. *Trends in Cognitive Sciences, 25*, 37–54.
Peer, M., Nadar, C., & Epstein, R. A. (2024). The format of the cognitive map depends on the structure of the environment. *Journal of Experimental Psychology: General, 153*(1), 224–240.
Pertzov, Y., & Husain, M. (2014). The privileged role of location in visual working memory. *Attention, Perception & Psychophysics, 76*(7), 1914–1924.
Schneegans, S., & Bays, P. M. (2017). Neural Architecture for Feature Binding in Visual Working Memory. *The Journal of Neuroscience, 37*(14), 3913–3925.
Siegel, A. W., & White, S. H. (1975). The development of spatial representations of largescale environments. In H. W. Reese (Ed.), *Advances in child development and behavior, 10* (pp. 10–55). New York: Academic Press.
Sommer, S., & Wehner, R. (2005). Vector navigation in desert ants, Cataglyphis fortis: Celestial compass cues are essential for the proper use of distance information. *Naturwissenschaften, 92*(10), 468–471.
Son, G., & Chong, S. C. (2023). Similarity-based clustering of multifeature objects in visual working memory. *Attention, Perception, & Psychophysics, 85*, 2242–2256.
Son, G., Oh, B. I., Kang, M. S., & Chong, S. C. (2020). Similarity-based clusters are representational units of visual working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 46*(1), 46–59.
Tamura, M., Spellman, T. J., Rosen, A. M., Gogos, J. A., & Gordon, J. A. (2017). Hippocampal-prefrontal theta-gamma coupling during performance of a spatial working memory task. *Nature Communications, 8*(1), 2182.
Taube, J. S. (1998). Head direction cells and the neurophysiological basis for a sense of direction. *Progress in Neurobiology, 55*, 225–256.
Taylor-Phillips, S., Jenkinson, D., Stinton, C., Kunar, M. A., Watson, D. G., Freeman, K., Mansbridge, A., Wallis, M. G., Kearins, O., Hudson, S., & Clarke, A. (2024). Fatigue and vigilance in medical experts detecting breast cancer. *Proceedings of the National Academy of Sciences, 121*(11), Article e2309576121.
Trullier, O., Wiener, S. I., Berthoz, A., & Meyer, J. A. (1997). Biologically based artificial navigation systems: Review and prospects. *Progress in Neurobiology, 51*, 483–544.
Utochkin, I. S., & Brady, T. F. (2020). Individual representations in visual working memory inherit ensemble properties. *Journal of Experimental Psychology: Human Perception and Performance, 46*(5), 458–473.
Warren, W. H. (2019). Non-Euclidean navigation. *Journal of Experimental Biology, 222* (Suppl 1).
Warren, W. H., Rothman, D. B., Schnapp, B. H., & Ericson, J. D. (2017). Wormholes in virtual space: From cognitive maps to cognitive graphs. *Cognition, 166*, 152–163.
Weisberg, S. M., & Newcombe, N. S. (2016). How do (some) people make a cognitive map? Routes, places, and working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 42*(5), 768–785.
Wittlinger, M., Wehner, R., & Wolf, H. (2006). The ant odometer: Stepping on stilts and stumps. *Science, 312*, 1965–1967.
Wyble, B., Hess, M., O'Donnell, R. E., Chen, H., & Eitam, B. (2019). Learning how to exploit sources of information. *Memory & Cognition, 47*(4), 696–705.
Yousif, S. R., Chen, Y. C., & Scholl, B. J. (2020). Systematic angular biases in the representation of visual space. *Attention, Perception & Psychophysics, 82*, 3124–3143.
Yousif, S. R. (2022). Redundancy and reducibility in the formats of spatial representations. *Perspectives on Psychological Science, 17*, 1778–1793.
Yousif, S. R., & Keil, F. C. (2021). The Shape of Space: Evidence for Spontaneous but Flexible Use of Polar Coordinates in Visuospatial Representations. *Psychological Science, 32*(4), 573–586.
Yousif, S. R., Forrence, A. D., & McDougle, S. D. (2024). A common format for representing spatial location in visual and motor working memory. *Psychonomic Bulletin & Review, 31*(2), 697–707.
Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature, 453*(7192), 233–235.