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When do sex differences manifest? Context-dependent modulation of spatial memory

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Abstract

Commuting to work or taking a trip to the nearby grocery store might seem as we are on autopilot, yet at the cognitive level it is anything but simple. Navigating in dynamic settings involves various complex processes, such as perception, attention, decision-making, adaptation and execution. Interestingly, research has shown that the ability to solve spatial problems is considered one of the most reliable domains to demonstrate sex differences, with distinct preferences for learning strategies. Beyond sex, environmental and cultural factors as well as personal experiences also play critical roles in shaping how, and how well, we find our way.

In response to this complexity, my research adopts a fundamentally different approach. In *Chapter 2*, we introduced a spatial memory paradigm that provides novel experience to both males and females. The environment was built on minimal information, where salient spatial cues, such as traditional landmarks and orientation cues, were omitted. By minimizing familiarity, the design reduced biases of culture, environment and prior knowledge, allowing memory processes to be observed in their most elemental form. By reintroducing familiar spatial elements, the goal was to pinpoint the specific instances and conditions under which gender differences may arise.

In *Chapter 3*, we extended this minimal framework with an incidental learning paradigm. While navigating the sparse environment, participants were exposed to floating images of faces and objects. This design allowed us to examine how spatial memory interacts with the incidental encoding of socially and perceptually meaningful information.

Moving beyond sex differences, *Chapter 4* focuses on individual variability. By implementing the Object Imagery and Verbal Questionnaire together with the Sensory Processing Sensitivity Questionnaire, it links spatial performance to broader cognitive styles and sensory sensitivity, offering a more nuanced perspective on how spatial memory is shaped.

Finally, in *Chapter 5*, we return to the original spatial memory paradigm and place the final piece of the puzzle. We introduce the most familiar setting, one that most closely resembles real-world experiences, allowing us to test whether, and in what way, sex differences manifest once everyday spatial cues are restored.

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Introduction

1.1 Mapping memories

1.1.1 The hippocampal system

Spatial cognition is fundamental to the survival and daily functioning of almost all species. This essential skill involves the encoding, storage and replay of a sequence of spatial locations, enabling individuals to navigate towards a goal. How does the brain encode and recall spatial locations with such precision?

Spatial cognition is one of the most flourishing fields in neuroscience ever since John O'Keefe's groundbreaking discovery of place cells, making the hippocampus central in spatial memory (O'Keefe and Dostrovsky, 1971). The hippocampus, located in the medial temporal lobe within the limbic circuitry, receives inputs from the septal nuclei, the amygdala, and the thalamus (Witter, 2007). It comprises the dentate gyrus and the cornu Ammonis (CA), also known as hippocampus proper. Together with the subiculum, these structures form the hippocampal formation. The hippocampus proper contains large pyramidal neurons, and it is organized into three zones: CA1, CA2 and CA3. Information flows unidirectionally within the hippocampal network: starting from the entorhinal cortex, it progresses to the dentate gyrus, then to CA3, CA1, and loops back to the entorhinal cortex (Vakilna et al., 2021, Figure 1.1).

The hippocampus is crucial for encoding complex sequences of events and spatial locations, as well as linking these sequences to form a comprehensive cognitive map that enables the retrieval of interconnected episodic memories, a type of declarative memory (Eichenbaum, 2004; Bird and Burgess, 2008). It also plays a key role in the consolidation of short-term memories into long-term storage, effectively connecting our daily experiences with our long-term memory (Squire et al., 2004). This function is vital for learning and adapting, as it allows for the recall of individual memories and the integration of these memories to form

new insights. The hippocampus integrates diverse memories over time and space, supporting our abilities in navigation, prediction, and future planning (Moscovitch et al., 2016). It also interacts with higher cortical areas to modulate attention and decision-making, providing a context for interpreting new information Preston and Eichenbaum (2013). The hippocampus therefore is more than just a storage unit for memories: it actively processes information that influences our perception and interaction with the environment.

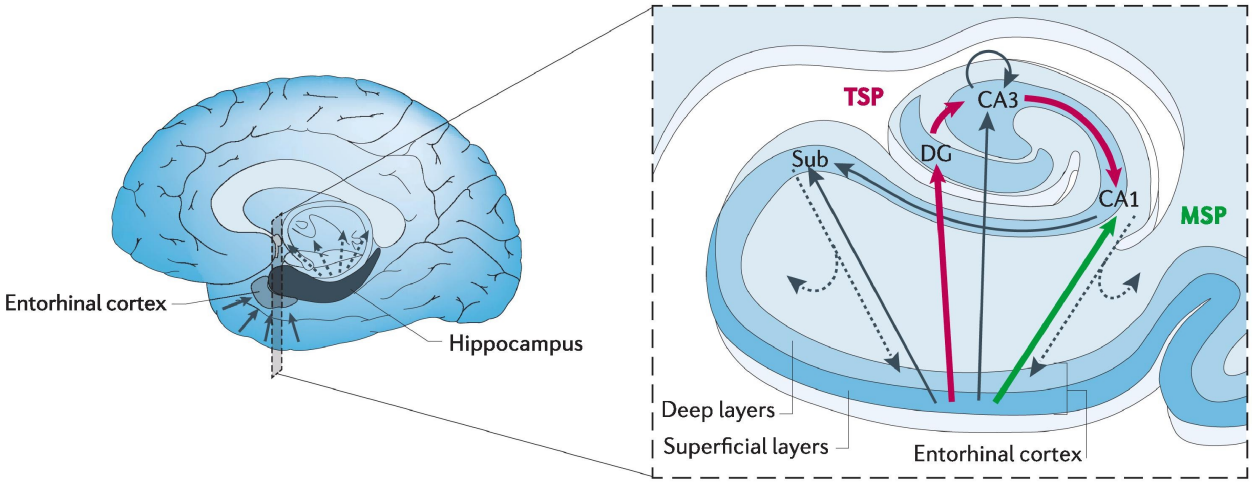


Figure 1.1: Hippocampal system. Reprinted from *"The hippocampus as a visual area organized by space and time: A spatiotemporal similarity hypothesis"*, by Turk-Browne (2019), retrieved from `https://doi.org/10.1016/j.visres.2019.10.007`.

1.1.2 Spatially selective cells

In 1971, while recording single units in the rat hippocampus, O'Keefe observed that a certain neuron was sensitive to a specific spatial location, activating exclusively when the rat visited that special place (O'Keefe, 2014a). He noted that other neurons behaved similarly: as the animal explored a new environment, a combination of neurons become active, and reactivated in the same fashion upon revisiting those places. Whenever the animal explored a new location, the place cells were remapped, leading to different combinations of cells representing different spaces (Muller and Kubie, 1987). Place cells are also influenced by the geometry of the environment: when environmental boundaries are altered, shape-based remapping occurs (Hartley et al., 2000). O'Keefe proposed that this dynamic representation of space must be Tolman's cognitive map (Tolman, 1948). Interestingly, the physical locations of the place cells in the brain have very little correlation with the spatial locations where they fire (place fields), which still baffles researchers (O'Keefe and Nadel, 1978; O'Keefe, 2014b).

O'Keefe's findings provided one of the first pieces of evidence for a neural correlate of a mental state, specifically the sense of space (Mallot, 2023). By now, a variety of spatially selective cells have been discovered in the hippocampal formation that form a comprehensive navigational system. In 2005, May-Britt and Edward Moser further expanded the understanding on how spatial information is processed in the brain, by identifying grid cells in the medial entorhinal cortex (Figure 1.2). Grid cells are named for their unique firing patterns that cover the spatial environment. As the animal moves through space, each grid cell fires periodically at multiple locations that form vertices of a hexagonal grid in the environment (Hafting et al., 2005). These cells enable the animal to track its position relative to a starting point by internally updating its coordinates based on movement cues, an ability known as path integration (Mittelstaedt and Mittelstaedt, 1980). Grid cells provide a scalable metric for mapping environments (Moser et al., 2015). In addition to varying scales, the firing patterns can also differ based on the direction in which the grid cells are aligned and the degree of overlap between one grid pattern and another, known as phase (Si et al., 2012). Grid cells are also highly organized into modules in the entorhinal cortex. Within each module, the firing patterns of the grid cells share the same scale and orientation but differ in phase. The deeper a module is located in the entorhinal cortex, the larger the scale of its grid cells' firing pattern (Pilly and Grossberg, 2014; Stensola et al., 2012). While grid cells might seem to solely provide precise metric for navigation, research suggests that they also aid in learning about space: grid patterns have been shown to be influenced by changing geometry of the environment (Fyhn et al., 2007; Krupic et al., 2015; Wernle et al., 2017), by walls (Barry et al., 2007; Keinath et al., 2018), by local cues (Ismakov et al., 2017), and even by goals (Boccara et al., 2019; Luo et al., 2022).

Since 2005, grid cells have been discovered in other parahippocampal areas, such as the presubiculum and parasubiculum (Boccara et al., 2010). Grid cells also interact with place cells as they influence the resolution of the place fields, and they also interact with head direction (HD) cells, which may potentially provide directional information to form their hexagonal pattern (Winter et al., 2015; Mallory et al., 2018; Gerlei et al., 2020). HD cells are found in the postsubiculum, as well as in the retrosplenial cortex and the entorhinal cortex (Figure 1.2). Receiving inputs from the vestibular system, they fire whenever the animal faces a certain direction to keep it oriented. Different HD cells respond to different angles, each firing at a specific angle relative to each other, making up all 360 degrees. Landmarks show strong control over their preferred direction: one type of HD cells aligns themselves to local landmarks, while another type aligns themselves to global ones (Taube, 2017).

Notably, HD cells are among the first spatially selective cells to develop, appearing by postnatal day 12 in rats, before they open their eyes and before they begin to actively

explore their environment. Moreover, they exhibit adult-like properties from the onset. This early emergence indicates that the HD system is capable of organizing itself without reliance on visual cues, (although visual cues rapidly improve the reliability of directional signals), suggesting its foundational role in the spatial orientation system (Tan et al., 2015, see also Section 1.2.3) . While grid cells and place cells develop more slowly, together with HD cells, they form a preliminary map of space as early as postnatal day 16 (Langston et al., 2010).

HD cells supply information not only to grid cells, but also to boundary vector cells (BVC), which further aid in orientation (Lever et al., 2009). BVCs, found in the subiculum, fire whenever the animal is at a specific distance and angle from a boundary, that is, anything that blocks navigation (Figure 1.2). These cells might be responsible for the shape-based remapping of place fields; moreover, the removal or addition of boundaries in an environment can cause place cells to stop firing completely (Muller and Kubie, 1987; Barry et al., 2006).

Border cells, located in the medial entorhinal cortex, are related to BVCs but their functional characteristics are different. While BVCs encode the distance and direction to environmental boundaries, and provide a vector-like representation that is useful for navigating relative to multiple boundaries, border cells fire when an animal is close to the actual boundary itself, such as the walls or edges of platforms. Border cells are therefore useful for immediate boundary detection, avoiding collisions and navigating along the edges of environments. Border vector cells have also been shown to be crucial to the formation of functioning grid cells in early development of rats, although the absence of boundaries in early life does not necessarily prevent the emergence of grid patterns if the animal gains some experience at a later stage (Ulsaker-Janke et al., 2023). Like head-direction cells, border cells are one of the first spatially selective cells to emerge in the developing brain, expressing adult-like firing fields from the first days of exposure to an open environment, further indicating their fundamental role in spatial representations (Bjerknes et al., 2014).

The range of spatially selective cells continues to expand, with new types being identified over time. Speed cells in the entorhinal cortex adjust their firing rate based on the animal's linear and angular navigational velocity (Kropff et al., 2015; Spalla et al., 2022). Landmark-controlled cells become active in response to specific landmarks within the environment (Gothard et al., 1996); (Rivard et al., 2004; Deshmukh and Knierim, 2013). Similarly, object vector cells fire when an animal is at a specific distance and direction from objects in its surroundings (Høydal et al., 2019).

To conclude, grid, head-direction, border, speed and object vector cells in the medial entorhinal cortex and adjacent parasubiculum, as well as place, boundary vector and landmark-controlled cells in the neighbouring hippocampal-parahippocampal regions, collectively form a sophisticated navigational system that provide a precise metric for mapping, and an un-

derstanding of space (Andersson et al., 2021).

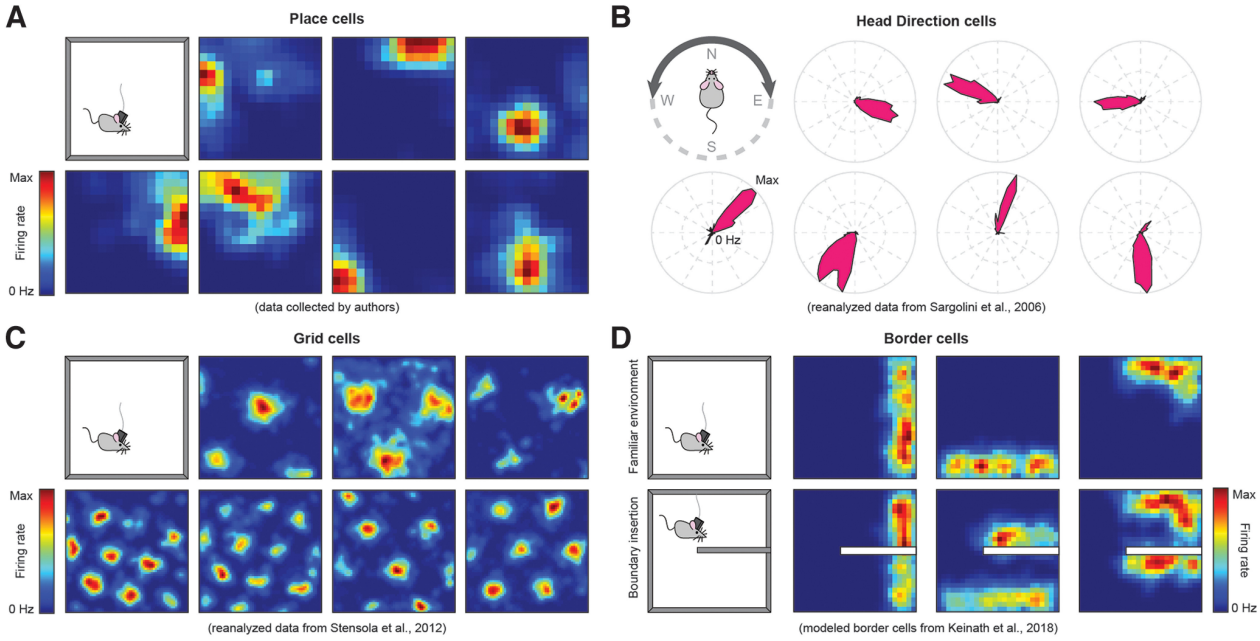


Figure 1.2: Examples of spatial cell types in the rat hippocampal formation. A, place cells activate in specific locations regardless of heading direction. The heat maps represent the firing rates of seven example place cells. B, head direction cells fire based on head orientation, independent of location. Radial plots of the firing rate for seven example head direction cells. C, grid and other periodic cells fire in symmetrical patterns across environments. The heat maps represent the firing rates of seven example grid cells. D, border or boundary cells in the subiculum, which fire at fixed distances from boundaries in an allocentric direction. Heat maps represent the firing rates of three example synthetic allocentric border cells in an open field and when a boundary is inserted. Reprinted from *"Making Sense of the Multiplicity and Dynamics of Navigational Codes in the Brain"*, by Maisson et al. (2022), (p. 8451). Retrieved from `https://doi.org/10.1523/JNEUROSCI.1124-22.2022.`.

1.2 Paths, places, and perspectives

1.2.1 Cognitive maps and graphs

Siegel and White's 1975 theoretical model describes how spatial representations are acquired and evolve over time in a new environment, a process they termed spatial cognitive microgenesis. This model was so influential, it was referred to as the dominant framework for decades (Montello et al., 1999). At the core of spatial representations are landmarks: in a new environment, we first recognize distinct objects and scenes that stand out due to their

shape, size, or colour (e.g., a large cathedral), and for their functionality in navigation (e.g., located by a cross-section). This initial stage is called landmark knowledge (Ishikawa and Montello, 2006). Once the identities of landmarks are established, we begin to connect them through sequences of environmental choice points (such as moves and turns), creating route knowledge. This stage is procedural, starts out non-metric, and it is often described as egocentric, since it relies on the observer's perspective and experience. Finally, we transition to the most advanced stage, survey knowledge. Here, we also learn the distances and the directional relationship among landmarks, even among the ones we never directly travelled to.

Survey knowledge forms the basis of cognitive maps, which represent spatial relationships in a globally consistent manner, structured within a unified coordinate system. Traditionally, it is thought to encode environmental features like places, landmarks, and goals within Euclidean space (Peer et al., 2021; Chrastil and Warren, 2014). By relying on this allocentric framework, cognitive maps enable us to understand spatial relationships and to navigate in an efficient, flexible way. For instance, if you know the locations of the train station, a store, and your home relative to one another, the unified coordinate system allows you to determine the shortest path between any of these points.

However, growing evidence has shown that people tend to disregard Euclidean metric when navigating towards a goal. Estimating distances and directions between locations tend to be influenced by the number of turns taken and can differ between inbounding and outgoing path directions (Jansen-Osmann and Wiedenbauer, 2004). People also tend to create simple, schematic representations of their environment. To address these tendencies, an alternative theory suggests that spatial knowledge is organized in a graph-like structure, composed of locations (nodes) connected by paths, without any reference to a global coordinate system, which may better reflect route-based navigation, an ordered sequence of stimuli and response (e.g., "when you see the bakery, turn right").

While these two models used to be viewed as conflicting concepts, a more recent theory suggests that the human brain encodes both types of spatial knowledge structures (Figure 1.3). According to Peer et al. (2021), these two types of representations are encoded in the hippocampal formation by partially distinct and partially overlapping neural systems, supporting both Euclidean-like and graph-like representations. This dual representation may provide the flexibility needed for navigation across different environments and navigational demands, allowing us to rely on a metric, map-like framework when precision is required, or to switch to a simpler, route-based structure when efficiency or familiarity makes it more beneficial.

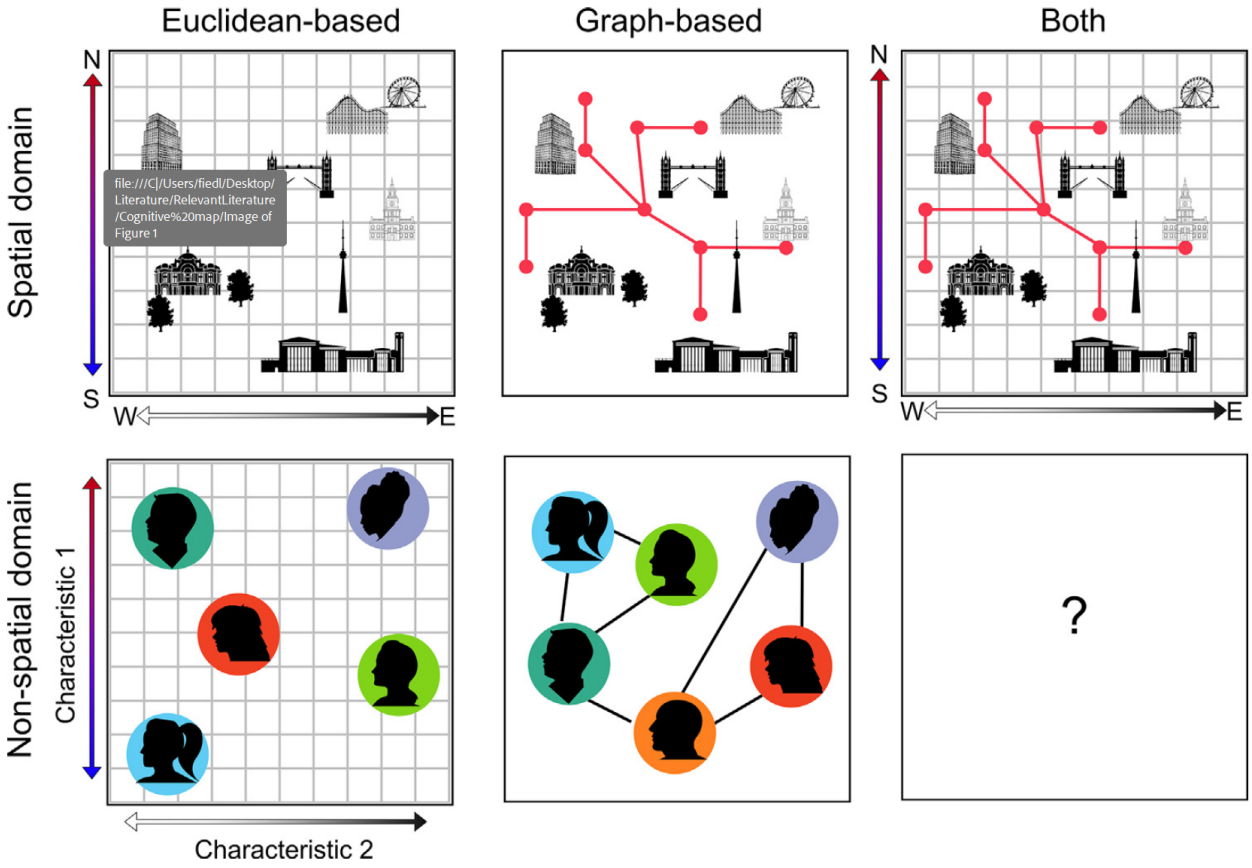


Figure 1.3: Map-based (Euclidean) and graph-based representations in the Peer et al. (2021) framework. In the spatial domain (top row), locations can be represented either in Euclidean coordinates, or by nodes (locations) and links (paths between the locations). These two representations can be used simultaneously for a more flexible and efficient navigation. Map-based and graph-based knowledge can also be represented in non-spatial domain (bottom row). For example, one's social circle can be continuously represented in terms of their personality characteristics, or they can be distinct entities (nodes) with specific social connections between one another (links). Reprinted from *"Structuring Knowledge with Cognitive Maps and Cognitive Graphs"*, by Peer et al., 2021 (p. 38). Retrieved from `https://doi.org/10.1016/j.tics.2020.10.004.`.

1.2.2 Landmarks

The hippocampus integrates sensory and spatial information to anchor landmarks within cognitive maps, providing a framework essential for navigating both familiar and novel environments O'Keefe and Nadel (1978). The role of the hippocampus in landmark processing is complemented by the parahippocampal gyrus, a neighbouring region crucial for encoding and recognizing the navigational relevance of landmarks. Janzen and van Turennout (2004) demonstrated that this brain region selectively increases its activity only for land-

marks located at decision-making points along a route, independent of the salience of all other landmarks. Remarkably, this selectivity is established after just one exposure and persists even when these landmarks are not consciously remembered. Janzen and van Turennout found that the parahippocampal response to decision-point landmarks is independent of explicit memory, suggesting that its role in spatial cognition is the automatic detection of landmarks that are useful and informative for navigation. These findings further indicate an efficient and cooperative brain system, crucial for survival, in which the parahippocampal gyrus selectively filters information that most benefits hippocampal functioning (Spiers and Maguire, 2004).

The retrosplenial cortex complements the hippocampus and parahippocampal gyrus by contextualizing landmarks and integrating them into flexible navigational strategies. A key function of the retrosplenial cortex is its ability to process both local and global landmarks, which differ based on their spatial visibility and utility. Local landmarks are in close proximity to the individual's current position, providing immediate navigational cues, while global landmarks are visible from greater distances or multiple perspectives, offering broader spatial orientation (Noble et al., 2020). In this region, two types of head direction (HD) cells have been identified: one type responds to local landmarks, while the other is attuned to global landmarks (Taube, 2017). The retrosplenial cortex plays a vital role in distinguishing reliable from unreliable landmarks, responding most strongly to stationary landmarks that serve as consistent spatial reference points (Page and Jeffery, 2018). Together, the hippocampus, parahippocampal gyrus, and retrosplenial cortex appear to form a dynamic network that encodes, evaluates, and integrates landmarks to guide navigation.

1.2.3 Orienting

The advancement in communication technology made pedestrian navigation systems widely accessible. However, this convenience might come at the cost of our spatial abilities. A recent meta-analysis by Miola et al. (2024) found that GPS use negatively impacts environmental knowledge and sense of direction. Ishikawa (2018) further investigated the long-term effects of navigation tools on spatial orientation and wayfinding accuracy. They determined participants' accumulated experience with navigation tools by taking the duration of use multiplied by frequency of use. Sense of direction was assessed by the Sense of Direction Scale (Hegarty, 2002). He observed that frequent pedestrian and in-car GPS users reported a lower sense of direction, made more wayfinding errors and were less efficient. In contrast, those who relied on paper maps reported a stronger sense of direction and demonstrated greater accuracy in finding their desired paths.

A key distinction between paper maps and navigation systems lies in the nature of learn-

ing: active versus passive. Pedestrian and in-car navigation systems enable users to follow directions passively, which eliminates two critical elements of wayfinding: on one hand, users are unable to associate environmental choice points to landmarks, since GPS systems primarily display road networks devoid of landmarks. Instead, the cue to turn at a choice point is solely provided by the GPS. In the absence of landmarks, GPS systems also automatically orient the user in the right direction, bypassing the need for individuals to actively orient themselves. As a result, the initial learning of the environment at the point of departure is effectively eliminated. This illustrates how removing the need to self-orient, as GPS systems do, can erode spatial abilities.

This behavioural evidence aligns with neurophysiological findings showing that orienting is the cornerstone of wayfinding. Within the brain's navigation system, HD cells (see Section 1.2.3) provide the simplest allocentric signal by encoding facing direction based on vestibular input and aligning it to external sensory cues, such as landmarks (Peyrache et al., 2017). This signal is conveyed by the antero-dorsal thalamic nucleus to the post-subiculum, which integrates it with other sensory information and projects it throughout the parahippocampal circuit. Developmentally, HD neurons emerge at the earliest stage of ontogenetic development, alongside border cells, which code for environmental boundaries (Bjerknes et al., 2015; Tan et al., 2015; Langston et al., 2010). Interestingly, both precede the maturation of grid and place cells, and their activity is critical for the later formation of these spatial representations.

In this perspective, orienting is not simply one of many components of wayfinding; it is the building block on which successful navigation depends. It is during self-orienting that individuals anchor themselves within the environment, link landmarks to choice points, and construct a coherent spatial framework. When this process is bypassed, environmental knowledge is often fragmentary.

1.3 Gendered geometry

1.3.1 Male advantage or (individual) difference in experience?

There is a widespread belief in a male advantage in spatial navigation tasks across many species, including humans. Moreover, the ability to solve spatial problems is considered one of the most reliable gender differences, with distinct preferences for learning strategies (Saucier et al., 2002; Jones and Healy, 2006; Pletzer, 2014; Andersen et al., 2012; Pletzer et al., 2017; Dahmani et al., 2023).

The male advantage in spatial cognition has often been explained by the sex-specific adaptation hypothesis, which suggests that males, due to larger home ranges for navigation or

natural selection, have evolved better spatial navigation skills (Jones et al., 2003). However, modern communities that primarily rely on hunting, gathering, fishing, or herding for their livelihoods, and therefore with lifestyles resembling those of ancestral societies, provide inconsistent evidence. A study conducted by Clint et al. (2012) analysed 11 animal species and found no relationship between sex differences in home range size and spatial ability. The authors aimed to address the limitations of this study by expanding it with 10 additional species, and by including human populations from non-Western cultures where both sexes have similar ranging behaviour. The study's updated analysis continued to find little evidence that could support the sex-specific adaptation hypothesis despite broadening the species profile (Hults et al., 2024). Specifically, in non-Western human populations, where both sexes travel long distances, the previously observed male advantage in spatial orientation tasks disappeared (Berry, 1966; Cashdan et al., 2012; Trumble et al., 2016; Davis et al., 2021; Jang et al., 2019). This lack of correlation suggests that other factors, such as cultural or environmental influences, could be key factors in developing spatial abilities, challenging the notion that these abilities are the result of species-specific evolutionary adaptations.

In addition to navigation, sex differences have been observed in memory consolidation during incidental learning. Torromino and colleagues have demonstrated that female mice show a lower memory consolidation capacity during an incidental learning paradigm (Torromino et al., 2021). They found that at a short delay (1 minute), male and female mice demonstrated similar (incidental) memory capacity. However, when the delay was long (1 hour or 24 hours), female mice remembered up to 4 objects, while male mice remembered up to 6. This may suggest that while male mice could consolidate all incidentally learned items to long-term memory, female mice can only do so in lower memory load conditions. In a subsequent brain mapping study, they found that the high memory load condition led to a higher activation of the dorsal hippocampus (dHP) in male mice than in female mice, whereas female mice demonstrated a higher activation in the thalamic nucleus reuniens (RE). Comparison of low, intermediate and high memory load conditions indicated that this sex difference in recruiting different pathways was load dependent. However, chemogenetic inhibition of the RE and stimulation of the dHP revealed that this capacity limit in female mice can be reversed, demonstrating similar performance to male mice. Conversely, stimulation of the RE in male mice lowered the capacity to the level seen in female mice.

These findings suggest that sex differences in spatial cognition cannot be explained solely by species-specific evolutionary pressures or task-specific demands. While differential neural mechanisms may contribute, their context dependence and reversibility indicate that they are not the whole story, motivating us to also consider stable individual traits. Blazhenkova and Kozhevnikov (2008) suggest that cognitive styles may also play a role in spatial mem-

ory performance, as individuals differ in their preferences for visual or verbal processing. They proposed a three-dimensional cognitive style model which categorizes individuals into three trait-like styles. Verbalizers prefer to process information verbally, spatial visualizers excel in tasks requiring mental manipulation of objects and navigation, while object visualizers are better at recognizing and recalling the detailed features of objects. These distinct cognitive traits may influence how individuals encode, store, and recall spatial information. Understanding a participant's cognitive style could help explain variations in spatial memory performance across individuals (Höffler et al., 2017; Blazhenkova and Kozhevnikov, 2008).

Taken together, the evolutionary, neurobiological, and individual differences perspectives raise several broad questions that motivate the present work. Does the male advantage reported in many studies of spatial navigation reflect hardwired, structural differences, or are such findings better explained by task-dependent neural activation? If structural explanations are insufficient, should we instead interpret observed sex differences as reflecting tendencies toward different navigation strategies, or even different motivational tendencies in males and females? Finally, to what extent are such strategy preferences determined by stable cognitive traits, and to what extent do they reflect dynamic choices shaped by the context and demands of the situation?

To address these questions, the remainder of this thesis is organised into five parts. *Chapter 2* introduces a novel virtual reality paradigm designed to minimise reliance on prior spatial experience. By systematically manipulating environmental familiarity (sparse vs. landmark-rich, flat vs. spherical layouts), we test the hypothesis that sex differences in sequential spatial recall emerge selectively with increasing environmental plausibility. *Chapter 3* extends the paradigm with an incidental learning task, asking whether sex differences become more apparent when faces or objects must later be recognised, whether retrieval modality (visual vs. verbal) and retention delay modulate these effects, and how incidental learning influences the original spatial memory task. *Chapter 4* moves beyond sex differences to examine individual differences, testing how cognitive style (object imagery, spatial imagery, verbal) and self-reported strategy preferences predict recall performance, and whether these predictors interact with sex. *Chapter 5* returns to spatial familiarity by combining Euclidean structure with traditional landmarks, testing whether this maximally familiar condition amplifies sex differences and their relationship with imagery abilities. Finally, *Chapter 6* provides a general discussion and proposes a novel mental rotation paradigm to further investigate whether the context-dependent nature of sex differences observed in navigation tasks extends to mental rotation.

A dynamic task in a sparse environment

2.1 Abstract

Sex differences in spatial cognition often show males outperforming females, especially in familiar environments rich with traditional landmarks. The present study explores these differences in a novel context: a sparse, spherical virtual reality environment devoid of familiar cues, such as traditional landmarks and other orientation aids. By manipulating spatial structure and the presence of familiar cues, we aimed to investigate how males and females differ in their Sequential Recall performances and spatial strategy use in this unfamiliar setting. In such a non-Euclidean and unusual space, without traditional landmarks, recall performance shows a surprising bimodal distribution, and males and females exhibit similar behaviours with no clear preference for a particular strategy. Across environments differing in familiarity, 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 a major 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.

2.2 Introduction

Navigation towards a goal in an unknown non-trivial environment involves the encoding, storage and replay of a sequence of spatial locations (Lee et al., 2023). Spatial sequential working

memory is limited both in capacity and duration (Miller, 1956; Cowan, 2001; Pertzov et al., 2017). Research across human and nonhuman 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; (e.g., mental rotation; Metzler and Shepard, 1974; Jansen and Heil, 2009; Maeda and Yoon, 2012) and large-scale (e.g., navigation) spatial abilities (Astur et al., 1998; Nazareth et al., 2019). In addition to performance differences, males and females often differ in their spatial strategies. Males tend to use "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 "route" or "egocentric" strategy, connecting landmarks through sequences of decision points from the observer's perspective (Lawton, 1994; Montello et al., 1999; Ishikawa and Montello, 2006; Jones and Healy, 2006; Tascón et al., 2021). 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 (Grön et al., 2000; Yagi and Galea, 2018; Rolls, 2023; Zhang et al., 2023). The greater hippocampal activation in males may in fact not be specific to spatial tasks (Torromino et al., 2021).

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 (Clint et al., 2012). 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 (Miner et al., 2014; Cashdan and Gaulin, 2016). 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 (Gallois et al., 2015; Davis et al., 2021). 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 (1981) 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 (Berry, 1966; Cashdan et al., 2012; Trumble et al., 2015; Jang et al., 2019; Davis and Cashdan, 2020). 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 (Cushman et al., 2013). 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 (Widdowson and Wang, 2022; Baumann and Mallot, 2023; Kim and Doeller, 2024), while distortions in spatial representation are observed, including in rodent grid cells (Stella et al., 2019; Ulsaker-Janke et al., 2023), highlighting the novelty of such unfamiliar settings. We then changed the environment by adding different familiar cues across the conditions. We hypothesized that the changes in familiarity/plausibility will be reflected in distinct sex trends of spatial memory performance. In a broader sense, we aim to understand how spatial behaviour in non-standard environments can be interpreted through cognitive maps and examine how varying degrees of familiarity influence memory performance.

2.3 Experiment 1 – Spherical, sparse environment

2.3.1 Methods

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; (Cohen, 2013)). 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 ((Nazareth et al., 2019)), 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. Ninety-six healthy adults participated through the online platform Prolific (48 females; mean age = 25.66 ± 7.25 years). All included participants indicated coinciding biological sex and gender, 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.

Materials

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 2.1). 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.

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 8 objects) and by using environments of differing complexity (cube vs. dodecahedron). These balls would always appear on one of the vertices of the coloured tiles. This required participants to rely on memorizing combinations of three colours of the faces and the relative positions of these faces.

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. As discussed earlier, the initial orienting process in wayfinding is crucial. To facilitate learning, participants were instantiated in the centre of the sphere, facing a randomized direction.

Unity technical specifications

The virtual environments were developed in *Unity* (version 2019.4.16f1, Unity Technologies), using C# scripts edited in Visual Studio. 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 rendering pipeline was set to the Universal Render Pipeline (URP) in high-quality mode,

with full-resolution textures, per-texture anisotropic filtering, real-time reflection probes enabled, and VSync set to every vertical blank, targeting a refresh rate of 60 Hz. No texture streaming or resolution scaling was applied. 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). Quality control procedures included pilot testing across machines and browsers, and excluding incomplete data uploads.

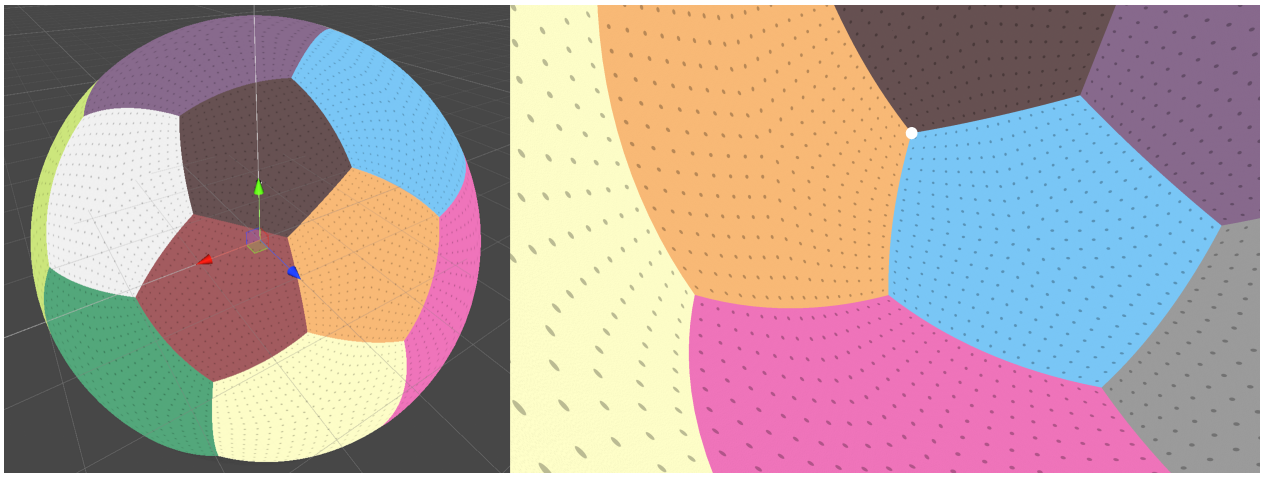


Figure 2.1: External view (left) and internal/game view (right), of the spherical (Dodecahedron) environment.

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 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.

Prior to the actual experiment, participants familiarized themselves with the task in a training session. Participants were then asked to locate and memorize the positions of white spheres ("balls") that appeared within the virtual environment. The balls appeared sequentially, each positioned at a vertex of the Platonic solid. In the cubic variants, the 6 different colours resulted in 8 possible location points (vertices) where the balls could appear, while in the dodecahedron variants, the 12 different colours resulted in 20 possible location points.

The number of balls participants were required to locate and memorize increased by one in each subsequent trial, starting with one ball in the first trial. There was a total of 8 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-second delay followed, and participants were then asked to recall and navigate to the locations in the correct order. 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. At the end of the experiment, participants were asked to describe the strategies they used to memorize the location points.

Data analysis

Statistical analyses were performed with RStudio (https://rstudio.com/).

Recall scores were calculated for each participant as the total number of correctly recalled location points in the correct order (Sequential Recall) and irrespective of order (Free Recall). Outliers, defined as values exceeding ± 3 standard deviations from the mean, were removed from recall performance variables (Sequential Recall, Free Recall), if any. To address the inherent skewness in reaction times, the data was log-transformed. Groups means for descriptive statistics were calculated.

To better understand participant behaviour in this novel task, Sequential Recall score distributions were analysed across variants. To formally assess whether the distributions deviated from unimodality, we conducted tests of multimodality. Specifically, we applied Hartigan's Dip Test ((Hartigan and Hartigan, 1985)), a conservative test of unimodality, using the `diptest package`, and the Excess Mass test ((Müller and Sawitzki, 1991)) using the `multimode` package.

Due to violations of normality and the bimodal distribution of Sequential Recall, a standard ANOVA was 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 in R. A total of 1,000 permutations were performed to assess the significance of main effects and interactions.

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

Using Pearson's product-moment correlations, mean Sequential Recall scores were corre-

lated with reaction times, across participants and between genders.

2.3.2 Results

Sequential Recall distributions

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

Figure 2.2 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.

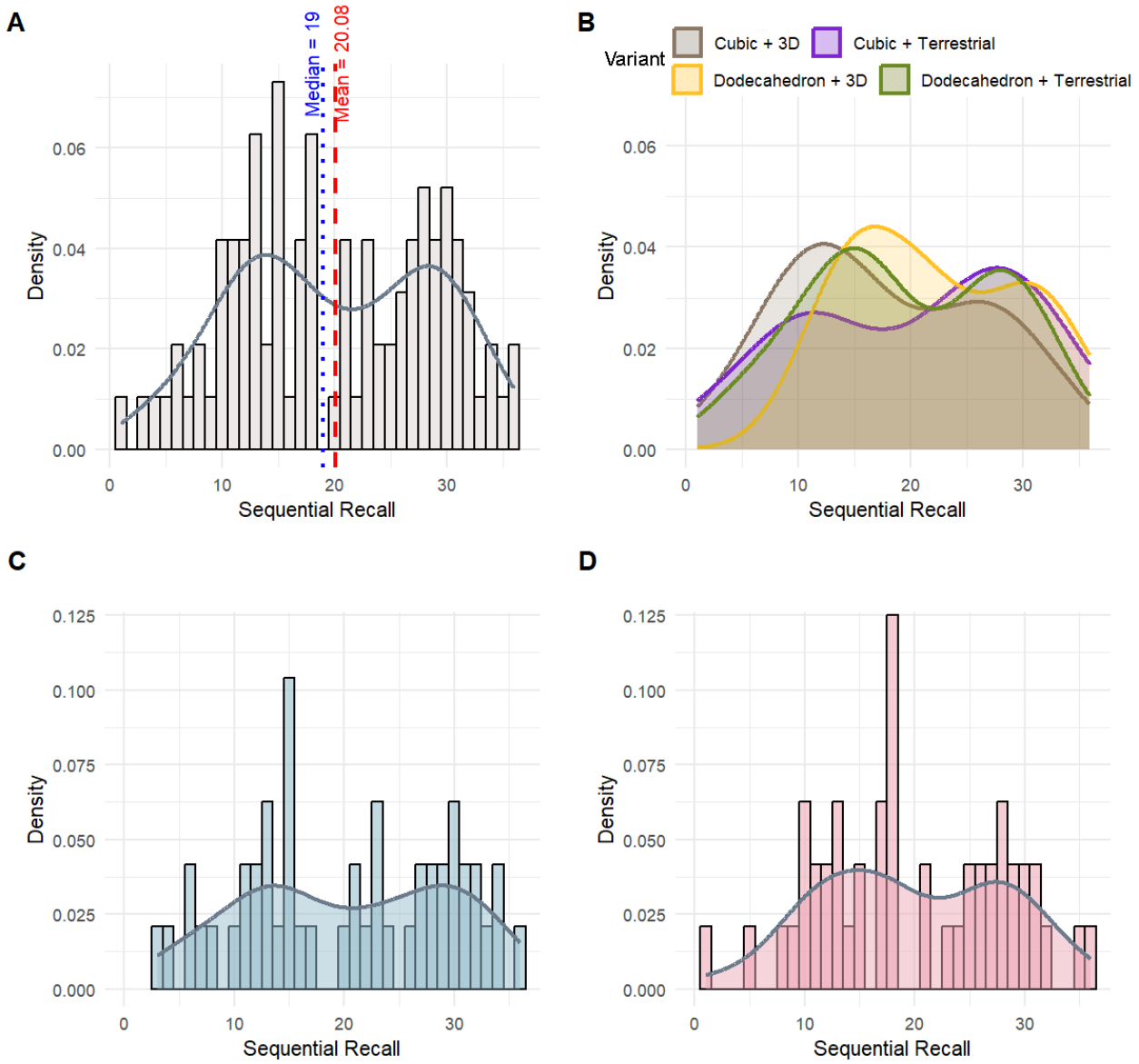


Figure 2.2: A) Sequential Recall score distribution across all participants, B) smoothed distributions across variants, and C) among males and (D) females. In these and similar panels, the continuous curves, serving merely as guides to the eye, represent kernel density estimates of the data, obtained using a Gaussian kernel with an automatically determined bandwidth in RStudio.

No Effects of Environment, Movement and Sex on Sequential Recall

A permutation-based three-way ANOVA revealed no significant main effects of Sex, ($F(1, 88) = 0.06$, $p = .803$), Environment, ($F(1, 88) = 1.00$, $p = .320$), or Movement Type, ($F(1, 88) = 0.01$, $p = .946$). Likewise, no significant interactions were found for Sex × Environment, ($F(1, 88) = 0.27$, $p = .602$); Sex × Movement Type, ($F(1, 88) = 0.35$, $p = .556$); En-

vironment × Movement Type, ($F(1, 88) = 2.05$, $p = .155$); or the three-way interaction, ($F(1, 88) = 1.19$, $p = .278$).

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 the later section, alongside with **Experiment 2**.

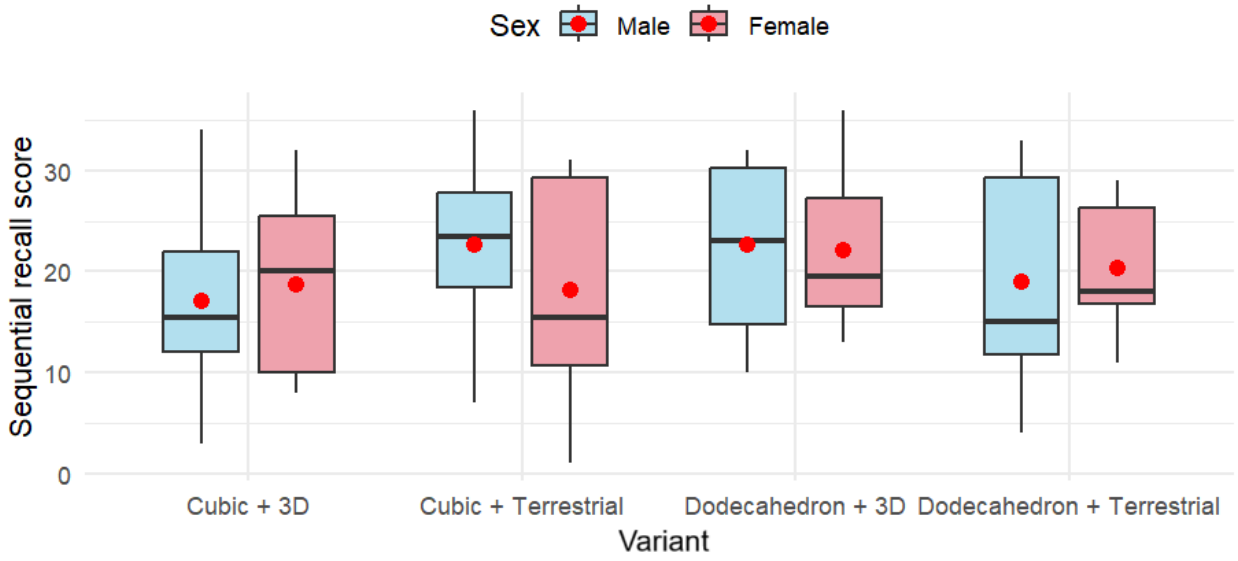


Figure 2.3: Sequential Recall score by variant and sex. We found no significant differences between the experimental variants. In this and similar figures, the bold line marks the median while the red dot shows the mean; the boxes represent the interquartile range (25th to 75th percentiles), and the whiskers extend to the minimum and maximum values within 1.5 times the IQR.

Table 2.1: Descriptive Statistics for Sequential Recall Scores by Variant (Environment × Movement Type) and Sex, in **Experiment 1**

Variant	**N**	**Mean**	**95% CI**
Cubic + 3D + Male	12	17.1	[11.9, 22.2]
Cubic + Terrestrial + Male	12	22.7	[17.5, 27.8]
Dodecahedron + 3D + Male	12	22.6	[17.4, 27.7]
Dodecahedron + Terrestrial + Male	12	18.9	[13.8, 24.1]
Cubic + 3D + Female	12	18.8	[13.6, 23.9]
Cubic + Terrestrial + Female	12	18.2	[13.0, 23.3]
Dodecahedron + 3D + Female	12	22.2	[17.0, 27.3]
Dodecahedron + Terrestrial + Female	12	20.3	[15.2, 25.5]

Note. Values represent estimated marginal means based on the full factorial model. Significance testing was performed using a permutation-based ANOVA. The standard error for all means is 2.59. 95% confidence intervals are shown. Group differences were not statistically tested due to the absence of significant effects in the permutation-based ANOVA.

No Effects of Environment, Movement and Sex on Free Recall

A three-way ANOVA was conducted to examine the effects of *Environment* (Cubic vs. Dodecahedron), *Movement Type* (3D vs. Terrestrial), and *Sex* (Male vs. Female) on Free Recall scores. The main effect of Environment approached significance ($F(1, 88) = 3.17$, $p = .078$, $\eta^2 = .03$), indicating a potential influence of environment type on average free recall scores. The *Sex* × *Environment* × *Movement Type* interaction also approached significance ($F(1, 88) = 2.92$, $p = .091$, $\eta^2 = .03$). However, no post-hoc comparisons were statistically significant (all $p_{\text{Tukey}} > .05$). None of the other main effects nor interactions yielded significant results.



Figure 2.4: Free recall score by variant and sex. We found no significant differences between the experimental variants.

Table 2.2: Descriptive Statistics for Free Recall Scores by Variant (Environment × Movement Type) and Sex in **Experiment 1**

Condition	**N**	**Mean**	**95% CI**
Cubic + 3D + Male	12	26.9	[23.6, 30.2]
Cubic + 3D + Female	12	29.0	[25.7, 32.3]
Dodecahedron + 3D + Male	12	27.3	[24.0, 30.6]
Dodecahedron + 3D + Female	12	26.8	[23.5, 30.0]
Cubic + Terrestrial + Male	12	30.1	[26.8, 33.4]
Cubic + Terrestrial + Female	12	27.2	[24.0, 30.5]
Dodecahedron + Terrestrial + Male	12	24.2	[20.9, 27.5]
Dodecahedron + Terrestrial + Female	12	26.7	[23.4, 30.0]

Note. Values represent estimated marginal means based on the full factorial model. Significance testing was performed using a permutation-based ANOVA. The standard error for all means is 1.65. 95% confidence intervals are shown. Group differences were not statistically tested due to the absence of significant effects in the permutation-based ANOVA.

2.4 Experiment 2 – Spherical environment, with traditional landmarks

2.4.1 Methods

Participants

Sixty-eight participants (34 females) were recruited through Prolific. Participants were aged between 20 and 38 years (M = 27.07, SD = 4.69). Participant eligibility, consent procedures, and ethical approval were identical to **Experiment 1**. Combined with **Experiment 1**, the full sample provided approximately 80% power to detect an effect of $f = 0.26$ (($\alpha = .05$), 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`.

Materials

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 sparse condition, in the *Spherical Landmark* one only the combination of the dodecahedron environment with 3D-movement was used. Eighteen landmarks were placed along some of the edges of the faces, 3 landmarks on each face. To facilitate participant motivation, we also added a time constraint of 40 seconds per ball (both in the encoding and recall sessions) and provided direct feedback (CORRECT/FALSE) upon each recorded location point.

Procedure

The procedure was identical to **Experiment 1**, except that a time constraint was introduced and participants also completed the OSIVQ and SPS questionnaires (see Chapter 4).

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 *Spherical Landmark* condition (**Experiment 2**)

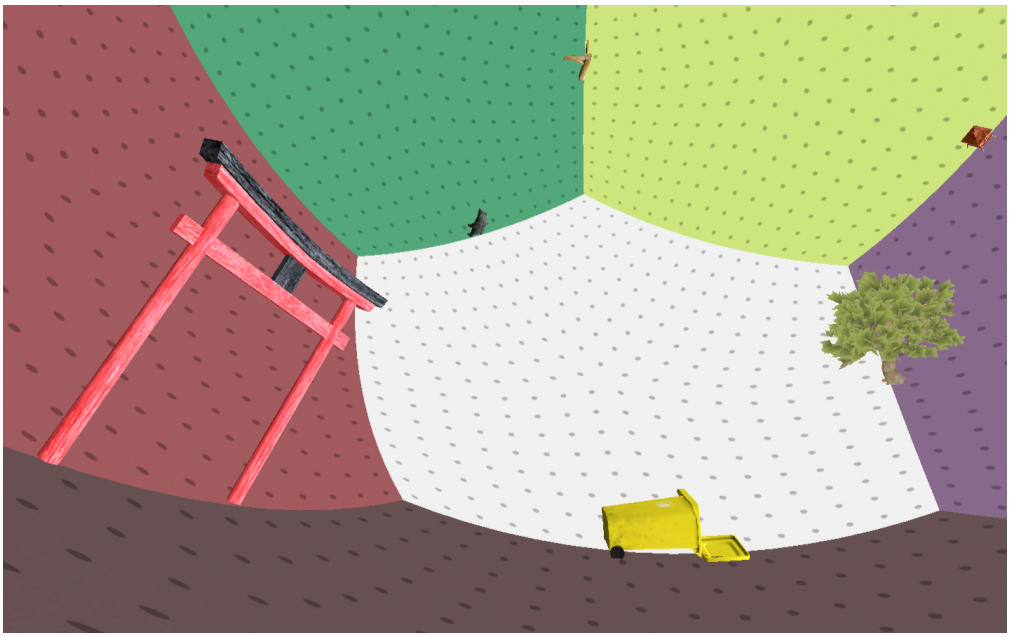


Figure 2.5: Game view of the *Spherical Landmark* Condition. The landmarks were placed on the centre of the edges.

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 1,000 permutations, in which the predictor labels (*Spherical Sparse* vs. *Spherical Landmark* and Male vs. 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 4 distinct strategy preferences. Separate Chi-square tests of independence were conducted to examine whether a basic dichotomic strategy preference (spatial vs. non-spatial) differed by sex within each condition. Given the binary nature of such basic strategy variable and potential small sample sizes, Yates' continuity correction was applied to each test.

2.4.2 Results

Sequential Recall distributions

Although the Excess Mass test did not reject unimodality ($p = .080$), visual inspection of the distribution of Sequential Recall scores across participants revealed a multimodal pattern. Compared to 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 2.6 C, D).

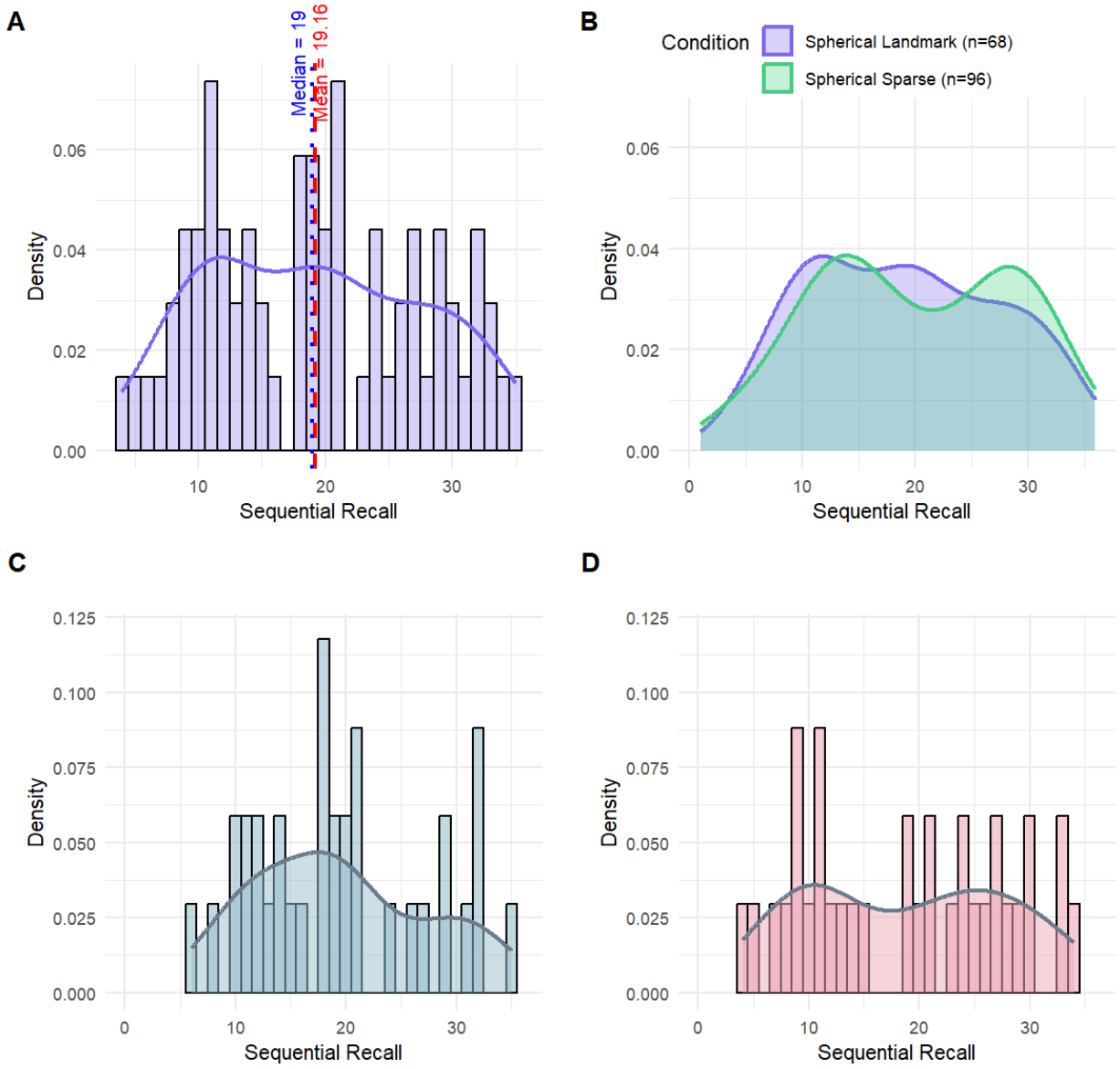


Figure 2.6: A) Sequential Recall score distribution across participants in the *Spherical Landmark* condition, B) smoothed distributions in the *Spherical Sparse* and *Spherical Landmark* conditions, and C) among males and (D) females in the *Spherical Landmark* condition.

No significant effects of Condition and Sex on Sequential Recall

The permutation-based ANOVA revealed no significant effect of the combination of Condition (*Sparse* vs. Landmark) and Sex (Male vs. Female) on (average) Sequential Recall performance. A permutation test with 1,000 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 A.1.

Complementary Bayesian analyses indicated moderate evidence for the absence of a Sex effect ($BF_{01} \approx 5.59$), moderate evidence for the absence of a Condition effect ($BF_{01} \approx 4.81$), and moderate evidence for the absence of a Sex $\times$ Condition interaction ($BF_{01} \approx 4.45$).



Figure 2.7: Sequential Recall score by condition and sex in **Experiment 1** vs. **Experiment 2**. The model could not identify a difference between the two sexes in either of the two conditions.

Strategy preference -Qualitative analysis

Self-reported strategy preferences were now categorically analysed, together with those from **Experiment 1**, based on classification criteria, reported in Supplementary Material, Section A). In the *Spherical Sparse* condition, three distinct basic strategy preferences were identified:

1. **Colour rehearsal**: mentally repeating or otherwise referencing colour combinations, either using 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 vs. 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 vs. non-spatial strategies. Participants who relied on 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 (Morris et al., 1982), some spatial reasoning. Therefore, the Landmark strategy was classified as part of the spatial strategy category in the collapsed analysis.

Figure 2.8 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 ($\chi^2(1) = 0.39$, $p = .535$). However, in the *Landmark* condition, a significant association was found ($\chi^2(1) = 4.20$, $p = .040$). Interestingly, this significant difference in strategy preference did not translate into a significant difference in Sequential Recall performance.

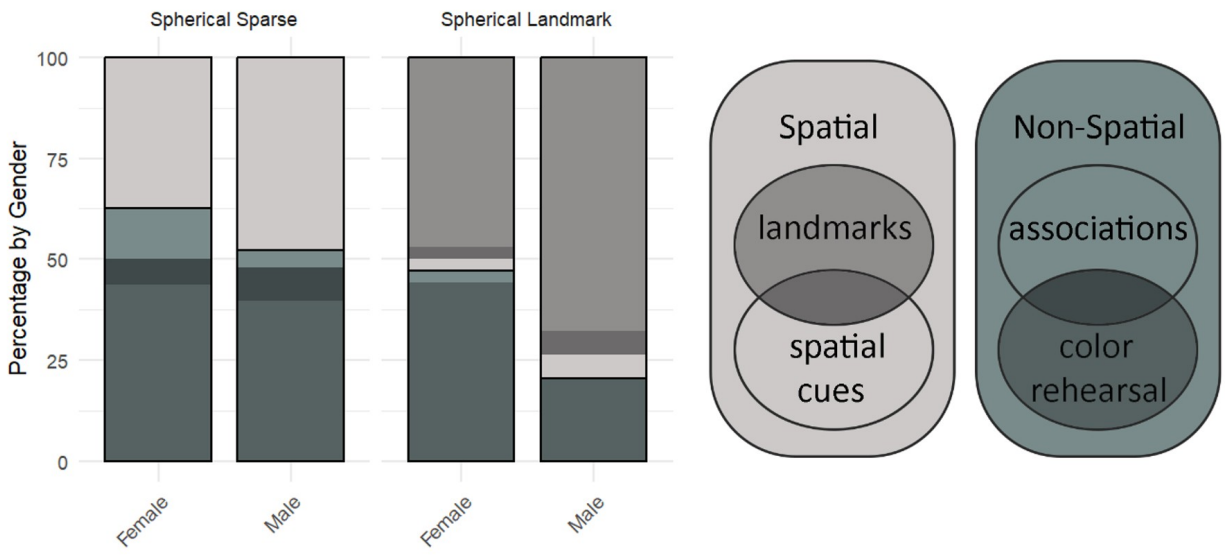


Figure 2.8: Spatial and non-spatial strategy preferences by condition and sex. Gray represents spatial strategies, green represents non-spatial strategies. The darkest shade within each colour indicates overlapping use of multiple sub-strategies within that category.

2.5 Experiment 3 – Flat, Sparse Environment

2.5.1 Methods

Participants

Sixty-eight participants (34 females) were recruited through Prolific. Participants were aged between 21 and 44 years (mean age = 28.22, ± 5.7 years). Participant eligibility, consent procedures, and ethical approval were identical to **Experiment 1**. Combined across all three experiments ($N = 232$), the full sample provides 80% power ($\alpha = .05$, $f = 0.22$) 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.

Materials

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 2.9), making it identical to the number of possible ball location points in the dodecahedron.

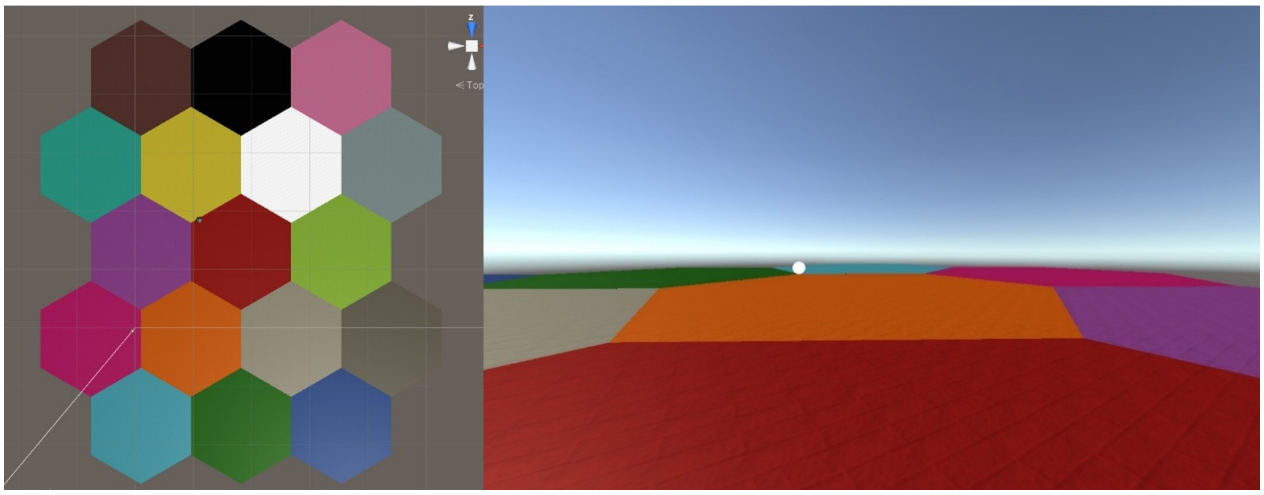


Figure 2.9: Map view (left) and game view (right) of the *Flat Sparse* condition.

Procedure

The procedure was identical to **Experiment 1** and **2**. Following the Sequential Recall task, participants first provided free verbal descriptions of their strategies, and then indicated them by selecting from predefined categories.

Data analysis

The distribution of Sequential Recall scores was examined to understand participant behaviour in such flat environment of increased (Euclidean) familiarity/plausibility. To compare the distributions of Sequential Recall scores across the three conditions, a series of Kolmogorov-Smirnov tests were conducted.

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 1,000 permutations, in which the predictor labels (*Spherical Sparse* vs. *Spherical Landmark* vs. *Flat Sparse* and Male vs. 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 or against 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.

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

A linear regression model was conducted to examine the effect of change of Condition (*Spherical Sparse*, *Spherical Landmark*, *Flat Sparse*) and Sex (Male vs. Female) on Sequential Recall performance among those who employed a spatial strategy. A separate analysis was conducted for participants who used a non-spatial strategy to complete the task.

Encoding means, recall means, total encoding path and total recall path were log transformed.

To investigate whether encoding and recall times predicted Sequential Recall performance by sex, linear regression models were fitted with Encoding Mean and Recall Mean as predictors, including Sex and their interaction terms, in each condition (*Spherical Sparse*, *Spherical Landmark*, *Flat Sparse*). When encoding and recall times were not strongly correlated, both predictors were entered in the same model. However, when multicollinearity was detected (Pearson's $r > .70$ between encoding and recall times), separate regression models were run for each predictor to avoid unstable estimates. The same analytic procedure was applied to total encoding and recall path lengths.

To examine potential sex differences in encoding and recall times within each condition, independent-samples tests were conducted. When measures were not normally distributed, Wilcoxon rank-sum tests were used, otherwise, Welch's two-sample t-tests were applied. P-values were adjusted for multiple comparisons using the Holm–Bonferroni method. Total encoding and recall path lengths were examined the same way.

2.5.2 Results

Sequential Recall distributions

The distribution of Sequential Recall scores across participants followed a roughly normal distribution. Compared to 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.

Statistically, the Kolmogorov-Smirnov tests revealed no significant differences between the distributions of Sequential Recall scores across the three conditions. Specifically, no significant difference was found between *Spherical Sparse* and *Spherical Landmark*, $D = 0.095$, $p = 0.71$; between *Spherical Sparse* and *Flat Sparse*, $D = 0.134$, $p = 0.34$; or between *Spherical Landmark* and *Flat Sparse*, $D = 0.074$, $p = 0.97$. These results suggest that, despite visual differences, the distributions of Sequential Recall scores are statistically similar across

the three conditions.

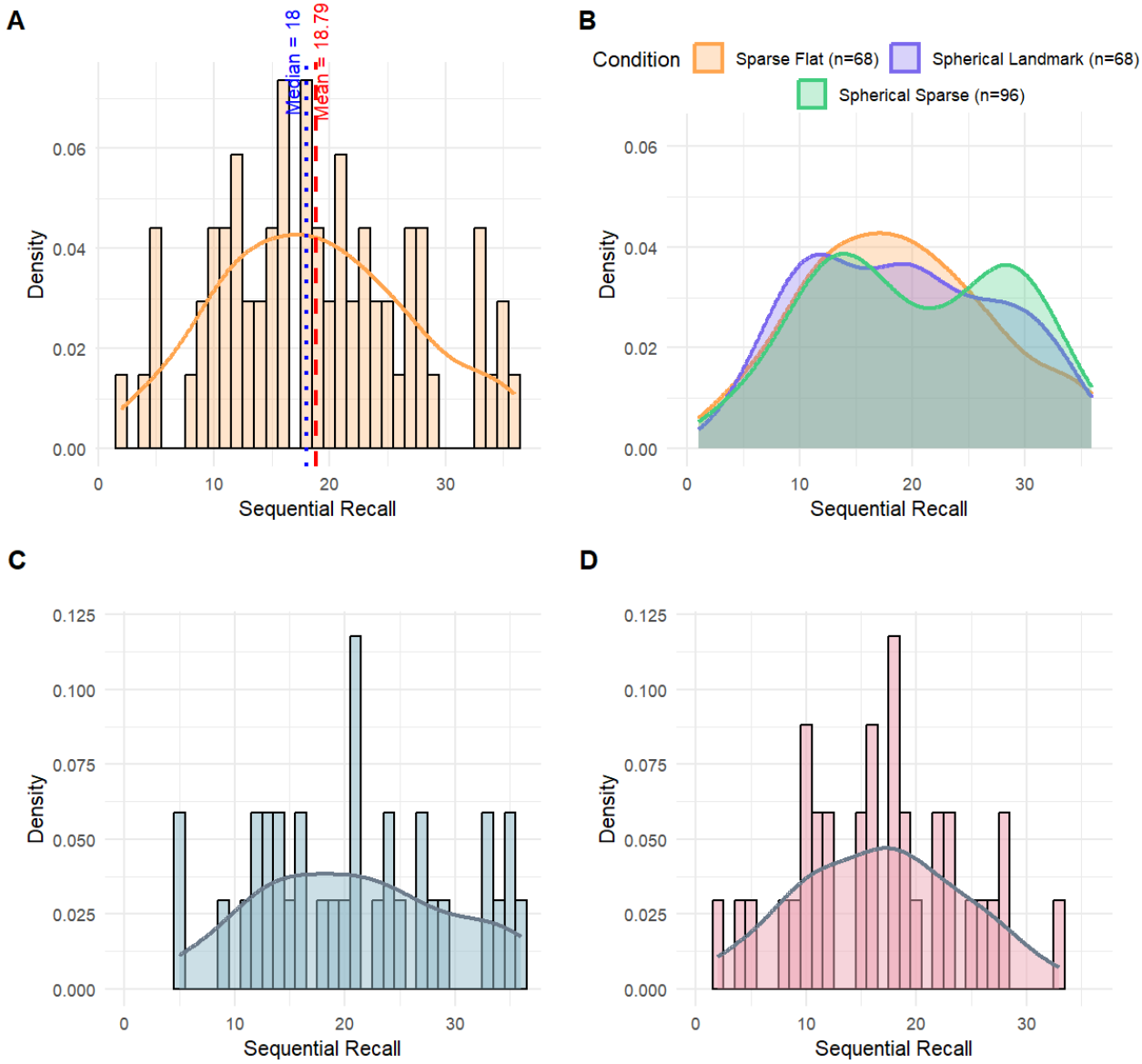


Figure 2.10: Sequential Recall score distributions of A) across participants in the *Flat Sparse* condition and B) in the *Spherical Sparse*, *Spherical Landmark* and *Flat Sparse* conditions, and C) among males and (D) females in the *Flat Sparse* condition.

Effects of Condition and Sex on Sequential Recall

The independent samples t-test revealed a significant difference in Sequential Recall between the sexes, with males outperforming females, $t(66) = 2.08$, $p < .05$, 95

The permutation-based ANOVA revealed no significant effect of the combination of Con-

dition and Sex on Sequential Recall performance. A permutation test with 1,000 iterations yielded a p-value of 0.428.

Complementary Bayesian analyses indicated anecdotal to moderate evidence for the absence of a Sex effect ($BF_{01} \approx 2.86$), 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 ($BF_{01} \approx 5.51$).

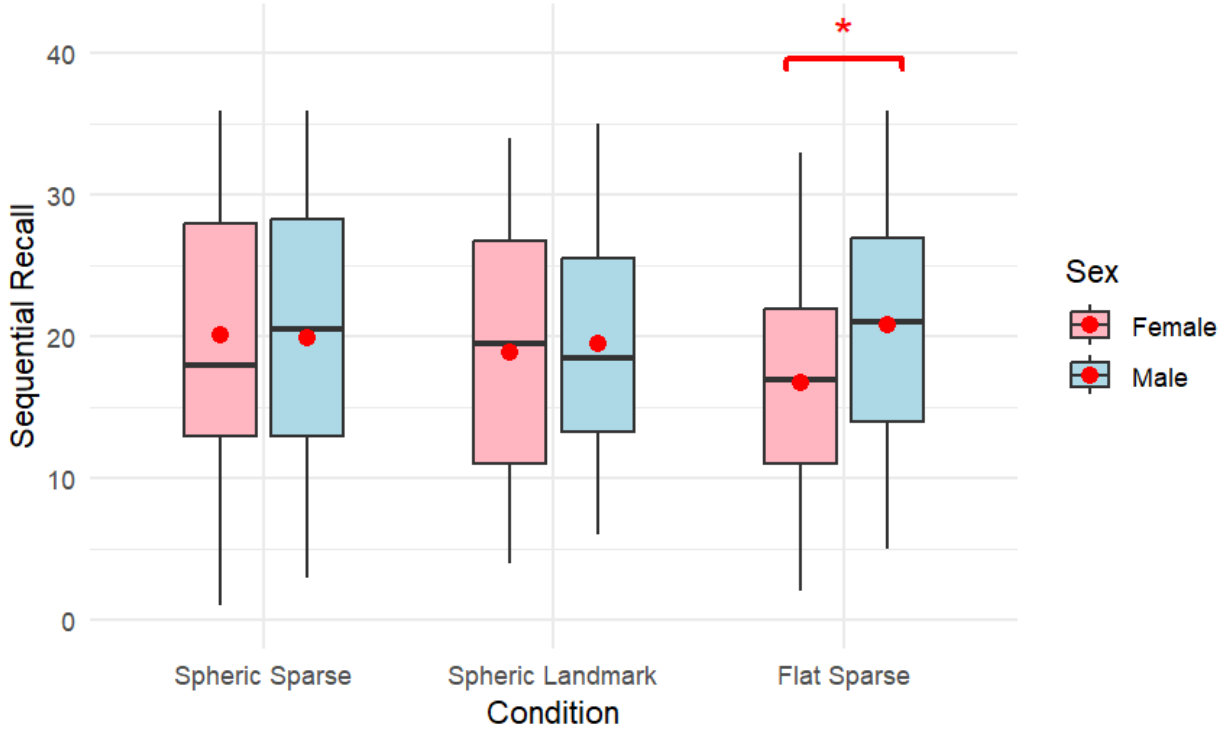


Figure 2.11: Sequential Recall score by condition and sex. The bold line marks the median and the red dot shows the mean.

Strategy preference

A Chi-square test showed no significant association between sex and strategy preference ($\chi^2(1) = 0.24$, $p = .624$). Participants in this condition showed similar sex-specific strategy preferences to participants in the *Spherical Sparse* condition. Figure 2.12 illustrates the proportions of spatial vs. non-spatial strategy users by sex and by condition.

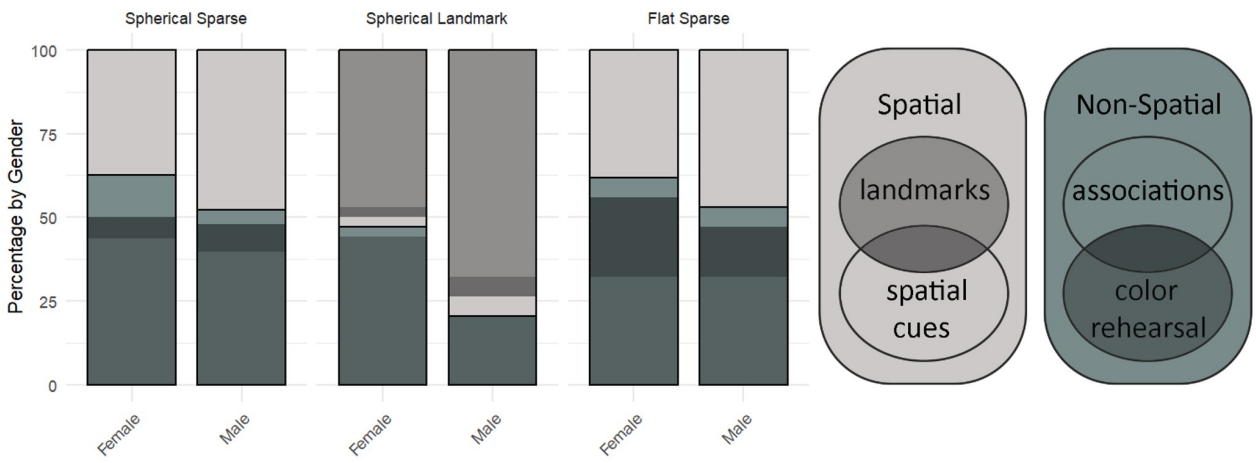


Figure 2.12: Spatial and non-spatial strategy preferences by condition and sex.

Effect of spatial vs. non-spatial strategy on Sequential Recall

The linear regression model revealed no significant main effect of Condition ($\beta = -3.18$, $p = .124$), indicating that Sequential Recall scores were similar in groups tested in later conditions. However, a significant linear Condition $\times$ Sex interaction ($\beta = 6.34$, $p = .024$) was observed, suggesting that males and females performed differently across conditions. Specifically, male spatial strategy users in the more plausible conditions showed increasingly higher recall performance compared to those in the less plausible conditions. Female spatial strategy users did not exhibit the same effect; however, female performance in the Euclidean condition was notably lower than female performances in the two less non-Euclidean conditions. Post-hoc pairwise comparisons indicated a significant sex difference in the *Flat Sparse* condition ($p = .035$), with males outperforming females. No significant sex differences were found in the *Spherical Sparse* ($p = .310$) or *Spherical Landmark* ($p = .958$) 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-values $> .05$). The overall model was not significant, $F(5, 112) = 1.30$, $p = .268$. 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.

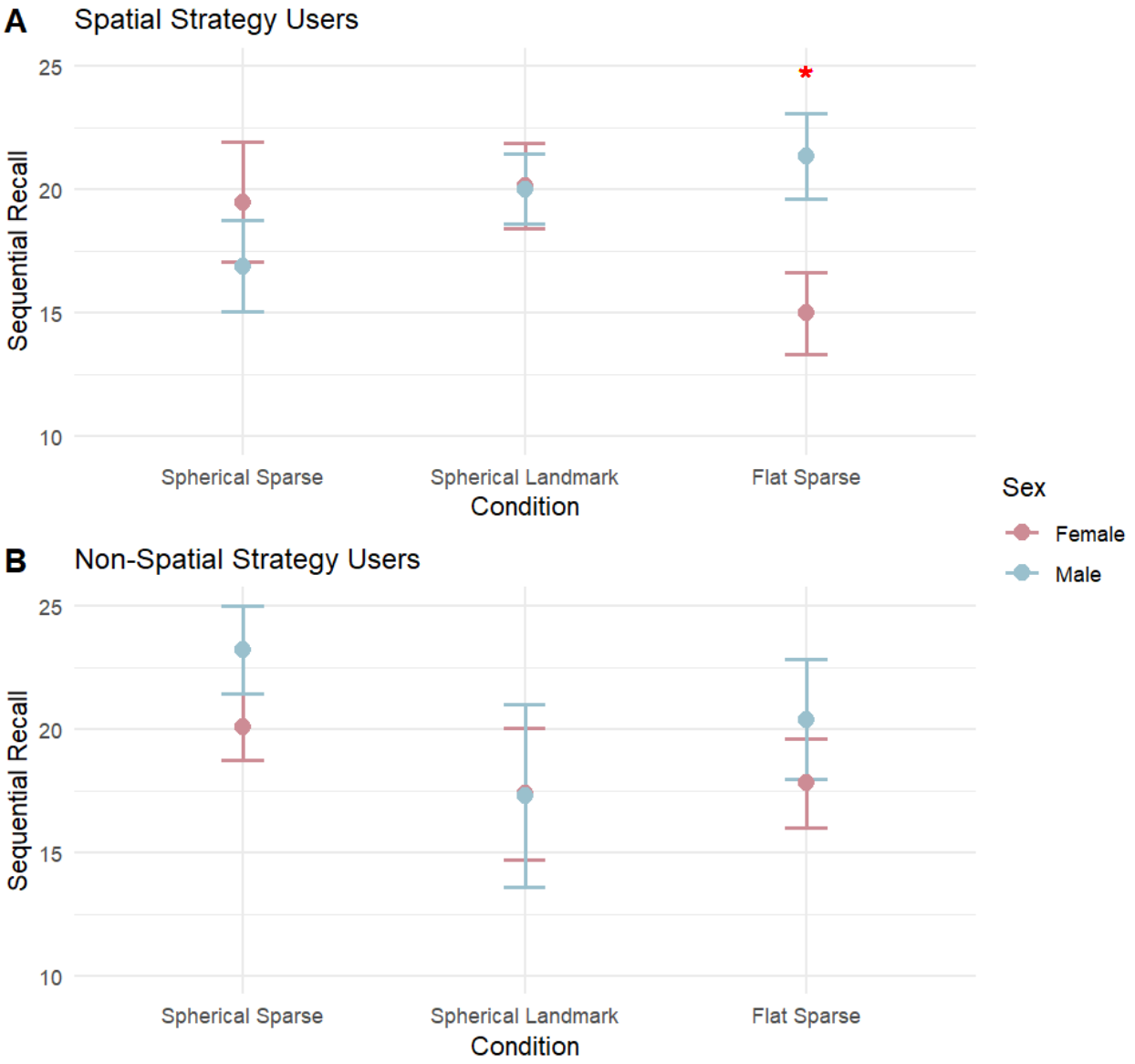


Figure 2.13: Effect of A) spatial strategy and B) non-spatial strategy, on Sequential Recall by condition and by sex.

2.6 Detailed Results

2.6.1 Encoding and recall means by sex

Longer encoding and recall times are linked to better Sequential Recall

Overall, both encoding and recall means were consistently associated with better Sequential Recall, regardless of sex. However, males tended to show stronger correlations than

females.

In the *Spherical Sparse* condition, a linear regression predicting Sequential Recall from Encoding Mean and Sex revealed a significant positive effect of Encoding Mean on Sequential Recall ($b = 10.33$, $t(92) = 4.43$, $p < .001$). Neither the main effect of Sex nor the Encoding Mean $\times$ Sex interaction reached significance. The model explained 20.0% of the variance in Sequential Recall scores.

A separate model predicting Sequential Recall from Recall Mean and Sex also showed a significant positive effect of Recall Mean on Sequential Recall ($b = 5.71$, $t(92) = 2.45$, $p < .05$). Neither the main effect of Sex nor the Recall $\times$ Sex interaction reached significance. This model accounted for 13.5% of the variance in Sequential Recall.

In the *Spherical Landmark* condition, the multiple regression model with Encoding Mean and Recall Mean and their interactions with Sex predicting Sequential Recall scores approached significance ($R^2 = .15$, $F(5, 62) = 2.27$, $p = .06$). A significant main effect of Recall Mean was observed ($\beta = 7.86$, $SE = 3.00$, $p < .05$). No significant main effect of Encoding Mean or interactions with Sex were found.

In the *Flat Sparse* condition, a linear regression predicting Sequential Recall from encoding times and sex was statistically significant ($F(3, 64) = 3.53$, $p < .05$), revealing a significant main effect of encoding times ($\beta = 4.56$, $SE = 2.08$, $p < .05$), such that longer encoding times predicted higher Sequential Recall scores. No significant effects of sex or the interaction were found.

The model with recall times and their interaction with sex was also statistically significant ($F(3, 64) = 6.88$, $p < .001$), and showed a significant main effect of recall times ($\beta = 7.11$, $SE = 1.81$, $p < .001$). Again, neither sex nor the interaction were significant.

Males are faster than females

Although in general, males were faster than females, this difference was only statistically significant in the *Spherical Landmark* condition, both for encoding and for recall means.

In the *Spherical Sparse* condition, encoding times did not differ significantly between males ($M = 2.43$) and females ($M = 2.53$), $W = 1009$, $p = .30$, and no sex difference was found for recall times, $t(79.81) = -1.16$, $p = .25$.

In the *Spherical Landmark* condition, females took significantly longer than males both during encoding, $W = 220$, $p < .001$ (Holm-adjusted $p < .001$), and during recall, $t(65.23) = -2.79$, $p = .007$ (Holm-adjusted $p = .034$).

In the *Flat Sparse* condition, no significant sex differences were observed in either encoding times, $W = 440$, $p = .09$, or recall times, $W = 538$, $p = .63$.

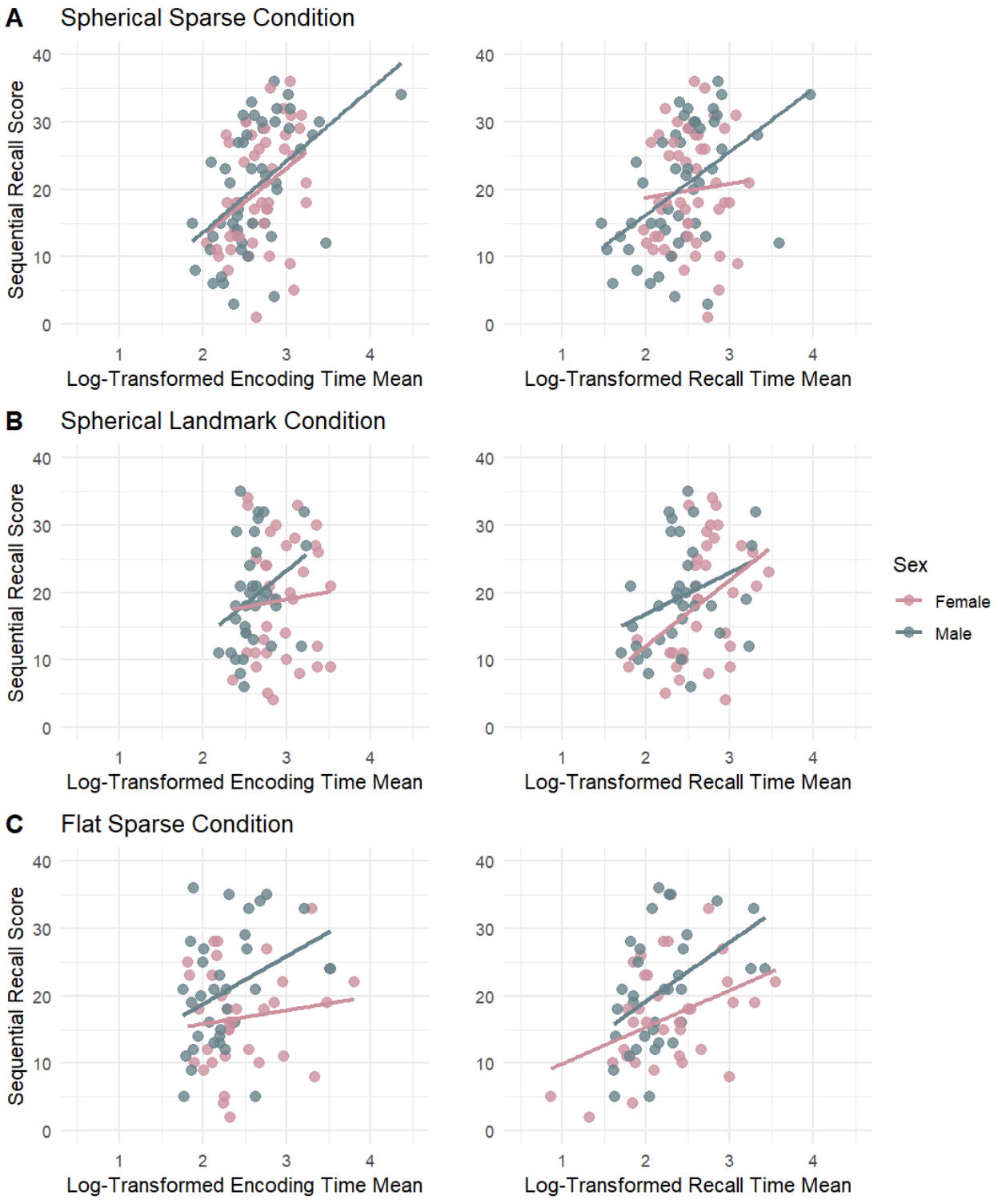


Figure 2.14: Correlations between encoding means and Sequential Recall, and between recall means and Sequential Recall, by sex across conditions. Overall, both encoding and recall means were positively associated with Sequential Recall, with stronger associations for males.

2.6.2 Encoding and recall path lengths by sex

Sex differences in travelled distance in the Flat Sparse condition

In the *Spherical Sparse* condition, a linear regression predicting Sequential Recall from Encoding Path and Sex was not statistically significant, and no main effects or interactions reached significance. Similarly, a regression with Recall Path and Sex as predictors was not significant. While no significant effects were found, there were marginal trends for Sex ($p = .08$) and for the interaction between Recall Path and Sex ($p = .079$), with females showing a tendency towards higher Sequential Recall at shorter recall path lengths.

In the *Spherical Landmark* condition, a linear regression predicting Sequential Recall from Encoding Path lengths and Sex was not statistically significant, and no main effects or interactions reached significance. Similarly, a regression with recall path lengths and sex as predictors was not significant, with no significant effects observed.

In the *Flat Sparse* condition, a linear regression including both Encoding Path and Recall Path, Sex, and their interactions was statistically significant ($F(5, 62) = 6.99$, $p < .001$). Longer encoding path lengths were associated with lower Sequential Recall scores ($\beta = -21.98$, $SE = 7.29$, $p < .01$), whereas longer recall path lengths predicted higher scores ($\beta = 36.17$, $SE = 8.90$, $p < .001$). There was a significant main effect of Sex ($\beta = 123.94$, $SE = 54.38$, $p < .05$), and a significant interaction between Recall Path and Sex ($p < .05$), as the positive relationship between Recall Path and performance was weaker for females than for males. No significant interaction was observed between Encoding Path and Sex.

Females travel longer distances than males

In the *Spherical Sparse* condition, females had longer Encoding Path than males, significant before correction ($W = 872$, $p = .04$) but not after Holm–Bonferroni adjustment ($p_{\text{adj}} = .127$). Recall Path did not differ significantly between sexes.

In the *Spherical Landmark* condition, females had longer encoding paths than males, significant before correction ($t(60.76) = 2.56$, $p < .05$) and approaching significance after adjustment ($p_{\text{adj}} = .06$). In contrast, Recall Path was significantly shorter for males, both before and after adjustment ($W = 296$, unadjusted $p < .001$, $p_{\text{adj}} < .01$).

In the *Flat Sparse* condition, females had longer Encoding Path than males, significant before correction ($W = 403$, $p < .05$) but not after adjustment. Recall path lengths did not differ significantly between sexes.

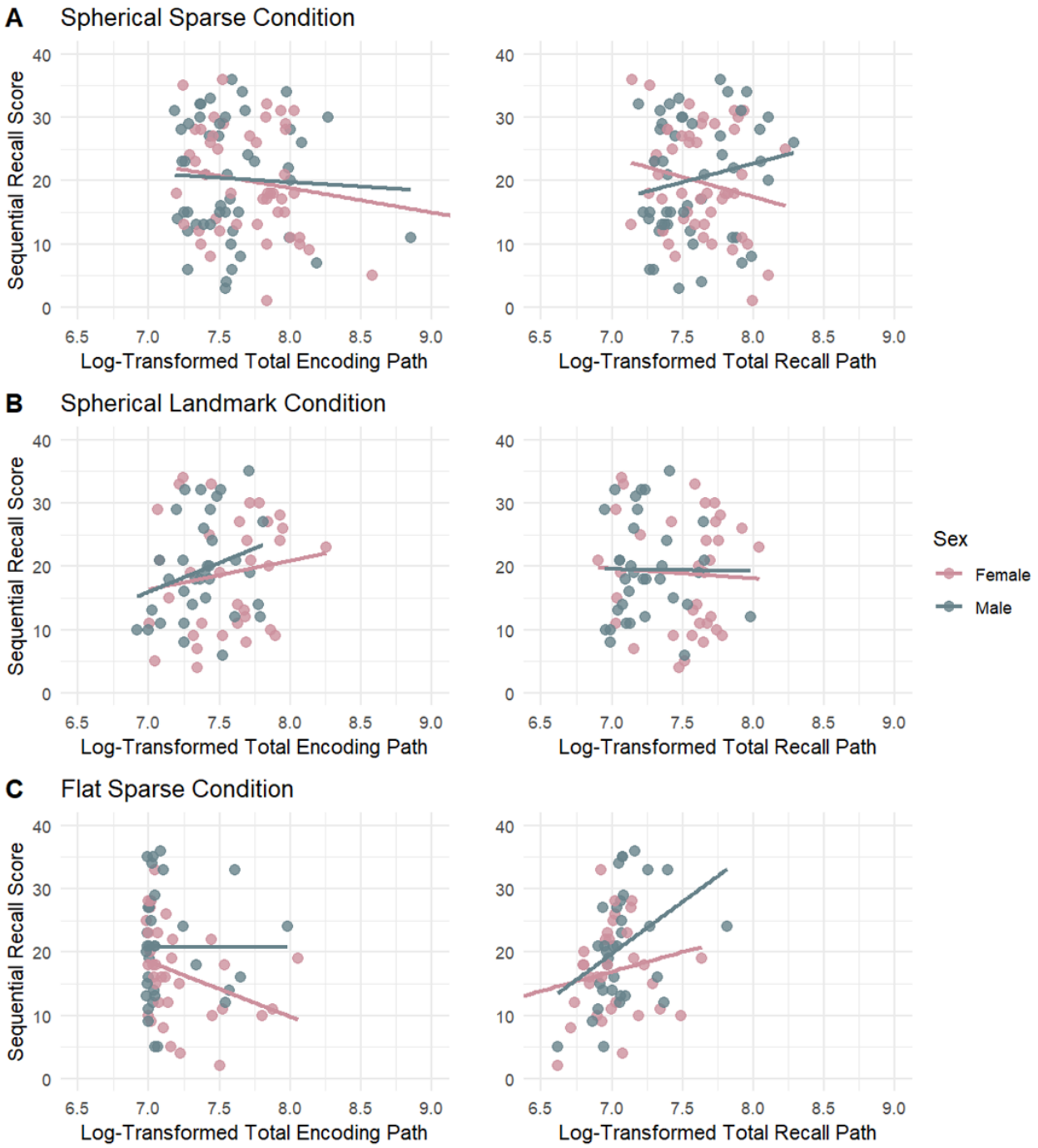


Figure 2.15: Correlations between total encoding path and Sequential Recall, and between total recall path and Sequential Recall, by sex, across conditions.

2.6.3 Paths and times across conditions

In the *Spherical Sparse* condition, the model was significant ($F(5, 90) = 8.52$, $p < .001$, $R^2 = .32$, $R^2_{\text{adj}} = .28$). Sequential recall was positively predicted by higher Encoding Mean ($\beta = 21.88$, $p < .001$) but shorter Encoding Path ($\beta = -15.93$, $p < .001$). By contrast, higher Recall Mean predicted worse performance ($\beta = -11.17$, $p < .01$), whereas longer Recall Path predicted better performance ($\beta = 11.91$, $p < .05$). Sex was not significant.

In the *Spherical Landmark* condition, the model was significant ($F(5, 62) = 3.74$, $p < .01$, $R^2 = .23$, $R^2_{\text{adj}} = .17$). Longer Encoding Path was associated with better Sequential Recall ($\beta = 21.10$, $p < .01$), whereas longer Recall Path predicted worse recall ($\beta = -21.47$, $p < .01$). Sex and mean times were not significant predictors.

In the *Flat Sparse* condition, the model was significant ($F(5, 62) = 7.78$, $p < .001$, $R^2 = .39$, $R^2_{\text{adj}} = .34$). During encoding, shorter path length predicted better recall ($\beta = -19.21$, $p < .001$), while during recall, longer path length predicted better recall ($\beta = 14.21$, $p < .01$). Neither sex nor Encoding and Recall Mean were significant predictors.

2.7 Discussion

The experiments reported in this chapter are at the core of the attempt, reported in this Thesis, to assess to what extent spatial behaviour can be understood in terms of evolutionarily versus culturally acquired cognitive traits. In 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 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 suggests that Euclidean space, even without traditional landmarks, enables a complex recall process with multiple contributions from a variety of sources. 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 (Yonelinas et al., 2024). 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 (Ciaramelli et al., 2006). In our spatial memory task, the reasoning could be, with more familiar and plausible environments participants may quickly adapt spatial memory schemata, or routines (Gilboa and Marlatte, 2017), 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 be seen as consistent with findings from Ciaramelli et al. (2010), who showed that egocentric navigation and the re-experiencing of spatial memories depend on posterior parietal cortex function, suggesting that familiarity-based processes may rely more heavily on neocortical regions.

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 (Torromino et al., 2021). 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 (O'Keefe and Nadel, 1978), and to be more effective in males. Such an extrapolation glosses over a complex phenomenology (Koss and Frick, 2016; Yagi and Galea, 2018). 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 (Lawton, 1994; Hugdahl et al., 2006).

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. In 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 and Healy (2006), 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 vs. 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 appeared to be higher in the environment with more spatial familiarity. Females did not show this pattern, suggesting that higher spatial familiarity primarily benefits male performance, specifically those who rely on spatial cues. It may lead to enhanced processing in a number of cortical areas, where higher activation has been observed in males (Spets and Slotnick, 2020). In contrast, females seem to benefit more by 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 diminishes. 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.

2.8 Conclusion

These findings reveal an effect of familiarity on both Sequential Recall of spatial locations and sex 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.

Incidental learning in a sparse, spherical environment

3.1 Abstract

This chapter examines sex differences in incidental learning and its potential influence on spatial memory performance and strategy preference. Across three virtual reality experiments, participants performed a Sequential Recall task in a sparse, traditional landmark-free spherical environment while being incidentally exposed to floating images of faces or objects, later tested in visual recognition tasks, with an additional condition in which object recognition was assessed using verbal descriptions. Recognition and rejection accuracy were tested after either a short (5-minute) or long (2-hour) delay. Consistent across retrieval modalities, participants were significantly better at rejecting new stimuli than recognising old ones. In experiment 4 (n = 96), males outperformed females in visual object and face recognition. In *Experiment 5* (with added famous faces, n = 96), males showed a larger rejection–recognition gap than females, and recognition accuracy was higher for female faces regardless of participant sex. Experiment 6 (n = 68), which required verbal recognition of objects, revealed no significant sex differences. Incidental stimulus type little effect on Sequential Recall performance, although object stimuli were associated with a tendency to rely on non-spatial strategies. These results suggest that incidental learning effects are robust across modalities but that sex differences are stimulus-dependent, likely influenced by social relevance and retrieval demands.

3.2 Introduction

What we remember depends not only on what we attend to, but also on the mental processes involved in encoding, consolidation, and retrieval. Encoding can be intentional, through deliberate effort, or incidental, where information is acquired without conscious attention (Wagnon et al., 2019; Tresselt and Mayzner, 1960). Working memory acts as a short-term buffer that is limited both in capacity (Miller, 1956; Cowan, 2001) and in duration (Baddeley et al., 2014). While some information remains in short-term memory, others undergo consolidation into long-term memory, a process that begins in the hippocampus and eventually involves cortical regions (Squire et al., 2015; Kitamura and Inokuchi, 2014).

As reviewed above, research has consistently shown sex differences in tasks involving spatial memory and hippocampus-dependent processing. Males typically outperform females in spatial navigation tasks and tend to rely on allocentric strategies based on Euclidean metrics. Females, by contrast, tend to prefer egocentric strategies guided by local landmarks or feature cues, strategies associated with the parietal cortex (Ishikawa and Montello, 2006; Jones and Healy, 2006; Tascón et al., 2021). Recent research with animals also suggests sex differences in memory consolidation under incidental learning conditions. Torromino et al. (2021) and colleagues found that female mice showed lower memory consolidation capacity compared to males in a modified object recognition task (the Different Object Task). While both sexes performed similarly at short delays, male mice retained more items after longer delays. C-Fos expression revealed that males recruited the dorsal hippocampus more strongly, while females showed greater activation in the nucleus reuniens (RE) of the thalamus. Interestingly, modulating the activity in these regions reversed the observed sex differences in performance, suggesting that consolidation capacity under high memory load may be controlled by the recruitment of specific neural pathways.

Building on this work, the current study investigated sex differences in both spatial memory and memory consolidation in humans using a novel virtual reality paradigm. Participants performed a spatial memory task in a sparse, three-dimensional environment lacking traditional landmarks and orientation cues. To assess memory consolidation under incidental learning conditions, in **Experiment 4** (so numbered after those described in another report), floating images of objects were presented during the spatial task without drawing explicit attention to them. Memory for these stimuli was tested in a recognition task after either a short (5-minute) or long (2-hour) delay. If the sex differences observed in mice generalize to humans, we expected both sexes to perform similarly at short delays, but a reduced memory capacity for females at longer delays. Additionally, we considered the possibility that the floating images may distract from the main spatial task, particularly for females if they allo-

cate more attention to incidental stimuli. This could even result in a trade-off: better object recognition in females but reduced spatial memory performance relative to males.

To test the role of stimulus salience, another condition replaced objects with faces, utilizing their social relevance (Tsao and Livingstone, 2008; McKone et al., 2007). We hypothesized that socially salient stimuli would draw more attention and enhance incidental memory, especially in females (Mast and Hall, 2006; Horgan et al., 2004; Casiere and Ashton, 1996), but may further interfere with spatial recall due to attentional competition between the task and the floating images. To further test social relevance, in **Experiment 5**, we extended the set of face images with 6 famous faces. Famous faces in this regard act as anchors for unfamiliar faces (Burton and Jenkins, 2011). We therefore hypothesized that face recognition would be improved, particularly among females.

To further investigate potential gender differences, in **Experiment 6** we modified the experimental design of the *Object* condition (from **Experiment 4**), where the subsequent recognition task was altered to an object recognition by description task. Instead of viewing visual stimuli, participants were asked to recognize objects based on verbal descriptions. This modification was introduced to engage verbal retrieval processes, which females are often found to rely on more during episodic memory processes (Voyer et al., 2021; Andreano and Cahill, 2009), however, whether this female advantage extends to incidental learning remains unclear in the literature (Kontaxopoulou et al., 2017; Chipman and Kimura, 1998; McGivern et al., 1998). We therefore aimed to examine whether shifting the cognitive demands of retrieval from visual to verbal representations would amplify sex differences in object recognition performance.

3.3 Experiment 4 – Incidental learning of faces and objects

3.3.1 Methods

Participants

A priori power analysis (conducted in R using the `pwr.anova.test` function from the `pwr` package) indicated that a target sample size of 96 participants would provide 80% power to detect medium-to-large main effects ($f = 0.35$; $\alpha = .05$, $1 - \beta = .80$) and approximately 66% power to detect interaction effects of similar size in a $2 \times 2 \times 2$ between-subjects design. therefore, a total of 96 healthy participants (48 females) were recruited through Prolific (Prolific Inc). Participants were aged between 19 and 57 years (mean age = 27.15, ± 8.49

years). The study was approved by the Ethics Committee of the International School for Advanced Studies (SISSA).

Materials

The *Spherical Sparse* space from **Experiment 1** was used as the base environment. In the *Face* condition, a set of 20 AI-generated face images (from https://thispersondoesnotexist.com) were inserted into the environment, drawn from a pool of 10 male faces and 10 female faces. Each face was displayed on a white circular background and floated in randomized directions. In the subsequent face recognition task, the already presented set of 20 face images were mixed with a new set of AI-generated 10 male and 10 female face images. In the *Object* condition, emoji images obtained from https://joypixels.com were used. Similarly, each object was displayed on a white circular background.



Figure 3.1: Example stimulus of the (left) *Face* condition, and (right) *Object* condition.

Procedure

The original spatial memory task remained: participants were instructed to locate and memorize white balls in the correct order. Participants were not informed about the presence of floating face/object images to ensure that any recollection of these images occurred unintentionally. The spatial memory task was followed by a face/object recognition task, which took place either after a 5-minute delay or a 2-hour delay. The set comprised 20 old face images and 20 new face images in the face recognition task, and 20 old object images and 20

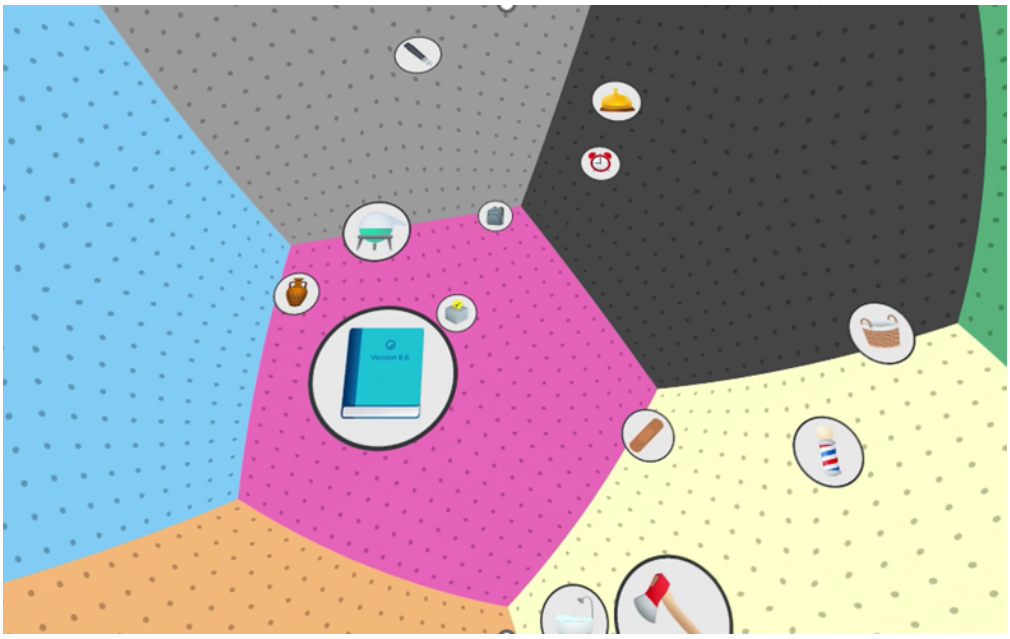


Figure 3.2: Game view of the *Object* condition.

new object images in the object recognition task. Images were presented one at a time, and participants were asked to indicate novelty using YES/NO responses.

Data analysis

Correct recognition of old images and rejection of new images were summed to obtain total Recognition Score and Rejection Score, respectively. To investigate how recognition and rejection performance varied by Sex, Delay, and Stimulus type, a series of multivariate and univariate analyses were conducted.

A three-way MANOVA was conducted with Sex, Delay, and Stimulus Type as between-subject factors and the two dependent variables, Recognition Score and Rejection Score. Following significant multivariate effects, separate univariate ANOVAs were conducted for recognition and rejection scores. When significant interactions emerged in the univariate ANOVAs, post hoc comparisons were performed using estimated marginal means with pairwise contrasts.

To explore whether participants were generally better at recognizing old images or rejecting new ones, a paired-samples t-test was conducted comparing each participant's total Recognition Score and Rejection Score across all conditions.

To assess whether recognition accuracy differed by face gender and participant sex in the *Face* condition, A 2×2 mixed-design repeated measures ANOVA was conducted with Face Gender (Male vs. Female) as a within-subject factor and Participant Sex (Male vs. Female) as a between-subject factor.

3.3.2 Main results

When recognition and rejection diverge

A paired samples t-test revealed that Recognition Score ($M = 11.91$, $SD = 4.19$) was lower than Rejection Score ($M = 14.69$, $SD = 3.01$; $t(95) = -6.51$, $p < .001$). The mean difference was -3.71, 95% CI $[-4.84, -2.58]$, indicating that participants performed significantly better at rejecting new images than recognizing old ones.

Significant effect of sex and stimulus on image recognition scores

On average, males ($M = 11.94$, $SD = 3.83$) outperformed females ($M = 10.02$, $SD = 4.34$). Participants also showed better accuracy for Objects ($M = 12.10$, $SD = 4.54$) than for Faces ($M = 9.85$, $SD = 3.49$). For the full report see Section 3.4.1.

3.3.3 Detailed Results

Significant effect of sex and stimulus on image recognition scores

Recognition and rejection accuracies varied between sexes and by stimulus type. A three-way MANOVA examined the effects of Sex, Delay (5-minute vs. 2-hour), and Stimulus Type (Face vs. Object) on Recognition Score and Rejection Score. The multivariate test (Pillai's trace) revealed a significant main effect of Sex (Pillai's Trace = 0.072, $F(2, 87) = 3.38$, $p < .05$, $\eta_p^2 = .07$), and a significant main effect of Stimulus Type (Pillai's Trace = 0.093, $F(2, 87) = 4.46$, $p < .05$, $\eta_p^2 = .09$). The Sex × Delay interaction was marginally significant ($p = .08$). No other main effects or interactions reached statistical significance.

Follow-up univariate ANOVAs further confirmed a significant main effect of Sex on Recognition Score ($F(1, 88) = 5.55$, $p < .05$, $\eta_p^2 = .06$), and a significant main effect of Stimulus Type ($F(1, 88) = 7.64$, $p < .01$, $\eta_p^2 = .08$).

In the 2-hour delay condition, females ($M = 15.70$, $SD = 2.66$) outperformed males ($M = 13.46$, $SD = 2.41$). Univariate ANOVA revealed a significant Sex × Delay interaction on Rejection Score ($F(1, 88) = 4.50$, $p < .05$, $\eta_p^2 = .05$). Post hoc comparisons using estimated marginal means revealed a significant sex difference in the 2-hour delay condition ($t(88) = 2.61$, $p = .011$). No significant difference was observed in the 5-minute delay condition.

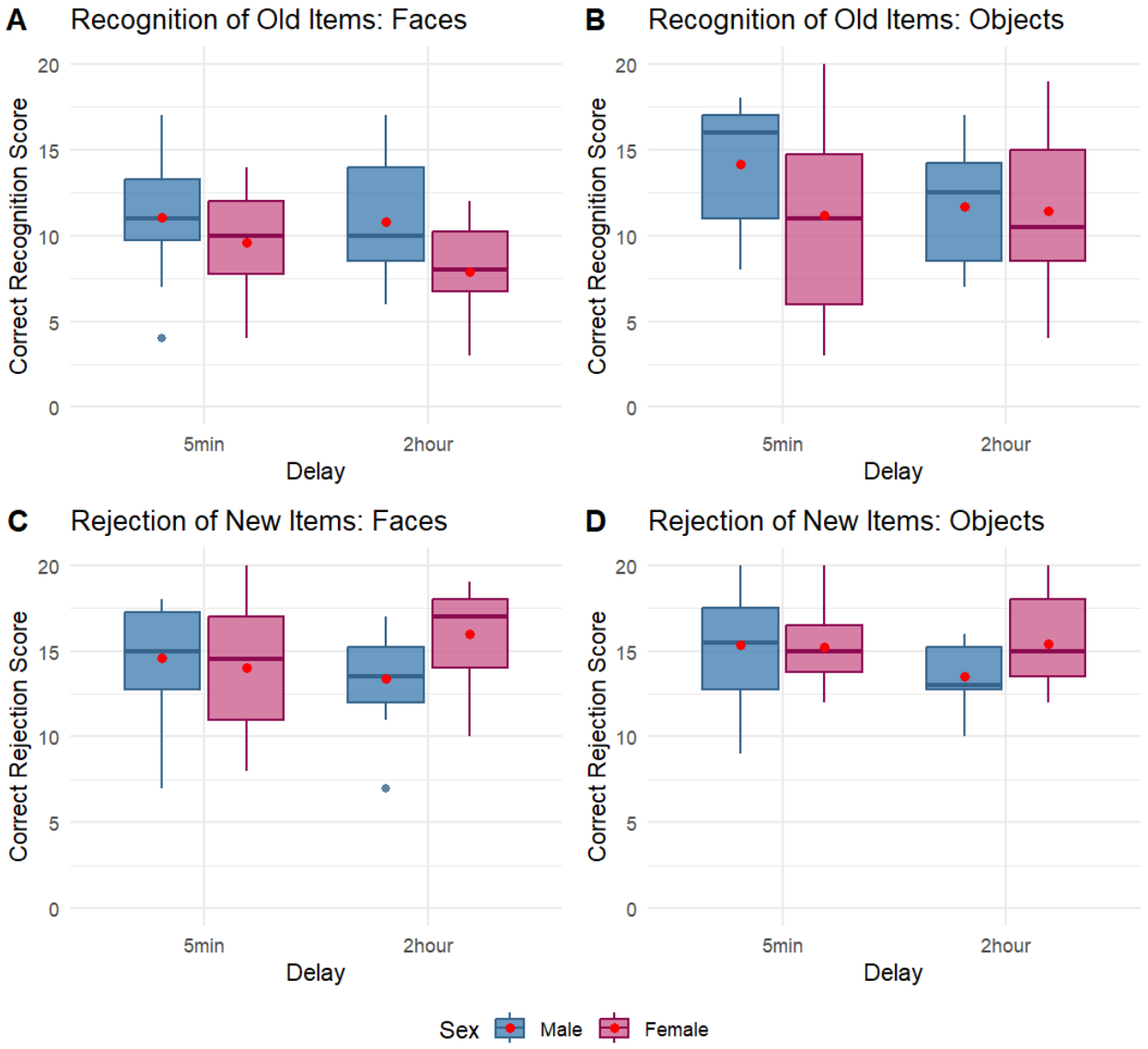


Figure 3.3: Correct old image recognition and new image rejection by Sex, Delay and Stimulus.

No effect of Sex or Face Gender on face recognition

A 2 (Face Gender: Male vs. Female) × 2 (Participant Sex: Male vs. Female) mixed-design repeated measures ANOVA was conducted to examine the effects of face gender and participant sex on face recognition accuracy, regardless of delay. The main effects of Face Gender, Participant Sex, and the Sex × Face Gender interaction were not statistically significant.

3.4 Experiment 5 – Incidental learning of faces with famous faces

3.4.1 Methods

Participants

A priori power analysis was conducted in R using the `pwr.anova.test` function from the `pwr` package. For a 2 × 2 between-subjects design (Sex × Delay), assuming a large effect size ($f = 0.40$, $\alpha = .05$, and $n = 24$ per group), the estimated power was 91%. A total of 96 healthy participants (48 females) were then recruited through Prolific (Prolific Inc). Participants were aged between 19 and 48 years (mean age = 26.9, ± 6.01 years). The study was approved by the Ethics Committee of the International School for Advanced Studies (SISSA).

Materials

Materials were identical to the *Face* condition from **Experiment 4**. The set of 20 images of faces was extended with 6 images of famous faces, both half Male and half Female. The number of famous face images was a compromise between sufficient exposure and minimizing visual overload.

Procedure

The procedure of **Experiment 5** was identical to **Experiment 4**. In the memory for trajectories task, the previously used 20 old face images were extended with 6 images of famous faces. The spatial memory task was followed by a face recognition task, which took place either after a 5-minute delay or a 2-hour delay. The set comprised 20 old face images, 6 famous face images, and 20 new face images. Images were presented one at a time, and participants were asked to indicate novelty using YES/NO responses. At the end, participants were asked to fill out a questionnaire (see Chapter 2).

Data analysis

Correct recognition of old face items and rejection of new ones were summed per to obtain total Recognition Score and Rejection Score. Responses to famous faces were excluded to obtain these measures.

A two-way MANOVA was conducted with Sex and Delay as between-subject factors and the two dependent variables, recognition score and rejection score. Following a marginally significant multivariate effect, separate univariate ANOVAs were conducted for recognition and rejection scores.

To explore whether participants were generally better at recognizing old face items or rejecting new ones, a paired-samples t-test was conducted comparing each participant's total Recognition score and Rejection score across all conditions.

Recognition Scores were subtracted from Rejection Scores to obtain the Rejection-Recogntion Gap). A $2 \times 2 \times 2$ ANOVA was conducted on Rejection Recogntion Gap scores, with Sex, Condition (**Experiment 4** vs. **Experiment 5**), and Delay (5-min vs. 2-hour) as between-subject factors, to assess the influence of the presence and absence of famous face stimuli. Levene's tests did not indicate violation of the homogeneity of variance assumption (all $ps > .35$), therefore we proceeded with the ANOVA despite the unbalanced group sizes.

To assess whether recognition accuracy differed by face gender and participant sex, A $2 \times 2 \times 2$ mixed-design repeated measures ANOVA was conducted with Face Gender (Male vs. Female) as a within-subject factor and Participant Sex (Male vs. Female) and Delay (5minute vs. 2-hour) as a between-subject factors.

Follow-up pairwise t-tests were conducted separately for male and female participants to examine differences in recognition accuracy for male versus female faces.

3.4.2 Main results

Whereas face gender had no effect on face recognition in the previous condition, it became highly significant with famous faces in the current sample, with higher accuracy for recognizing female faces than male faces (3.6). This may suggest that familiarity with a face activates additional semantic and socially relevant information which does not only produce sex-dependent effects, but also influences how participants respond to female and male faces. Analysing the Rejection-Recognition Gap in the presence and absence of famous face stimuli revealed a striking sex difference: males had significantly higher Rejection-Recognition Gap scores than females when exposed to famous face stimuli (3.5).

Recognition vs. rejection

A paired samples t-test revealed that Recognition Score ($M = 7.98$, $SD = 4.26$) was significantly lower than Rejection Score ($M = 15.90$, $SD = 2.84$: $t(95) = -12.17$, $p < .001$).

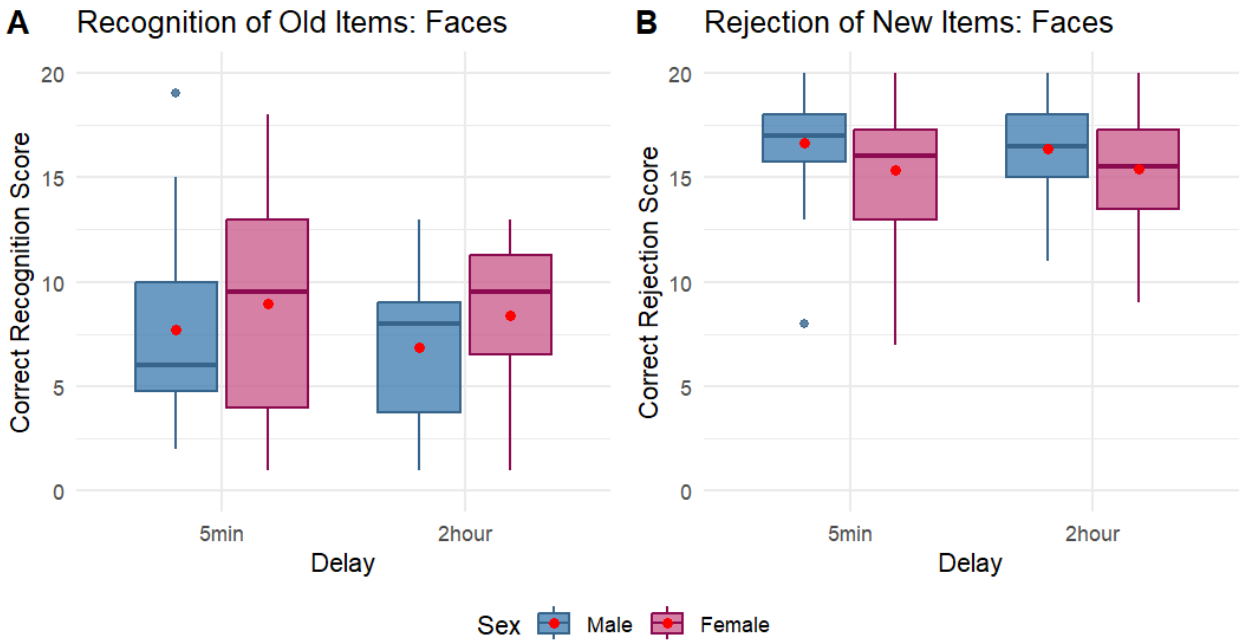


Figure 3.4: Recognition Score and Rejection Score by sex and delay, with famous faces included among the floating images (but not tested for novelty).

Significant effect of famous face stimuli on males

Rejection–Recognition Gap scores were larger in the famous-faces condition compared to the no-famous condition ($F(1, 136) = 9.52$, $p = .002$, $\eta_p^2 = .07$). Furthermore, there was a Sex × Condition interaction ($F(1, 136) = 6.97$, $p = .009$, $\eta_p^2 = .05$).

Collapsing across delay, the Rejection-Recognition Gap for males increased from $M = 3.04$ in the no-famous condition to $M = 9.21$ in the famous-faces condition, whereas this gap for females remained stable ($M = 6.25$ vs. $M = 6.73$, respectively). Follow-up pairwise comparisons confirmed that for males, this difference was statistically significant ($t(136) = -4.05$, $p < .001$). For females, the gap did not differ significantly between conditions.

No other main effects or interactions were significant.

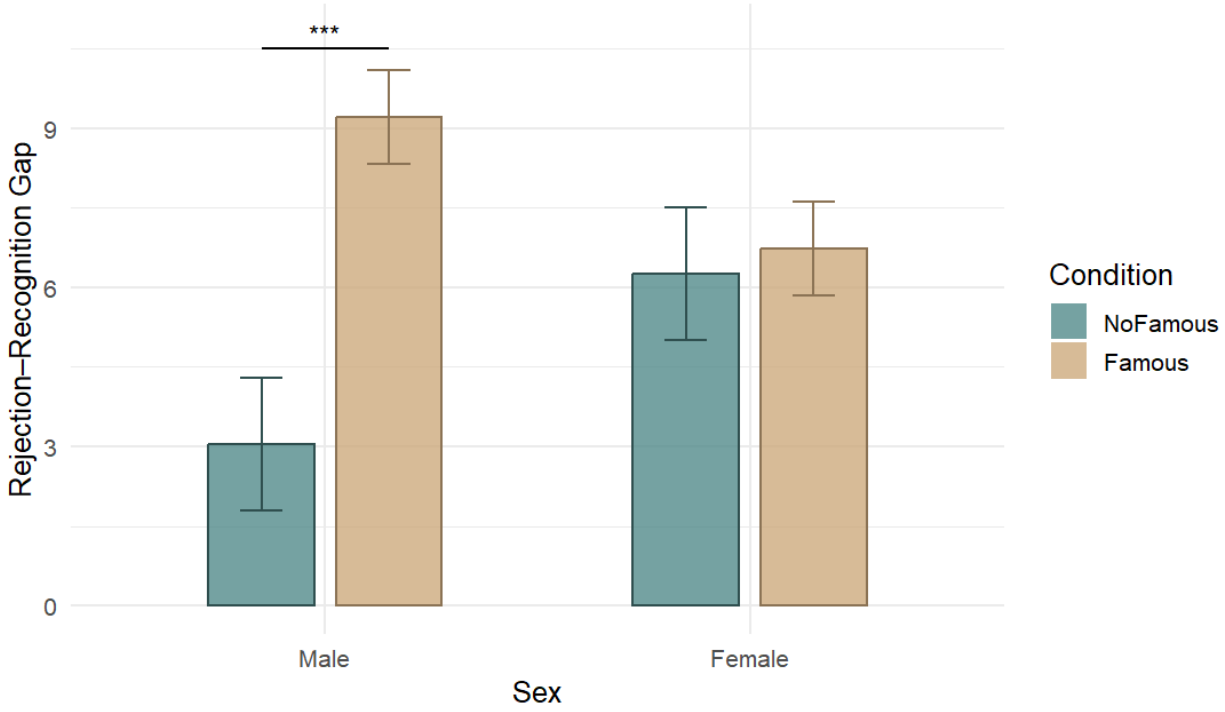


Figure 3.5: Model-adjusted means (± SE) for the Rejection-Recognition Gap (Rejections Score minus Recognition Score) by Sex and *Face* condition (no-famous vs. famous faces), averaged over delay. The gap was significantly larger for males in the famous-faces condition than in the no-famous condition ($p < .001$), whereas no difference was observed for females.

Significant effect of face gender on face recognition

Recognition accuracy was higher for female than male faces ($F(1, 92) = 73.53$, $p < .001$, $\eta_p^2 = .44$). Follow-up comparisons confirmed this effect in both sexes: males recognised female faces more accurately ($M = 0.658$, $SE = 0.015$) than male faces ($M = 0.529$, $SE = 0.017$; $t(92) = -6.26$, $p < .001$). Likewise, females recognised female faces more accurately ($M = 0.665$, $SE = 0.015$) than male faces ($M = 0.541$, $SE = 0.017$; $t(92) = -5.87$, $p < .001$).

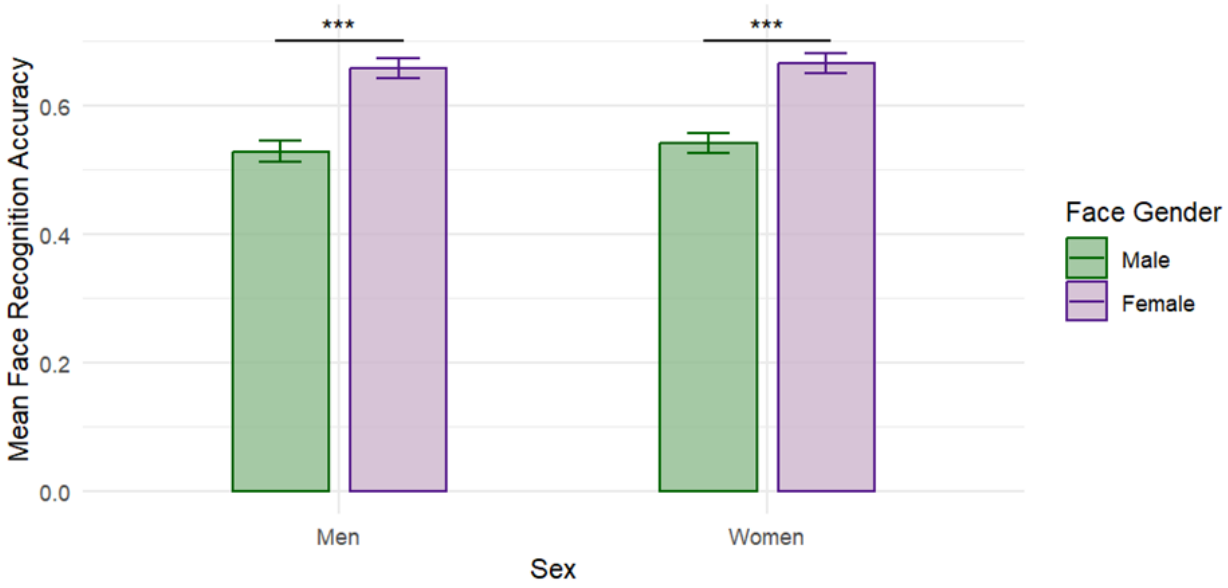


Figure 3.6: Mean face recognition accuracy by participant sex and face gender. Bars show group means, error bars indicate SEM. Accuracy was significantly higher for female faces across both male and female participants (both $p < .001$).

3.4.3 Detailed Results

Significant effect of sex on face recognition

A two-way MANOVA was conducted to examine the effects of Sex and Delay on Recognition Score and Rejection Score. The multivariate test revealed no significant main effect of Sex. Main effect of Delay and the Sex × Delay interaction were not significant.

Females showed slightly higher recognition scores ($M = 8.67$, $SD = 4.61$) than males did ($M = 7.29$, $SD = 3.81$). However, follow-up univariate ANOVAs revealed that the main effect of Sex was not statistically significant with Recognition Scores. On average, males ($M = 16.50$, $SD = 2.43$) outperformed females ($M = 15.40$, $SD = 3.13$) in rejecting new

faces. The univariate ANOVA with Rejection Scores was marginally statistically significant ($F(1, 92) = 3.65$, $p = .06$, $\eta_p^2 = .05$).

Significant effect of face gender on face recognition

While the 2×2×2 mixed-design repeated measures ANOVA examining the effects of Sex (Male vs. Female), Delay (5 minutes vs. 2 hours), and Face Gender (Male vs. Female) on Recognition Score revealed a significant main effect of Face Gender, the main effects of Sex (Male vs. Female participants) and Delay (5-minute vs. 2-hour delay) were not statistically significant. No interaction effects between Sex and Face Gender, Sex and Delay, or Delay and Face Gender were significant.

3.5 Experiment 6 – Incidental learning of objects and verbal recognition

3.5.1 Methods

Participants

Sixty-eight healthy participants (34 females) were recruited through Prolific (Prolific Inc). Participants were aged between 19 and 52 years (mean age = 28.65, ± 6.26 years). The study was approved by the Ethics Committee of the International School for Advanced Studies (SISSA).

Materials

Materials were identical to those used in the *Object* condition of **Experiment 5**. The subsequent object recognition task consisted of 40 descriptive questions: 20 targeting old objects and 20 targeting new ones. Procedure The procedure for **Experiment 6** was the same as in **Experiment 5**. The initial spatial memory task was followed by an object recognition-by-description task, which was administered after either a 5-minute delay (n = 44) or a 2-hour delay (n = 24). The task included 40 prompts (e.g., "Do you remember a red balloon?"), each presented individually. Participants responded YES or NO to indicate novelty. At the end, participants were asked to fill out a questionnaire (see Chapter 2).

Data analysis

Correct verbal recognition of old object and rejection of new object scores were summed per participant to obtain total recognition and rejection accuracy. A two-way MANOVA was

conducted with Sex and Delay as between-subject factors and the two dependent variables, recognition score and rejection score. Since the two-way MANOVA revealed no significant multivariate main effects nor interactions, no follow-up univariate analyses were conducted. To explore whether participants were generally better at recognizing old objects or rejecting new ones, a paired-samples t-test was conducted comparing each participant's total Correct Recognition score and Correct Rejection score across all conditions.

3.5.2 Main Results

As with faces, participants showed significantly higher accuracy for rejecting new objects than for recognizing old ones. Furthermore, males exhibited better rejection accuracy than females.

Consistent divergence of recognition and rejection across modalities

A paired samples t-test revealed that Recognition Score ($M = 10.68$, $SD = 4.16$) was significantly lower than Rejection Score ($M = 14.51$, $SD = 3.74$: $t(67) = -5.38$, $p < .001$). The mean difference was -3.85, 95% CI $[-5.28, -2.42]$, indicating that participants performed significantly better at rejecting new images than recognizing old ones.

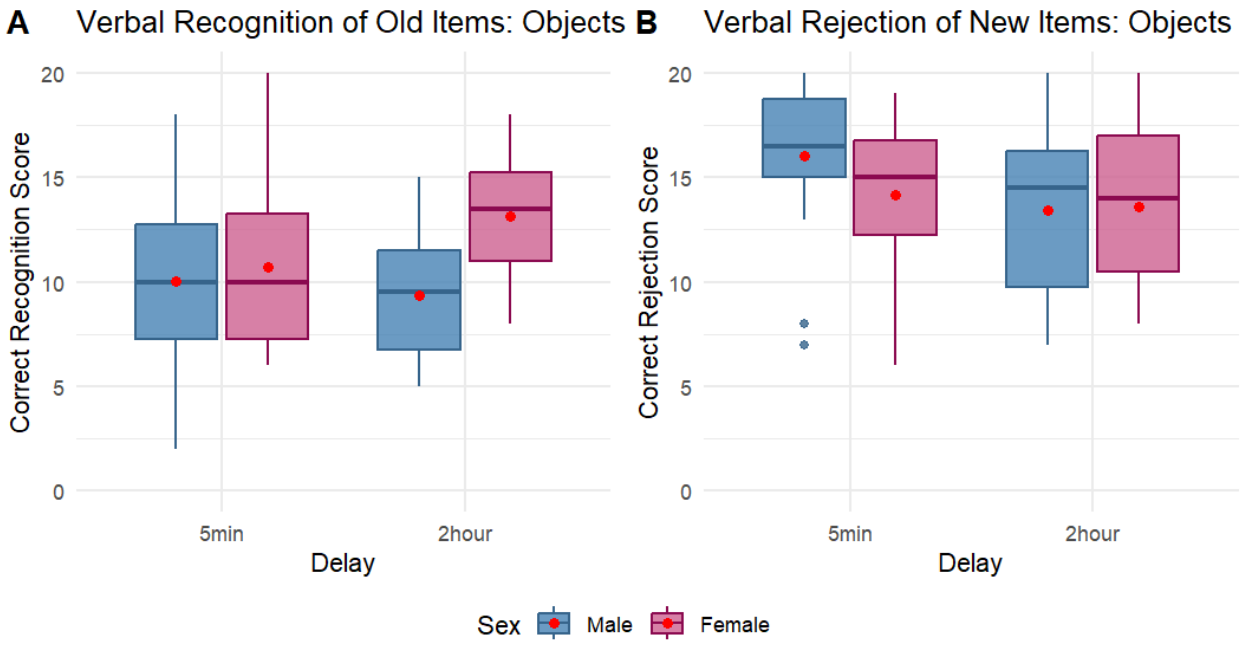


Figure 3.7: Correct old object recognition and new object rejection from verbal descriptions, by sex and delay.

3.5.3 Detailed Results

No effect of sex or delay on object recognition results

A two-way MANOVA was conducted to examine the effects of Sex and Delay on Correct Recognition of Presented Objects and Correct Rejection of New Objects. The multivariate test (Pillai's trace) revealed no significant main effects of Sex, Delay, and the Sex × Delay interaction.

Females showed slightly higher Recognition Score than males. Univariate ANOVAs revealed that the effect of Sex on Recognition Score was marginally significant ($F(1, 64) = 3.22$, $p = .08$, $\eta_p^2 = .05$). The effect of Delay on Rejection Score also approached significance ($F(1, 64) = 2.93$, $p = .09$, $\eta_p^2 = .03$), suggesting a possible influence of retention delay on Rejection Score.

3.6 Memory for trajectories

3.6.1 Methods

Participants, materials, procedure

The Sequential Recall task was identical to the one discussed in Chapter 2. Participants were instructed to locate and memorize sequences of locations of white balls in a sparse, spherical environment where the only available spatial cues were the relative positions of coloured tiles. At this stage, the sole difference between the three incidental learning paradigms (Experiments 5, 6, and 7) was the type of floating stimuli presented.

Participant data from these experiments were therefore split into two conditions based on what type of stimuli (floating images of faces vs. objects) they were exposed to during the spatial memory task. The *Face* condition resulted in a sample size of 144 (72 females, $M = 27.40$, ±7.53 years), and the *Object* condition in 116 (58 females, $M = 27.66$, ±6.54 years).

To investigate whether the floating object or face images influenced Sequential Recall performance, the two incidental learning conditions were analysed alongside the two other spherical conditions: *Spherical Sparse* (n = 96) and *Spherical Landmark* (n = 68).

Data analysis

The distributions of Sequential Recall scores were examined in the *Face* and *Object* conditions.

Due to violations of normality and unequal group sizes, a permutation-based ANOVA was conducted to investigate the effects of Sex and Condition in the spherical environments, by fitting a linear model and computing the F-statistic across 1,000 permutations, in which the predictor labels (*Sparse* vs. *Landmark* vs. *Face* vs. *Object* and Male vs. Female) were randomly shuffled while keeping the Sequential Recall scores fixed.

To further examine whether incidental exposure to floating images during the spatial memory task influenced spatial memory, Spearman correlations were conducted between Sequential Recall scores and recognition scores for old images, and rejection scores for new images, between sexes in both conditions. Spearman's rho was chosen due to non-normal data distributions. False discovery rate correction (Benjamini & Hochberg, 1995) was applied to control for multiple comparisons.

Self-reported strategies were categorized into distinct strategy preferences. To test whether the proportion of participants using spatial versus non-spatial strategies differed by sex across the four experimental conditions, a binary logistic regression was performed with strategy type (spatial vs. non-spatial) as the dependent variable, and Sex, Condition, and their interaction as predictors.

A permutation-based one-way ANOVA (1,000 permutations) was conducted separately for spatial and non-spatial strategy users to test for differences in Sequential Recall scores across conditions (Sparse Female, Sparse Male, Landmark Female, Landmark Male, Face Female, Face Male, Object Female, Object Male). 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.

3.6.2 Main Results

Sequential Recall distributions

In the incidental learning conditions, the spatial environment was identical to the *Spherical Sparse* condition (Figure 2.1), with the only difference being the added floating face or object images. In the *Spherical Sparse* condition, Sequential Recall showed a bimodal distribution. The *Object* condition did not substantially change this pattern, with the bimodal shape remaining similar to that observed in the *Spherical Sparse* condition (3.8). In contrast, the *Face* condition introduced a distinct middle peak that was particularly pronounced in males, suggesting that faces acted as stronger distractors than objects when participants encoded and recalled sequences of location points (3.9).

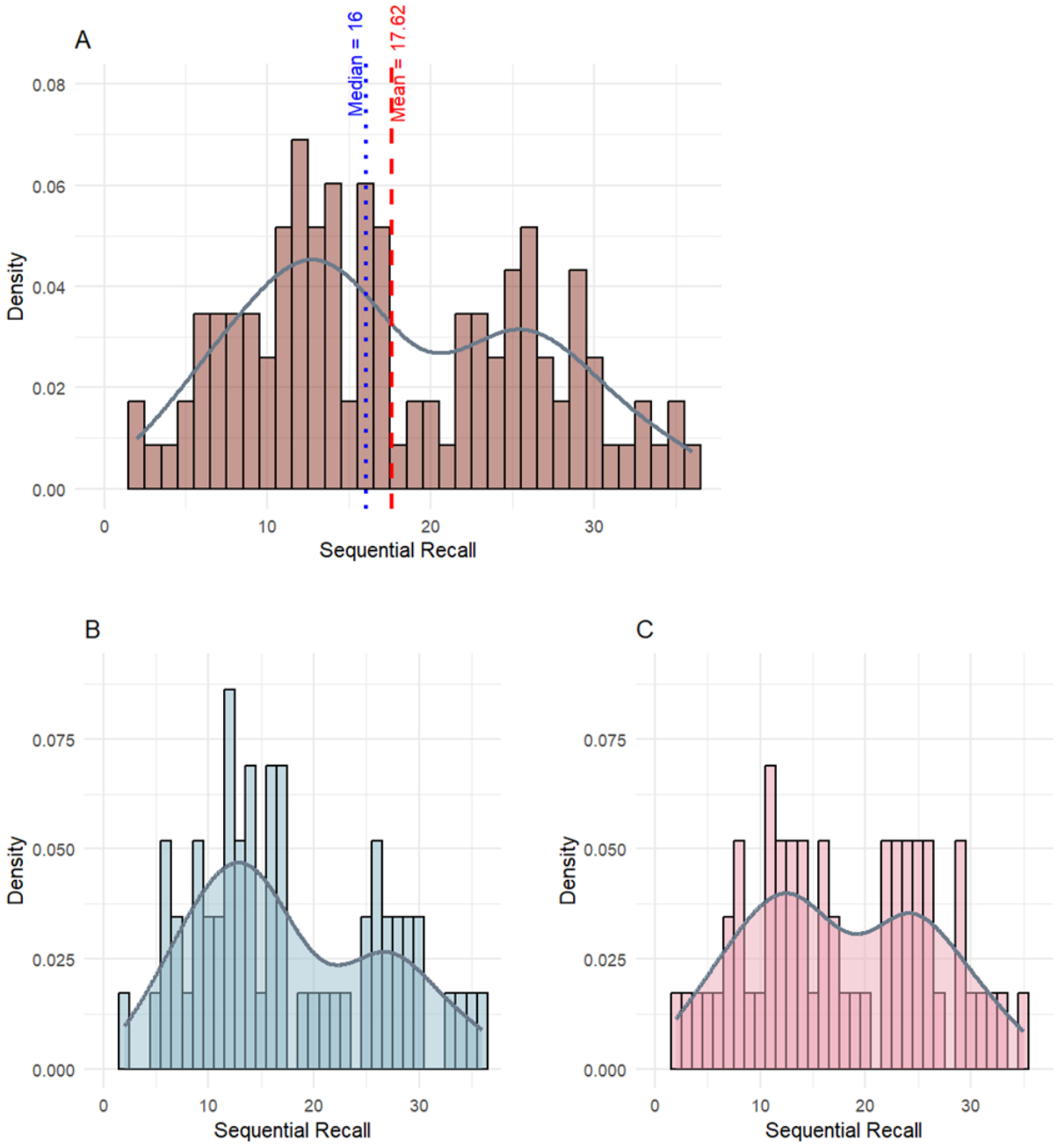


Figure 3.8: A) Sequential Recall score distribution across participants in the *Object* condition, and B) among males and (C) females.

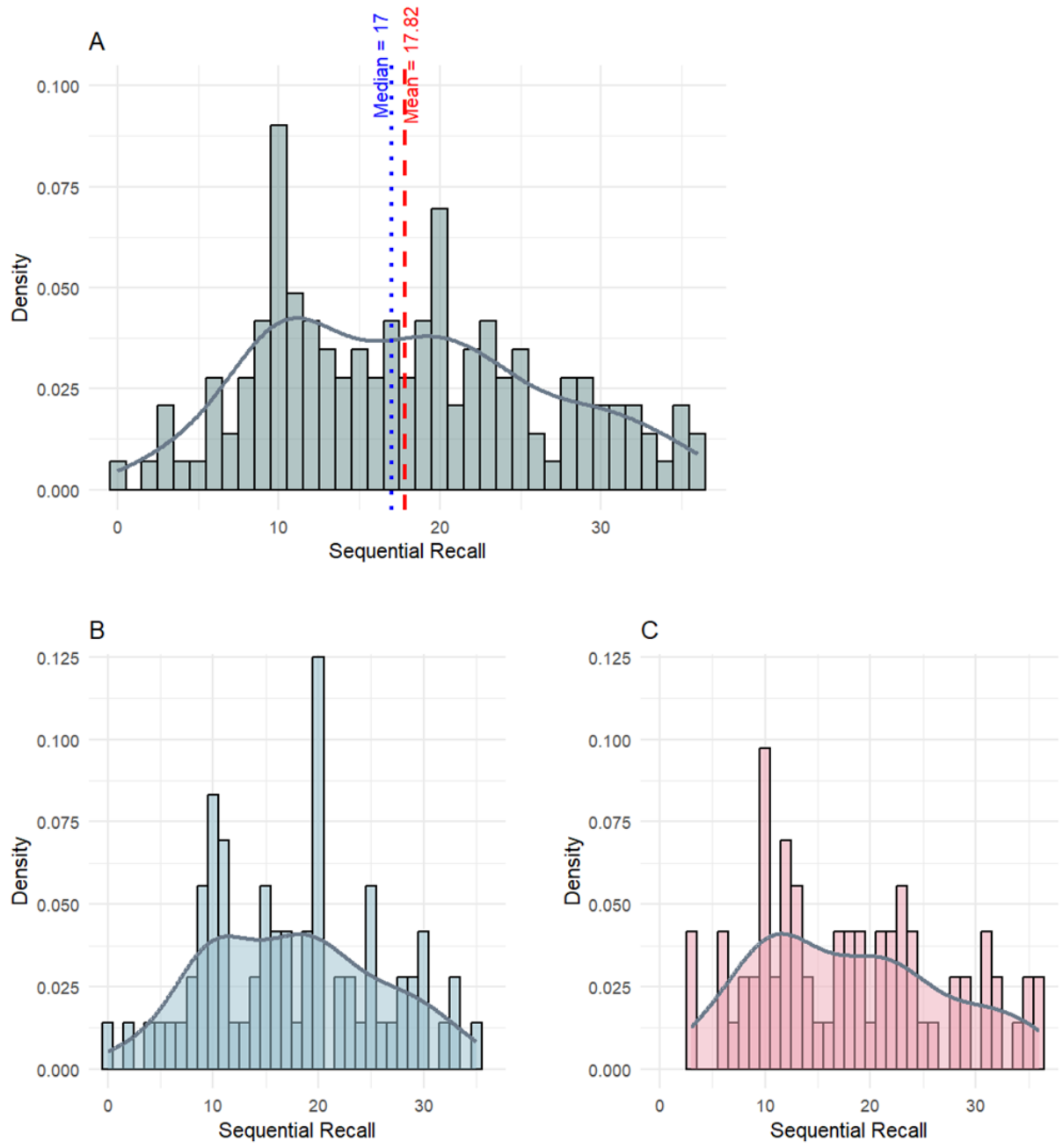


Figure 3.9: A) Sequential Recall score distribution across participants in the *Face* condition, and B) among males and (C) females.

Strategy preference between sexes

The proportions of spatial versus non-spatial strategy use in the two incidental learning conditions were similar between sexes, consistent with the pattern observed in the *Sparse* condition (Figure 3.10). However, compared to the *Sparse* condition, here participants relied more on non-spatial strategies, especially when they were incidentally exposed to floating

object images in the *Object* condition ($\beta = -1.78$, $SE = 0.68$, $p < .01$).

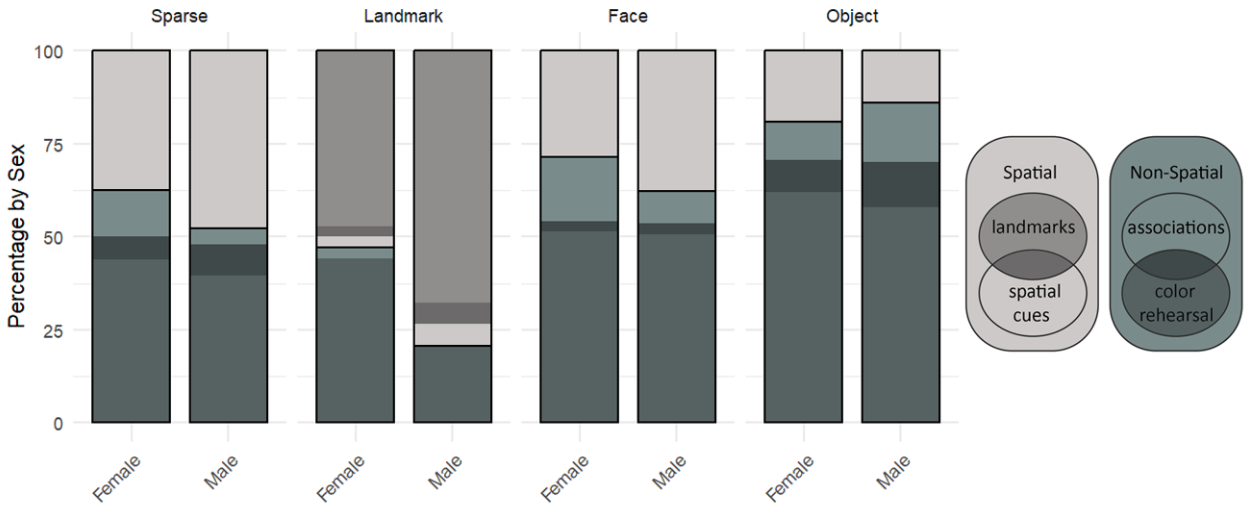


Figure 3.10: Spatial and non-spatial strategy preferences by sex across the spherical conditions (*Sparse* (n = 96) vs. *Landmark* (n = 68) vs. *Face* (n = 139) vs *Object* (n = 115).

3.6.3 Detailed Results

No effect of Condition on Sequential Recall

Although average Sequential Recall scores were lower for both males and females in the two incidental learning conditions, suggesting a potential distracting effect of the floating images, the permutation-based ANOVA revealed no significant effect of the combination of Condition (*Sparse* vs. *Landmark* vs. *Face* vs. Object) and Sex (Male vs. Female) on Sequential Recall performance. A permutation test with 1,000 iterations yielded a p-value of 0.548. Regression coefficients showed very slight variation of recall scores across conditions.

Complementary Bayesian analyses indicated moderate evidence for the absence of a Sex effect ($BF_{01} \approx 8.53$), moderate evidence for the absence of a Condition effect ($BF_{01} \approx 6.99$), and strong evidence for the absence of a Sex $\times$ Condition interaction ($BF_{01} \approx 35.15$).

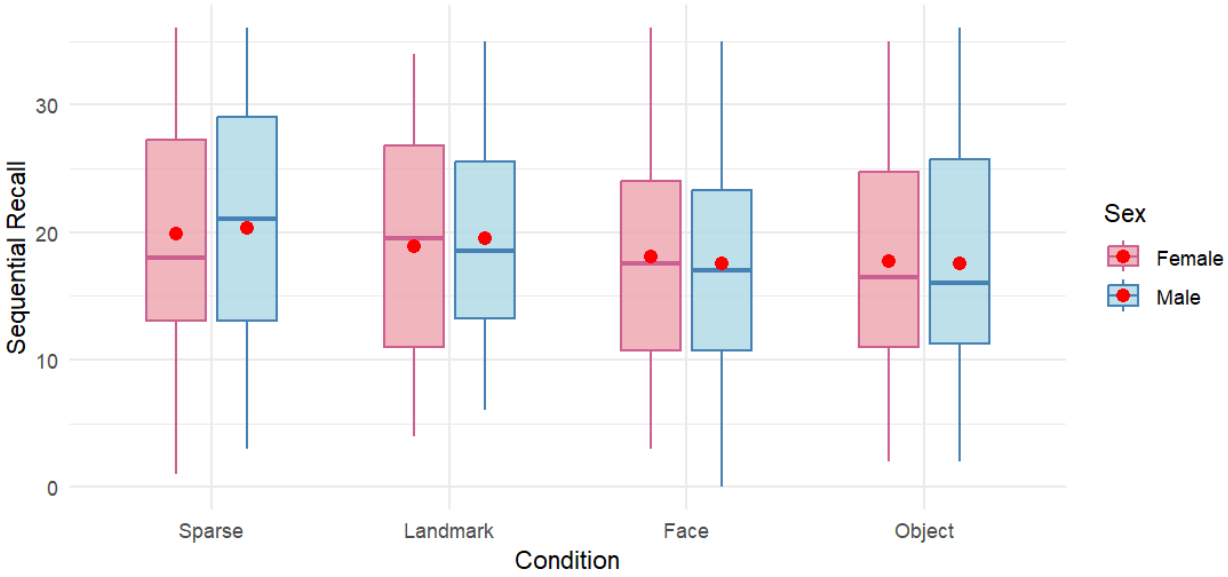


Figure 3.11: Sequential Recall score by condition and sex in the spherical environments (*Sparse* (n = 96) vs. *Landmark* (n = 68) vs. *Face* (n = 144) vs *Object* (n = 116) conditions. The permutation-based ANOVA could not identify a difference between the two sexes in any of the conditions.

Some effect of incidental learning on Sequential Recall in males

Spearman's correlation revealed a positive association between Sequential Recall and recognition of object stimuli in males ($\rho = .33$, $p < .05$); however, this did not remain significant after correction for multiple comparisons ($p_{\text{adj}} = .09$). No other correlations reached significance.

Strategy preference between sexes

Responses of participants who did not provide strategy preference reports were discarded in these analyses. Two females and 3 males were eliminated in the *Face* condition, and one male in the *Object* condition.

A binomial logistic regression predicting strategy preference from Sex and Condition revealed significant main effects of condition; participants in the *Landmark* condition were more likely to use a spatial strategy compared to those in the *Sparse* condition ($\beta = 1.52$, $SE = 0.51$, $p = .003$), replicating the difference observed in Chapter 2, whereas participants in the *Object* condition were less likely to use a spatial strategy ($\beta = -1.78$, $SE = 0.68$, $p = .009$). The main effect of Sex and the Sex × Condition interactions were not significant.

Strategy preference and Sequential Recall

Permutation-based one-way ANOVAs (1,000 permutations) revealed no significant differences in Sequential Recall scores across conditions for spatial strategy users or non-spatial strategy users.

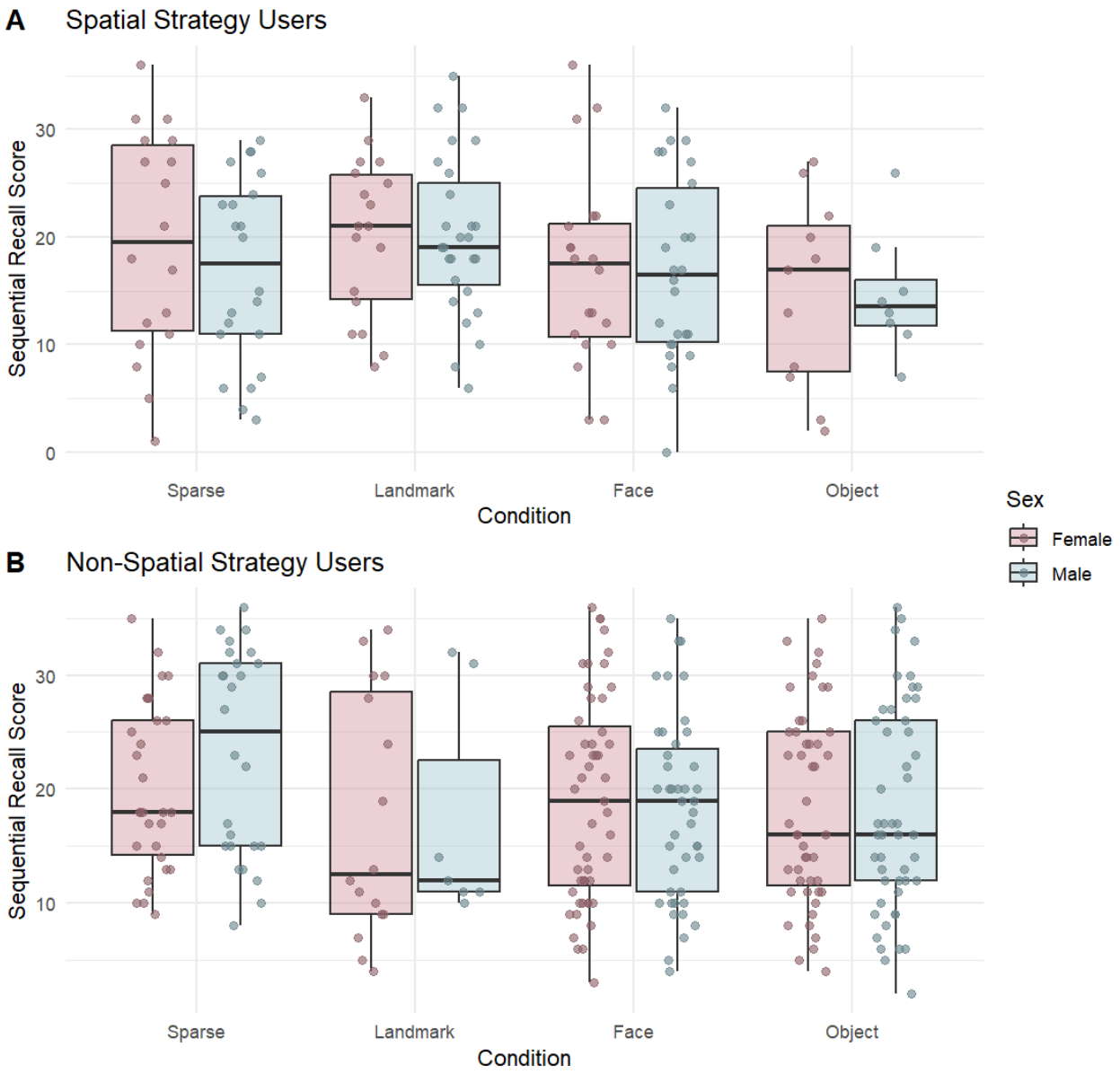


Figure 3.12: Effect of A) spatial vs. B) non-spatial strategy on Sequential Recall across the spherical conditions.

3.7 Discussion

In all three experiments, a consistent pattern emerged: participants were significantly better at rejecting new stimuli than at recognising old ones. This effect held across the different modalities of retrieval, and at both short and long delays. This robust asymmetry can be interpreted within two complementary theoretical frameworks. According to dual-process theory, recognition memory relies on two distinct mechanisms. Recollection is a slower and effortful retrieval of contextual details, which strongly benefits from semantic encoding and depends on the hippocampus and prefrontal cortex (Yonelinas, 2002). Familiarity, in contrast, is a faster and more automatic process associated with the perirhinal and parahippocampal regions. In the context of this study, recognition accuracy may have depended more heavily on recollection and was therefore more deliberate, whereas rejection of new items could be handled by the familiarity process. Because participants were only incidentally exposed to the stimuli, without explicit instructions to attend to them or form semantic associations, recollection was likely disadvantaged. Familiarity, being less sensitive than recollection to semantic encoding and related contextual demands, may have provided a relatively fast and accurate rejection responses throughout these experiments.

A complementary account comes from signal detection theory (Macmillan and Creelman, 2005; Green and Swets, 1966). According to this framework, a decision criterion is set relative to memory strength, determining whether there is enough evidence to judge an item as "old" (Aminoff et al., 2015). If test items fall below this criterion, they are judged as "new." Since participants were only incidentally exposed to the face and object stimuli, memory for these items was fragile, and participants may have adopted a conservative response criterion, tending to respond with "new" rather than "old." Such a criterion produces a higher proportion correct rejections scores (and misses), and a lower proportion of correct recognition (and false alarms).

Sex differences in recognition performance emerged selectively, indicating that they are not a general feature of incidental learning but stimulus and task dependent. In **Experiment 4**, males outperformed females in visual recognition of both faces and objects. However, in **Experiment 5**, the exposure to famous faces increased the rejection–recognition gap in males, whereas female performance remained stable. Both sexes also showed higher accuracy for female faces, but only in the *Famous Face* condition, suggesting that social relevance may modulate incidental memory of males and females in a similar fashion. By contrast, **Experiment 6**, which replaced the visual recognition with verbal object descriptions, revealed no sex differences.

Individual nuances: sex, cognitive style and sensory sensitivity

4.1 Abstract

This chapter examines how individual personality traits contribute to spatial cognition and sex differences in spatial memory. Across four virtual reality experiments, participants performed a sequential recall task and completed the Object–Spatial Imagery and Verbal Questionnaire (OSIVQ) and the Sensory Processing Sensitivity Questionnaire (SPSQ). Cognitive style, particularly object and spatial imagery, correlated with sequential recall. Notable sex differences only emerged in the condition with floating images of objects, where females high in object imagery showed better performance, regardless of strategy preference, whereas for males this imagery style appeared disadvantageous. However, pairing it with a spatial strategy in other conditions reversed this effect. For females, verbal style strongly supported recall in a landmark-rich environment. Furthermore, in the *Object* condition, spatial imagery correlated with rejection accuracy differently depending on the length of delay. By contrast, sensory sensitivity showed no consistent relationship with spatial performance. These findings provide further evidence that sex and individual differences in spatial memory are context dependent and may be shaped by cognitive traits.

4.2 Introduction

Beyond sex and strategy, individual cognitive traits can also influence performance in spatial navigation tasks. Cognitive traits, which regulate how individuals acquire and process information (Klein, 1951), are stable through life and affect strategies, preferences, and ways of perceiving and learning information (Höffler et al., 2017; Jonassen and Grabowski, 1993).

A cognitive trait that plays an important role in navigation is the visual component of the verbal/visual cognitive style, which refers to a preference for processing information visually rather than verbally (Kraemer et al., 2009). This style can be further divided into object-visualization and spatial-visualization cognitive styles, for instance based on the scores in the Object-Spatial Imagery Questionnaire (OSIQ; Blazhenkova and Kozhevnikov, 2008). While object-visualizers excel in picture recognition, spatial visualizers tend to perform better in mental spatial transformation and in navigation tasks (Chabris et al., 2006). These two cognitive styles are largely uncorrelated and associated with different abilities and preferences (Haciomeroglu and LaVenia, 2017). Neuroimaging evidence supports these differences, with distinct brain activity patterns for each style (Motes et al., 2008). Moreover, spatial-visualizers are more accurate and faster than object-visualizers (Vandenberg and Kuse, 1978), and they excel in tasks requiring spatial orientation and navigation (Chabris et al., 2006).

Sensory processing sensitivity (SPS) is a personality trait, often referred to as the highly sensitive person, characterised by heightened sensitivity to internal and external stimuli and rooted in deeper cognitive processing of sensory input (Aron and Aron, 1997). Individuals high in sensory sensitivity often show stronger awareness of subtleties in their environment, greater emotional reactivity and increased susceptibility to overstimulation (Lionetti et al., 2019). Interestingly, individuals high in sensory sensitivity often perform in an all-or-nothing manner: in supportive environmental conditions (e.g., positive parenting styles during childhood) they show enhanced socio-emotional wellbeing, heightened creativity, and superior performance on various cognitive tasks due to greater awareness of detail. In contrast, in unsupportive or stressful environments, they tend to perform worse than less sensitive individuals, as a result of increased vulnerability to stress and anxiety (Greven et al., 2019). In this study, we assessed SPS in relation to our spatial memory paradigm, using the Sensory Processing Sensitivity Questionnaire (Malinakova et al., 2021), which evaluates individual differences in sensitivity across two domains: sensitivity to physical stimuli (Sensory Sensitivity) and sensitivity to emotional and social stimuli (Other Sensitivity).

The present chapter examines cognitive styles in spatial navigation and sequential working memory. Specifically, we examine whether males and females, as well as individuals with varying levels of Object Imagery, Spatial Imagery, or Verbal cognitive styles, differ in how they encode and recall sequences of spatial locations in a novel virtual reality environment. Additionally, we explore whether sensory processing sensitivity to physical and emotional stimuli influences Sequential Recall performance. We hypothesise that higher Spatial and Object Imagery scores will be associated with better Sequential Recall, particularly among males, whereas higher Verbal scores will be more predictive of recall performance among females. We also expect individual differences in sensory sensitivity to be reflected in high

Sequential Recall performance variability, with more, or highly sensitive individuals potentially performing either better or worse than average.

4.3 Methods

4.3.1 Participants

Sixty-eight participants from each experiment, **Experiment 2** (34 females, mean age = x, $\pm$ x years), **Experiment 3** (34 females, mean age = x, $\pm$ x years), **Experiment 5** (34 females, mean age = x, $\pm$ x years), **Experiment 6** (34 females, mean age = 28.65, $\pm$ 6.26 years), were used for these analyses.

4.3.2 Materials

In addition to the spatial memory and subsequent face/object recognition tasks, participants filled out the Object-Spatial Imagery and Verbal Questionnaire (OSIVQ), and Sensory Processing Sensitivity Questionnaire (SPSQ; see Supplementary Material X). The OSIVQ questionnaire consists of 15 items per dimension (Object Imagery, Spatial Imagery and Verbal), 45 items in total. The SPSQ consists of two subscales, sensory processing sensitivity other sensitivity items, each with including 8 items, 16 items in total.

4.3.3 Procedure

The procedure was identical to the one in **Experiment 5** and **6**. Following the face/object recognition task, participants were instructed to fill out the OSIVQ questionnaire. They were presented 45 statements and indicated their response using a 5-point Likert scale: (1) Strongly Disagree; (2) Disagree; (3) Neither Agree nor Disagree; (4) Agree; (5) Strongly Agree. Finally, they were asked to fill out the SPSQ questionnaire, using a 10-point Likert scale: (0) Compared to others, I am not sensitive to them at all; (5) About the same as the people around me; (10) Much more sensitive than the people around me.

4.3.4 Data analysis

Object Imagery, Spatial Imagery, and Verbal scores were estimated as latent variables using confirmatory factor analysis based on the OSIVQ structure (Blazhenkova & Kozhevnikov, 2009). The model showed acceptable fit (RMSEA = .078, SRMR = .107), therefore the standardised factor scores were extracted using lavPredict in lavaan for use in subsequent analyses.

To explore the relationship between individual differences in cognitive style and memory performance, Pearson correlation matrices were computed separately for each experimental condition and sex. These exploratory correlations served only as descriptive guidelines to identify potential patterns between OSIVQ traits (Object Imagery, Spatial Imagery, and Verbal scores) and key task performance measures (Sequential Recall, Encoding Mean, Recall Mean, Recognition Score, Rejection Score).

To examine whether sex and cognitive style predicted performance in Sequential Recall across different experimental conditions, we ran a multiple linear regression model. The dependent variable was Sequential Recall, and the predictors included Object Imagery, Spatial Imagery, and Verbal factor scores (derived from CFA), along with Sex (Male vs. Female), Condition (*Famous Face* vs. *Object* vs. *Spherical Landmark* vs. *Flat Sparse*), and all two- and three-way interactions.

To interpret the significant three-way interaction between Object Imagery, Sex, and Condition, separate linear regression models were conducted by sex within the *Object* condition.

To explore how strategy preference and cognitive style relate to Sequential Recall performance across the entire sample, we ran separate linear regression models by sex and condition, including interactions between strategy group (Spatial vs. Non-Spatial) and cognitive styles.

Because splitting the data by sex, strategy preference, and condition resulted in small sample sizes in some subgroups, exploratory scatterplots with linear fits were first generated to identify potential patterns between cognitive style, strategy use, Sequential Recall performance, and sex. Follow-up regression models were then conducted only for combinations where visual trends appeared meaningful.

Due to the small number of participants in some subgroups (e.g., $n = 5$), no formal statistical comparisons were conducted. Instead, group-level trends were explored descriptively and through visual inspection. Where sample sizes allowed, interaction models comparing regression slopes were conducted to assess whether the relationship between cognitive style and recall differed by sex and by condition.

To explore how individual differences in cognitive style relate to incidental learning performance in the *Famous Face* and *Object* conditions, we computed correlation matrices.

To examine the effects of cognitive style (Spatial Imagery, Object Imagery, Verbal score), Sex, and Delay (5-minute vs. 2-hour) on Recognition Score, we first ran a full linear regression model with all traits and their interactions included, for each condition. Due to high multicollinearity, we fitted reduced models with recognition score and rejection scores separately, excluding three-way terms.

To test whether sensory sensitivity measures predicted Sequential Recall, we ran a linear regression model including Sensory Sensitivity and Other Sensitivity, together with sex and

condition, and all their interactions. Due to small and unequal sample sizes in the *Famous Face* condition, this condition was excluded in this analysis. We therefore anlaysed only the *Object Verbal*, *Spherical Landmark*, and *Flat Sparse* conditions. Analysing separately by sex resolved the collinearity problem, therefore we ran separate regression models for each sex, including all conditions (*Famous Face*, *Object Verbal*, *Spherical Landmark*, and *Flat Sparse*)

4.4 Main Results

In the *Object* condition, Spatial and Object Imagery scores predicted performance differently for males and females. Notably, females with stronger Verbal cognitive styles showed better Sequential Recall performance in the *Spherical Landmark* condition, regardless of strategy preference. For males, Spatial Imagery supported better recall, while Object Imagery was linked to poorer performance, except when paired with a spatial strategy, which appeared to reverse the effect.

4.4.1 Cognitive style vs. Sequential Recall

Cognitive traits are correlated with Sequential Recall

The multiple regression model predicting Sequential Recall from Object Imagery, Spatial Imagery, Verbal scores, Sex, and Condition (including all interactions) was significant ($F(31, 240) = 3.04$, $p < .001$), explaining approximately 28% of the variance in Sequential Recall scores (adjusted $R^2 = .19$).

Spatial Imagery showed a trend toward a positive association with Sequential Recall ($\beta = 4.13$, $p = .08$). A two-way interaction between Verbal scores and Condition in the *Spherical Landmark* approached significance ($\beta = 6.37$, $SE = 3.33$, $p = .06$), and among females, Verbal scores were significantly associated with better Sequential Recall performance ($\beta = 5.50$, $SE = 2.57$, $p < .05$; Figure A.7, C), whereas no comparable effect was found among males.

In the *Object* condition, Object Imagery predicted performance differently for males and females (($\beta = -17.86$, $p < .05$); Figure A.5, B), and a similar sex-dependent pattern was observed for Spatial Imagery ($\beta = 11.05$, $p < .05$); Figure A.6, B). Follow-up regressions revealed that among females, Object Imagery tended to predict better Sequential Recall ($\beta = 4.73$, $SE = 2.82$, $p = .1$), whereas among males, the relationship was slightly negative and non-significant. Follow-up analyses revealed no comparable sex-dependent patterns for Spatial Imagery.

No significant cognitive trait related effects were observed in the *Flat Sparse* condition.

4.4.2 Cognitive style vs. strategy preference

Sequential Recall by strategy preference and cognitive style, regardless of condition

Among males, higher Spatial Imagery predicted better Sequential Recall ($\beta = 6.94$, $SE = 1.65$), and this effect was highly significant ($p < .001$). By contrast, higher Object Imagery predicted poorer Sequential Recall ($\beta = -5.16$, $SE = 2.43$, $p < .05$). However, this negative relationship was moderated by strategy use: when males employed a spatial strategy, higher Object Imagery predicted better performance ($\beta = 8.02$, $SE = 3.94$, $p < .05$). Overall, the model explained a substantial proportion of variance in Sequential Recall ($R^2 = .26$, $p < .001$).

4.5 Detailed Results

4.5.1 Exploratory correlations

Exploratory Pearson correlations between the three cognitive styles (Object Imagery, Spatial Imagery, and Verbal scores) performance measures from the original memory for trajectories task (Sequential Recall, Encoding Mean, Recall Mean, Total Encoding Path, and Total Recall Path), performance in the incidental learning paradigm where applicable (Recognition Score, Rejection Score), and sensory sensitivity measures (Sensory Sensitivity, Other Sensitivity), by Condition and by Sex, are presented in Figure A.1 for the *Spherical Landmark* condition, in Figure A.2for the *Flat Sparse* condition, in Figure A.3 for the *Famous Face* condition, and in Figure A.4for the *Object (Verbal)* condition.

4.5.2 Cognitive style vs. strategy preference

Sequential Recall by strategy preference and cognitive style, regardless of condition

Among females, Spatial Imagery showed a statistically significant positive relationship with Sequential Recall ($\beta = 3.20$, $SE = 1.61$, $p = .050$). No other main effects or interactions were significant.

Exploratory scatterplots with linear regression lines illustrating the relationship between Sequential Recall performance and each cognitive style: Object Imagery (Figure A.8), Spatial Imagery (Figure A.9), and Verbal (Figure A.8), separately by strategy preference, sex, and

condition, can be viewed in the Appendix.

Sequential Recall by strategy preference, cognitive style, and by condition

Object Imagery style

A linear regression model revealed that in the *Flat Sparse* condition, among spatial strategy users, females showed a negative association between Object Imagery and performance, whereas males showed a positive one. This interaction between Sex and Object Imagery was statistically significant ($\beta = 9.94$, $SE = 4.75$, $p < .05$).

In the *Object* condition, exploratory scatterplots revealed that among spatial strategy users, males and females showed opposing trends in how Object Imagery related to Sequential Recall: a negative slope for males and a positive slope for females (Figure A.8). However, due to limited sample sizes in this subgroup (n $<$ 6 per sex), no formal statistical comparison was conducted. In the non-spatial strategy group, similar opposing trends were observed with larger samples.

A linear regression model revealed that although in the *Object* condition, non-spatial strategy user females showed a positive association between Object Imagery and Sequential Recall, and males showed a negative trend, the interaction between Sex and Object Imagery was not statistically significant.

Spatial Imagery style

Spatial Imagery scores showed consistent positive associations to varying degrees with Sequential Recall scores for both sexes and across all conditions (Figure A.9). The only exception was apparent in the *Flat Sparse* condition, where males showed a positive, while females showed a slight negative trend between Spatial Imagery and Sequential Recall scores.

A linear regression model revealed that in the *Flat Sparse* condition, among spatial strategy users, higher Spatial Imagery predicted better Sequential Recall for males, while females showed a slight negative trend. This interaction between Sex and Spatial Imagery was statistically significant ($\beta = 8.76$, $SE = 3.23$, $p < .05$).

Verbal style

A linear regression model in the *Famous Face* condition among spatial strategy users revealed a positive trend between Verbal scores and Sequential Recall for males, and a negative trend for females. This interaction between Sex and Verbal scores approached significance ($\beta = 10.12$, $SE = 5.71$, $p = .09$). Although the sexes showed similar trends in the non-spatial subgroup, that interaction did not reach statistical significance.

4.5.3 Cognitive style during incidental learning

Cognitive styles predict incidental learning only in the Object condition

While the linear regression model predicting Recognition Score revealed no significant main effects or interactions in the *Object Verbal* condition, there was a marginal effect of Sex, with males tending to perform worse than females ($p = .06$). There were also trends for an Object Imagery × Sex interaction ($p = .09$) and a Verbal × Delay interaction ($p = .1$).

Spatial Imagery positively predicted Rejection Score ($p < .05$; Figure 4.1). The linear regression model predicting Rejection Score was significant in this condition ($F(11, 56) = 2.49$, $p < .05$, adjusted $R^2 = .20$). This effect was moderated by delay, such that higher Spatial Imagery predicted poorer rejection performance at the 5-minute delay but better performance at the 2-hour delay ($\beta = -5.57$, $p < .01$). In addition, the interaction between Object Imagery and Delay approached significance ($p = .07$).

Cognitive styles in the Famous Face condition

While the correlation matrices revealed considerable variation in cognitive style, sex, and incidental learning performance, the separate regression models for the *Famous Face* condition did not yield significant results. The linear regression model predicting Recognition Score revealed no significant main effects or interactions.

The linear regression model predicting Rejection Score also revealed no significant main effects or interactions in this condition. Although not significant, there were trends for a main effect of Sex, with males tending to score higher than females ($p = .1$), and a Spatial Imagery × Sex interaction ($p = .07$).

4.5.4 Sensory processing sensitivity

The linear regression model predicting Sequential Recall from Sensory Sensitivity, Other Sensitivity, sex, and condition (*Object Verbal*, *Spherical Landmark*, *Flat Sparse*) was not statistically significant overall. No significant main effects or interactions emerged.

For males, the regression model predicting Sequential Recall from sensory processing sensitivity, other sensitivity, and condition approached significance overall ($F(11, 113) = 1.63$, $p = .1$, adjusted $R^2 = .05$). No significant effects of sensory sensitivity or other sensitivity emerged, although the interaction between other sensitivity and condition in the *Flat Sparse* condition approached significance ($p = .1$).

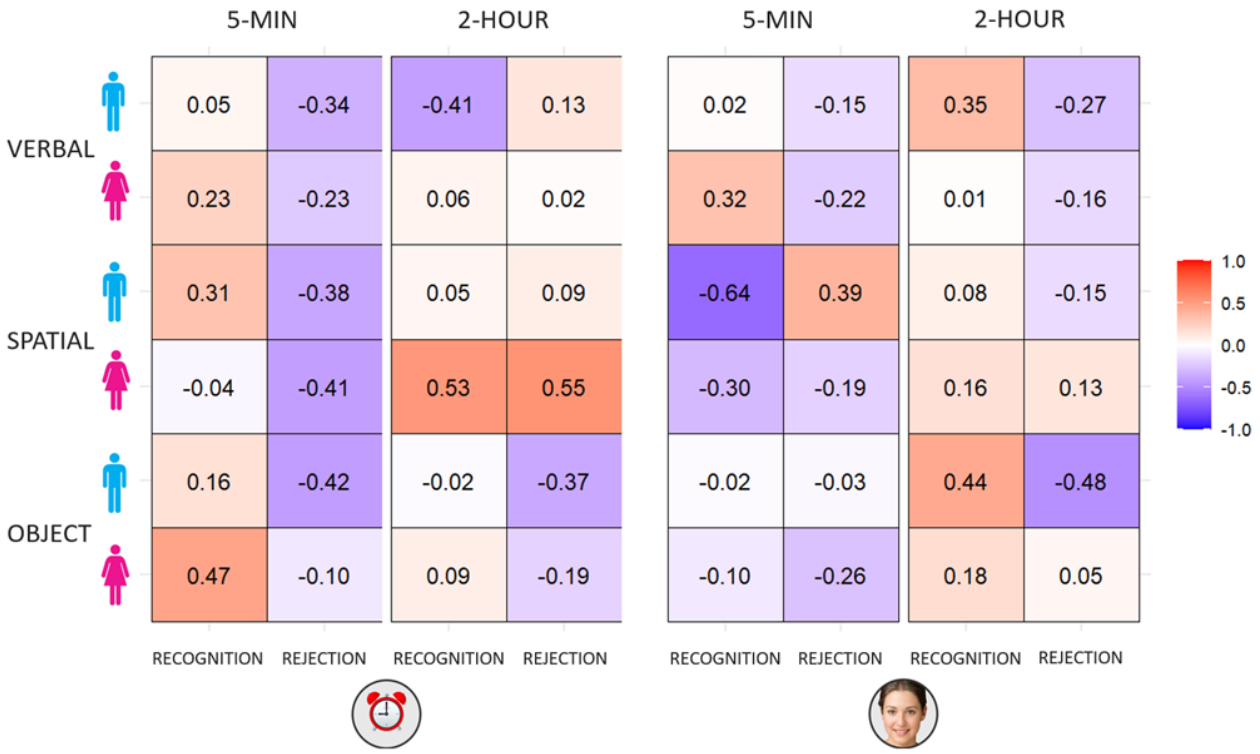


Figure 4.1: Exploratory Pearson correlations between cognitive styles and incidental learning measures, by Sex, Delay and Condition. Both in the *Object Verbal* and *Famous Face* conditions,the 5-minute delay condition included 44 participants, whereas the 2-hour delay condition comprised 24 participants, both sex-balanced.

4.6 Discussion

Notably, sex differences only emerged reliably in the *Object* condition, where females high in Object Imagery performed better than their male counterparts. This effect was not influenced by strategy preference, as females benefitted from Object Imagery regardless of the strategy they reported. By contrast, for males, higher Object Imagery was associated with poorer Sequential Recall, unless paired with a spatial strategy, which appeared to reverse this disadvantage. The fact that such a difference emerged only in the *Object* condition, provides further evidence for the context-dependent nature of sex-specific effects in spatial memory.

Across conditions, Spatial Imagery tended to support Sequential Recall performance, particularly among males, consistent with previous findings that spatial visualisers excel in navigation and mental rotation tasks (Chabris et al., 2006; Kozhevnikov et al., 2005). For females, however, this advantage was overall less pronounced, unless paired with supportive contextual elements (such as the *Spherical Landmark* condition). Interestingly, in the *Flat Sparse* condition, females high in Spatial Imagery performed worse if they relied on a spatial strategy, while adopting a non-spatial strategy appeared to mitigate this disadvantage.

Verbal style revealed a different, and perhaps more versatile, profile. In the *Spherical Landmark* condition, higher Verbal scores predicted better Sequential Recall among females, irrespective of strategy preference. It is possible that, particularly in this condition, females could leverage their well-documented advantage in verbal episodic memory (Hirnstein et al., 2022; Golchert et al., 2019; Herlitz et al., 1999), both when applying spatial strategies (e.g., verbally rehearsing landmarks) and when relying on non-spatial strategies (e.g., rehearsing associations or colour combinations.

Sensory sensitivity did not show consistent associations with Sequential Recall performance. One likely explanation is that our sample contained relatively few individuals at the high end of the sensitivity spectrum, with most participants scoring in the average range. The relatively small, and in one condition unequal, sample sizes, may have reduced statistical power, limiting the ability to detect significant effects, despite the patterns observed in the exploratory correlation matrices. There, males appeared more affected by sensory sensitivity, especially in the incidental learning conditions, whereas females showed little to no influence.

These results suggest that sex influences not just the strength but also the direction of the relationship between Imagery abilities and strategy preferences. The opposing trends could reflect underlying cognitive or motivational differences between sexes in how they approach tasks involving imagery and spatial processing.

Back to familiarity: flat space with landmarks

5.1 Abstract

This chapter introduces the final stage of the spatial familiarity paradigm developed in Chapter 2, adding the *Flat Landmark* condition (n = 68) as the most familiar and plausible environment in the series. Across the four stages, Sequential Recall distributions shifted gradually: bimodal in the *Spherical Sparse* condition, multimodal with added landmarks, normal in the sparse, flat environment, and left-skewed in the current *Flat Landmark* condition. Despite the marked changes in distributions, average performance remained similar across all conditions. In the *Flat Landmark* condition, males and females showed comparable Sequential Recall, but unlike in the spherical version of this condition where only males showed a significant preference for a spatial strategy, here strategy use converged, with the majority of participants now relying on spatial strategies. Cognitive traits, which previously reliably predicted performance, especially Object and Spatial Imagery, revealed no significant associations with Sequential Recall in this most familiar environment. Most strikingly, the relationship with Spatial Imagery was essentially flat, an unexpected finding given its consistent predictive value in less familiar environments.

5.2 Introduction

In Chapter 2, we proposed a series of tasks, with those in the first stage set in a highly unusual and minimalistic environment. Platonic solids (a Cube in one condition and a Dodecahedron in another) were projected onto a sphere as navigable spaces, and combined with unfamiliar movement experiences: zero gravity/flying in one condition and terrestrial movement on the

sphere's surface in another. We then manipulated the familiarity of the environment by changing spatial structure, or adding traditional landmarks. Therefore, in the next stage, we placed traditional landmarks in our sparse, spherical space. While the non-Euclidean spatial structure remained, the landmarks provided additional familiarity. In the third stage, we created the Euclidean version of the sparse, spherical environment.

We hypothesised that the change in each stage is gradual, such that each stage increases in familiarity in the proposed order, and participant behaviour would reflect that. Indeed, the shifts from a bimodal, to multimodal, and to a roughly normal distributions of Sequential Recall across the experimental conditions, suggested that the novelty of the first stage led only to individual differences, while sufficient plausibility evoked the sex difference widely observed in the literature.

The current experiment introduces the final piece of this spatial paradigm, the *Flat Landmark* condition, designed as the maximally familiar environment. Here, participants navigate a Euclidean space enriched with both orientation cues and traditional landmarks, a setting that combines sources of familiarity present in everyday navigation. Based on the proposed framework, we hypothesised that this condition would amplify sex differences in Sequential Recall and strengthen their associations with individual cognitive traits, especially with spatial imagery, further extending our series of tests of whether environmental familiarity/plausibility modulates the expression of sex differences in spatial memory.

5.3 Methods

5.3.1 Participants

Sixty-eight participants (34 females) were recruited through Prolific. Participants were aged between 20 and 40 years ($M = 28.85$, $SD = 4.92$). Participant eligibility, consent procedures, and ethical approval were identical to previous experiments. Combined with **Experiment 1**, **Experiment 2** and **Experiment 3**, the full sample provided 90% power ($\alpha = .05$, $f = 0.25$) to detect small-to-medium effects in a 2×4 between-subjects design, as determined using the `pwr.anova.test` function from the `pwr` package in R, assuming an average of 37.75 participants per group across 8 groups.

5.3.2 Materials

The materials used were identical to **Experiment 3** (*Flat Sparse* condition). Twelve traditional landmarks were added to the flat, sparse space, such that the environmental design of the current experiment shared numerical symmetry with the *Spherical Landmark* condition

(see Chapter 2). The landmarks were placed at the centre of the hexagonal edges.

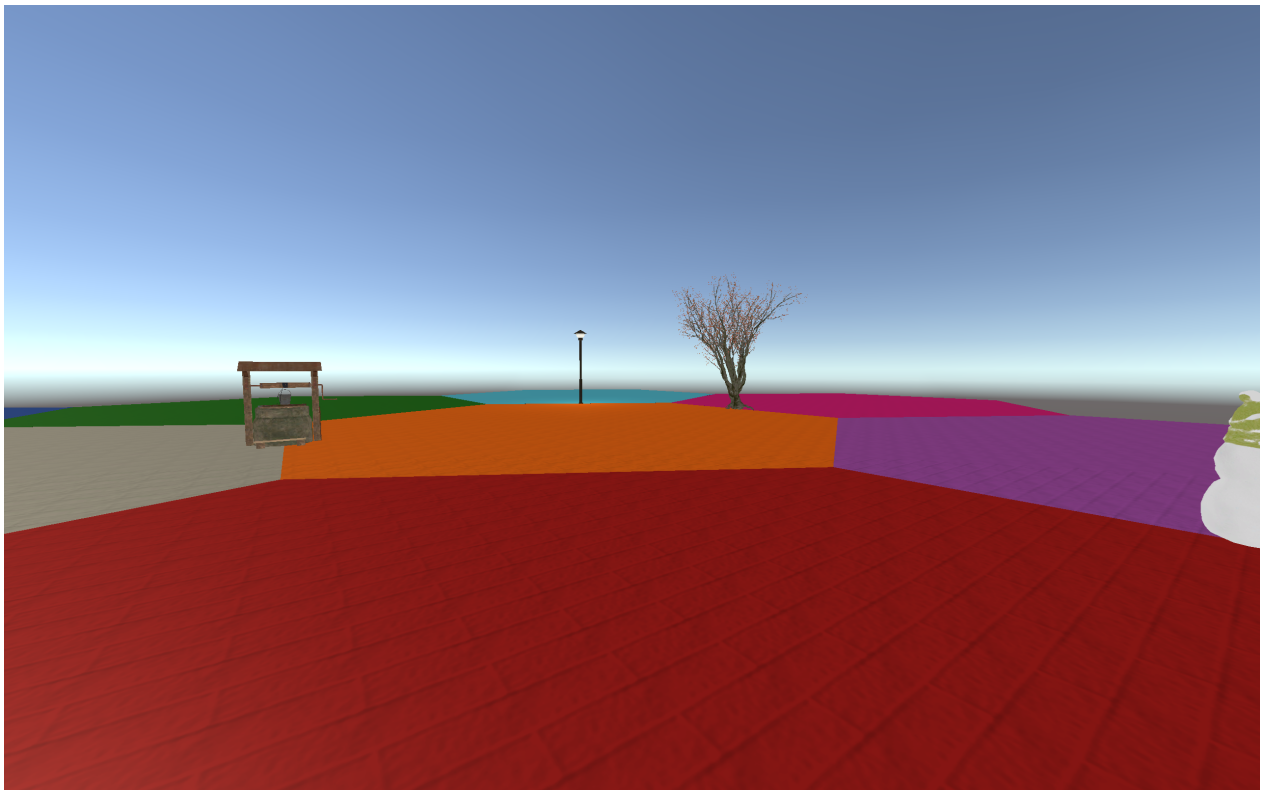


Figure 5.1: Game view of the *Flat Landmark* condition. As in the *Spherical Landmark* condition, the traditional landmarks were placed at the centre of the hexagonal edges.

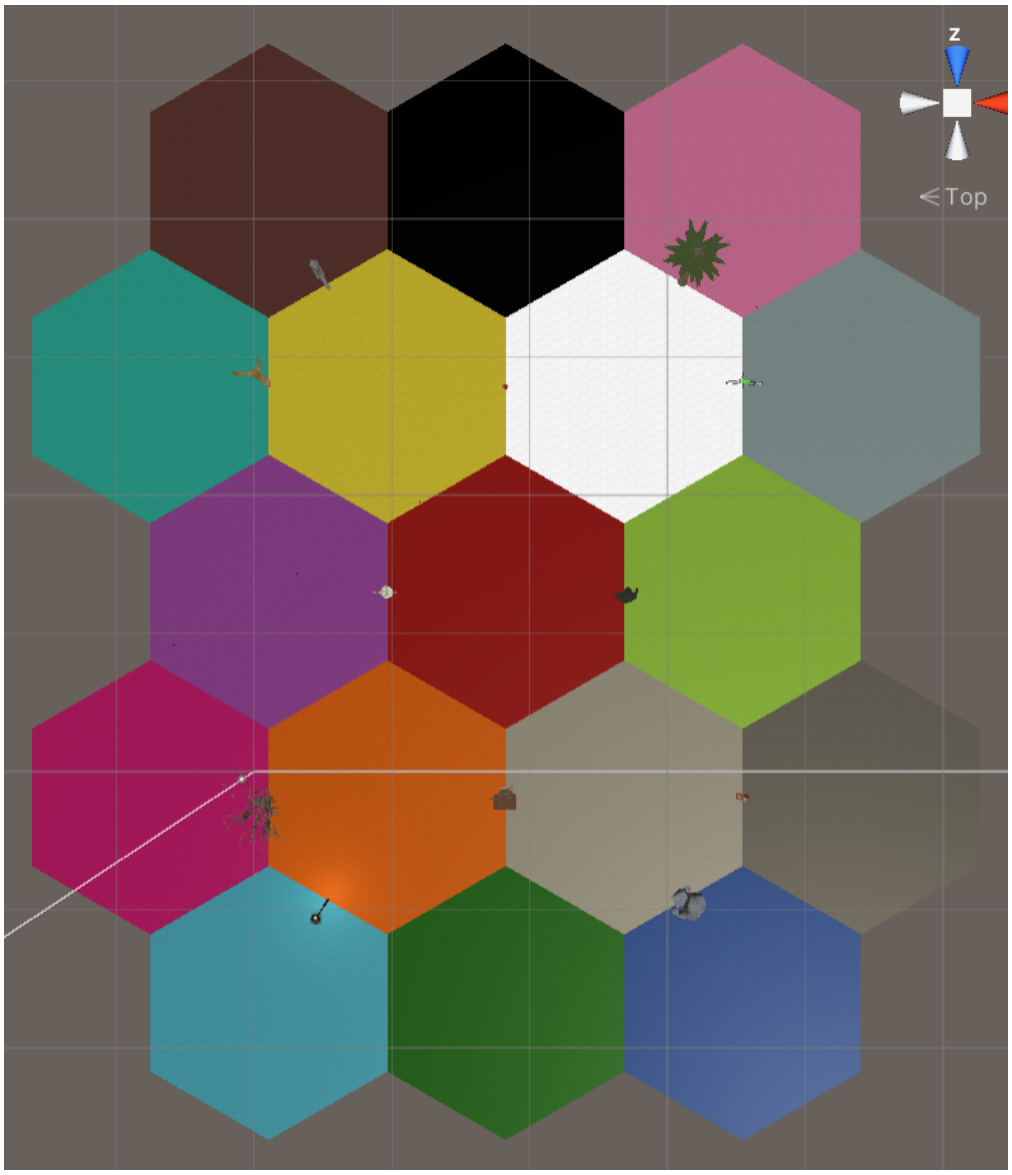


Figure 5.2: Map view of the *Flat Landmark* environment. This design featured 20 vertices, identical to the structure of the *Spherical Landmark* space. Interestingly, there was additional numerical symmetry between the two traditional landmark rich conditions: the *Flat Landmark* condition used 17 colours and 12 landmarks, while the *Spherical Landmark* condition featured 17 landmarks and 12 colours.

5.3.3 Procedure

The procedure was identical to *Experiment 3*. Following the Sequential Recall task, participants completed the OSIVQ and SPS questionnaires (see Chapter 4).

5.3.4 Data analysis

The distribution of Sequential Recall scores was examined across participants and between sexes to understand their behaviour in this most plausible flat environment with traditional landmarks.

To further investigate the effects of increased familiarity/plausibility of Condition, and Sex, Sequential Recall scores from the *Spherical Sparse* Condition (**Experiment 1**), *Spherical Landmark* Condition (**Experiment 2**), *Flat Sparse* Condition (**Experiment 3**) and *Flat Landmark* Condition (**Experiment 7**) 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 1,000 permutations, in which the predictor labels (*Spherical Sparse* vs. *Spherical Landmark* vs. *Flat Sparse* vs. *Flat Landmark* and Male vs. 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 or against each effect.

A Fisher's exact test was conducted to examine the association between sex and strategy use (spatial vs. non-spatial) in the *Flat Landmark* condition. Since visual inspection of strategy distributions suggested that females were the only group showing a marked change in strategy preference between the two landmark conditions, a follow-up Fisher's exact test was conducted to compare strategy use between females in the *Flat Landmark* and *Spherical Landmark* conditions.

A linear regression model was conducted to examine the effect of change of Condition (*Spherical Sparse*, *Spherical Landmark*, *Flat Sparse*, *Flat Landmark*) and Sex (Male vs. Female) on Sequential Recall performance among those who employed a spatial strategy. A separate analysis was conducted for participants who used a non-spatial strategy to complete the task.

Encoding means, recall means, total encoding path means and total recall path means were log-transformed. A multiple regression model predicting Sequential Recall from Total Encoding Path, Total Recall Path, and Sex (including their interactions) was conducted.

Confirmatory factor analysis (CFA) was conducted on all participants who completed the OSIVQ questionnaire (Experiments 2, 3, 5, 6, and 7; see Chapter 4). Although the CFA showed only moderate model fit (CFI = 0.670, RMSEA = 0.078), the factor structure remained consistent across participants. As the model was based on the full sample (N = 340), the resulting factor scores for Object Imagery, Spatial Imagery, and verbal styles are considered sufficiently stable for use in exploratory analyses.

To examine whether sex and cognitive style predicted performance in Sequential Recall across different experimental conditions, we ran a multiple linear regression model. The dependent variable was Sequential Recall, and the predictors included Object Imagery, Spatial Imagery, and Verbal factor scores, along with Sex (Male vs. Female), and Condition (*Spherical Landmark*, *Flat Sparse*, *Flat Landmark*).

5.4 Main Results

5.4.1 Sequential Recall

Distributions across participants and between sexes

The Sequential Recall distributions shifted across the four conditions of increasing familiarity: bimodal in the *Spherical Sparse* environment, multimodal with added traditional landmarks, normal in the *Flat Sparse* condition, and left-skewed in the *Flat Landmark* condition (Figure 5.3). These shifts suggest that the increase in familiarity/plausibility of the environment influenced how participants approached the task. However, these shifts in distribution were not accompanied by changes in average performance, as confirmed by the permutation-based ANOVA.

Similar average performance across conditions

The permutation-based ANOVA assessing group differences (by Condition and by Sex) in Sequential Recall yielded a non-significant result. Regression coefficients from the original model showed no significant group differences. Complementary Bayesian analyses indicated moderate evidence for the absence of a Sex effect (BF01 ≈ 3.58), very strong evidence for the absence of a Condition effect (BF01 ≈ 31.87), and strong evidence for the absence of a Sex $\times$ Condition interaction ($\text{BF}_{01} \approx 11.56$).

Path length matters - but differently at encoding and at recall

The multiple regression model predicting Sequential Recall from Total Encoding Path, Total Recall Path, and Sex (including their interactions) was significant, $F(5, 62) = 7.90$, $p < .001$, $R^2 = .389$, adjusted $R^2 = .340$. Total Encoding Path negatively predicted Sequential Recall ($\beta = -15.80$, $p = .014$), whereas Total Recall Path positively predicted it ($\beta = 18.40$,

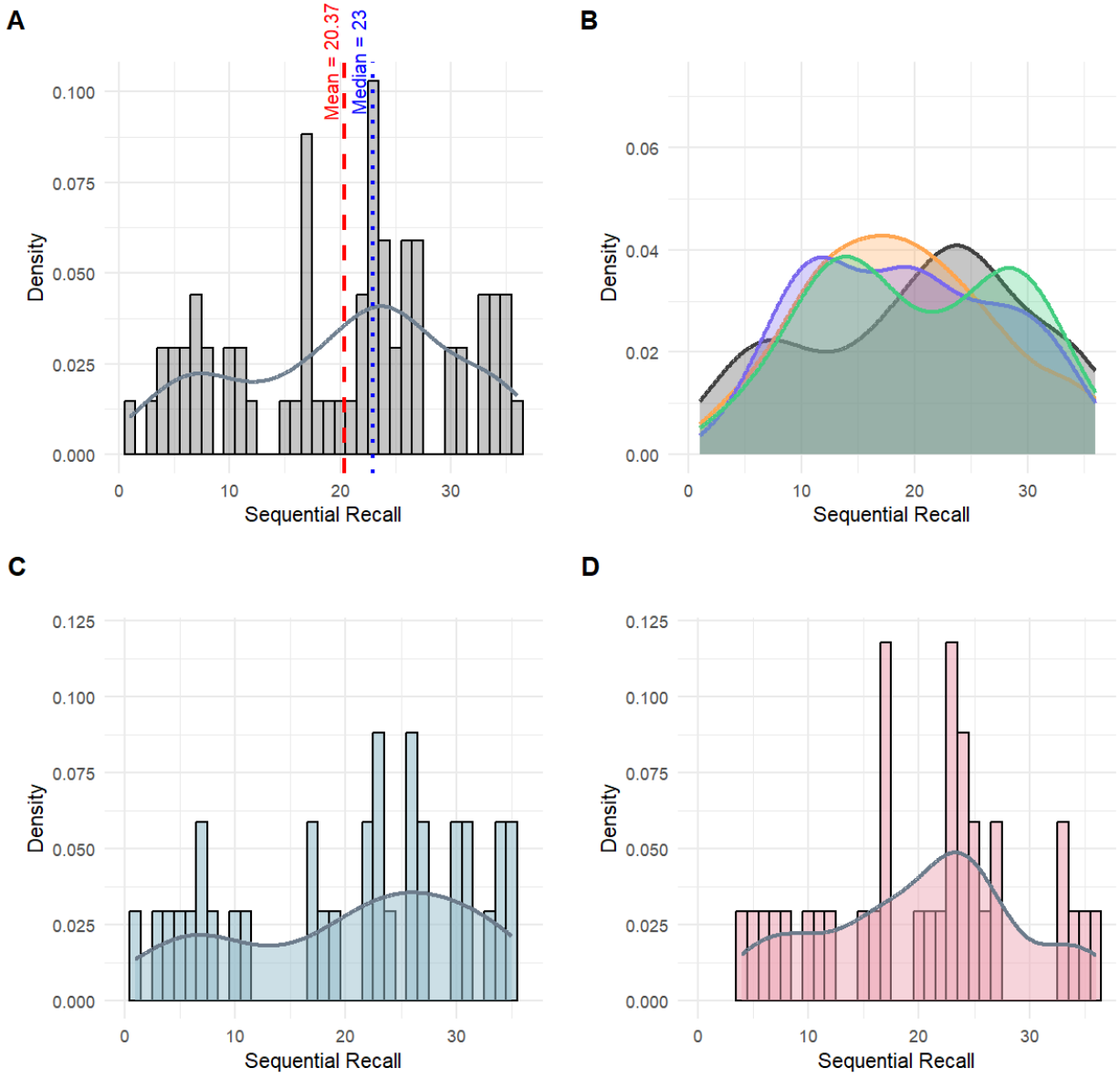


Figure 5.3: Sequential Recall score distributions of A) across participants in the *Flat Landmark* condition and B) in the *Spherical Sparse*, *Spherical Landmark*, *Flat Sparse* and *Flat Landmark* conditions, and C) among males and (D) females in the *Flat Landmark* condition.

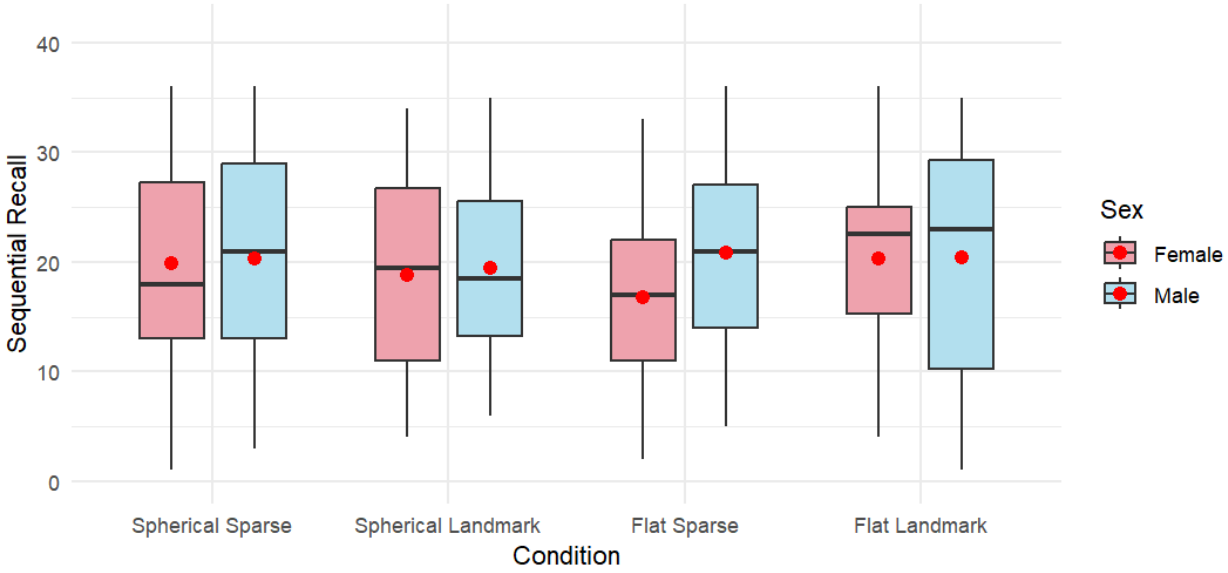


Figure 5.4: Sequential Recall by condition and sex. Although no significant group differences were found in the current permutation-based ANOVA, a significant sex difference in the *Flat Sparse* condition was observed in a previous analysis (see Chapter 2).

$p = .005$). Neither Sex nor the Sex × predictor interactions were significant (largest $|t| = 1.63$, $ps \geq .108$).

5.4.2 Strategy preference

Females abandon non-spatial strategies

There were significant differences in non-spatial strategy use across the four conditions ($\chi^2(3, N = 300) = 39.53,\ p < .001$), with lower non-spatial strategy use observed in conditions with more familiarity (Figure 5.5).

The Fisher's exact test did not yield a statistically significant association between sex and strategy use in the *Flat Landmark* condition, suggesting no evidence of a sex difference in strategy preference. However, a separate Fisher's exact test revealed a significant difference in strategy use between females in the *Flat Landmark* and *Spherical Landmark* conditions ($p < .05$).

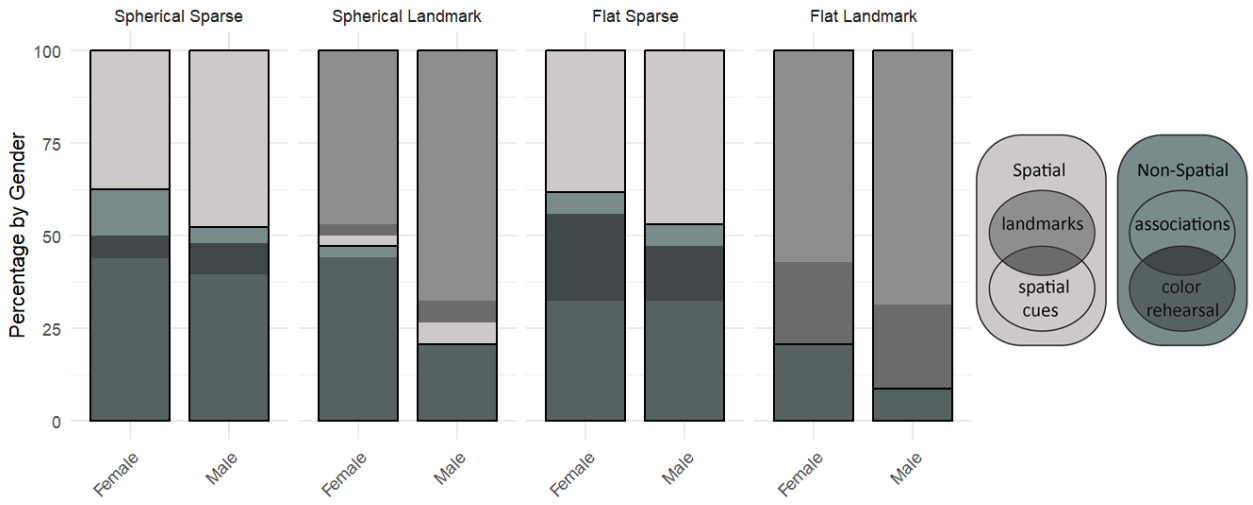


Figure 5.5: Strategy preference by condition and by sex. Participants in the *Flat Landmark* condition showed the strongest preference for spatial strategies (85%), compared to 66% in the *Spherical Landmark*, 42% in the *Flat Sparse*, and 42% in the *Spherical Sparse* conditions.

5.5 Detailed Results

5.5.1 Sequential Recall and strategy preference

Strategy use did not moderate performance

The linear regression model examining the effect of Condition (*Spherical Sparse*, *Spherical Landmark*, *Flat Sparse*, *Flat Landmark*) and Sex on Sequential Recall among participants who employed a spatial strategy, was not significant. There were no significant main effects of Condition, Sex, or significant Condition × Sex interactions.

Although the overall interaction between condition and sex was not significant in this analysis, pairwise comparisons revealed that in the *Flat Sparse* condition, spatial strategy user males (emmean = 21.4, SE = 2.22) tended to outperform spatial strategy user females (emmean = 15.0, SE = 2.46), with the difference approaching statistical significance ($t(164) = -1.93$, $p = .06$). This trend is consistent with the significant sex difference observed in the *Flat Sparse* condition in Chapter 2, where only three conditions were included in the model.

A separate linear regression with non-spatial strategy users was also not significant. No significant pairwise differences were observed between sexes within any condition.



Figure 5.6: Effect of A) spatial strategy and B) non-spatial strategy, on Sequential Recall by Condition and by Sex.

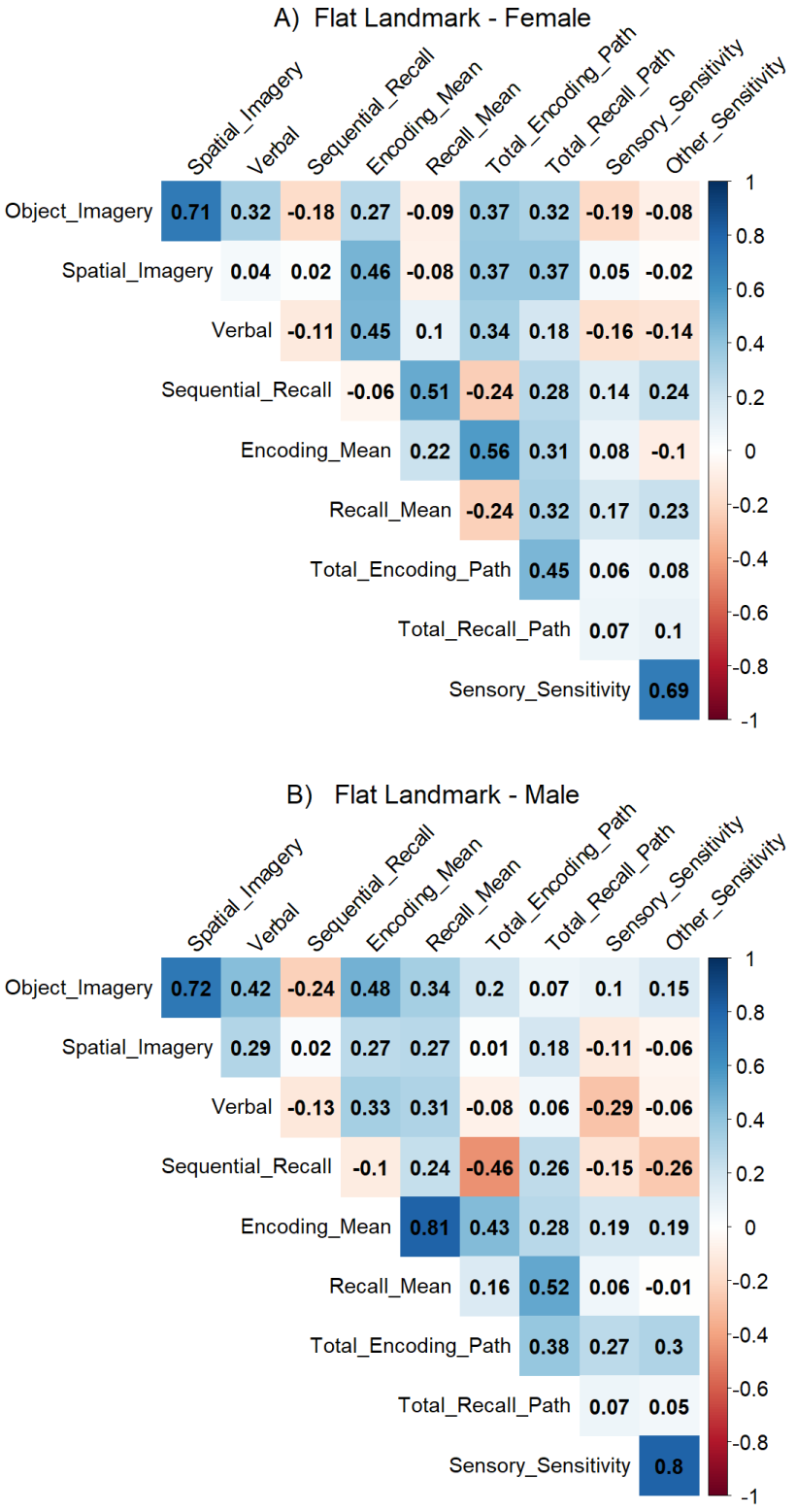


Figure 5.7: Exploratory correlation matrices for the *Flat Landmark* condition by A) females and by B) males.

5.5.2 Cognitive styles and sensory sensitivity

Cognitive traits did not predict Sequential Recall

The multiple regression model predicting Sequential Recall from Object Imagery, Spatial Imagery, verbal scores, sex, and condition (including all interactions) was significant ($F(23, 180) = 2.28$, $p < .01$), explaining approximately 13% of the variance in Sequential Recall (adjusted $R^2 = .13$). Using *Flat Landmark* as the baseline, performance was marginally lower in the *Flat Sparse* condition ($\beta = -3.92$, $p = .06$) and did not differ in the *Spherical Landmark* condition. No main effects were observed for Sex, Object Imagery, Spatial Imagery, or Verbal scores, and no cognitive trait $\times$ Sex, cognitive trait $\times$ Condition, or three-way interactions reached significance.

Sensory sensitivity did not predict Sequential Recall

The multiple regression model predicting Sequential Recall from sensory sensitivity, other sensitivity, sex, and their interactions (predictor $\times$ sex) was not significant. There was, however, a marginal Sex $\times$ Other Sensitivity interaction ($\beta = -3.79$, $p = .08$). All other effects were non-significant.

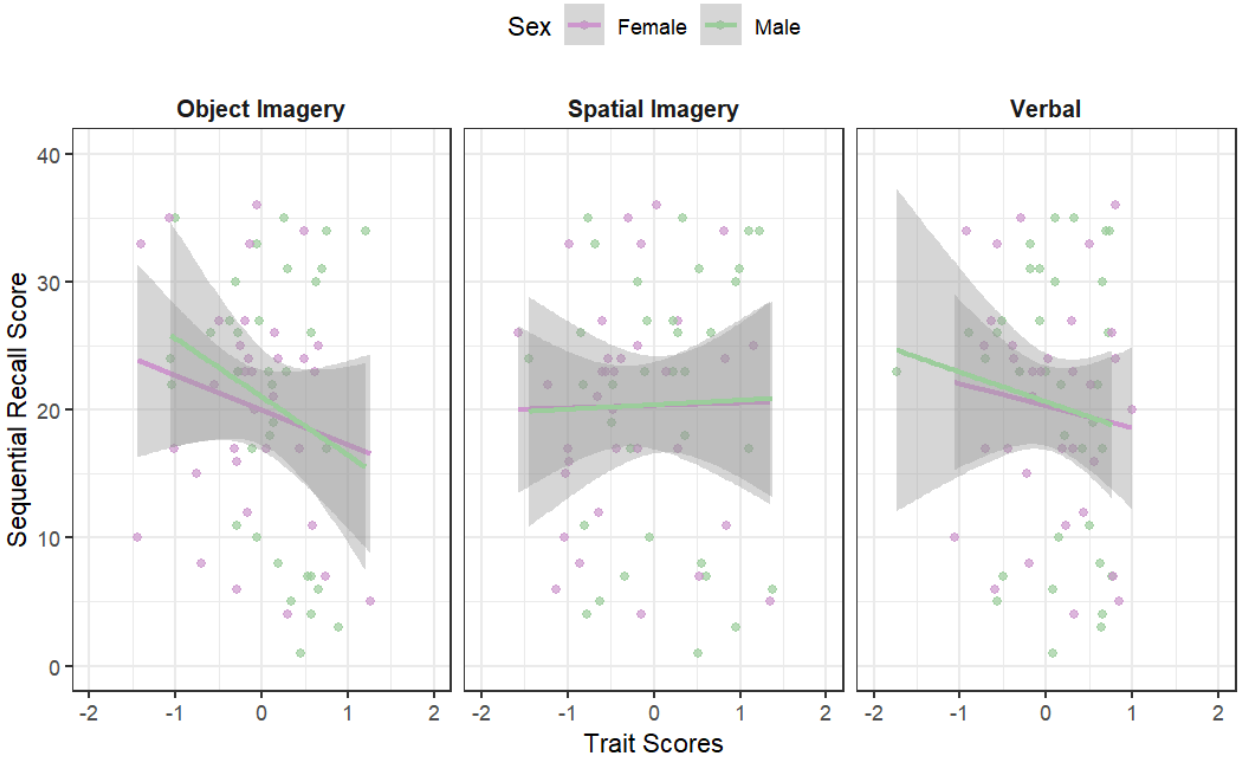


Figure 5.8: Correlations between Sequential Recall scores and cognitive styles in the *Flat Landmark* condition.

5.6 Discussion

The Sequential Recall distributions showed gradual changes across the four stages (*Spherical Sparse*, *Spherical Landmark*, *Flat Sparse*, *Flat Landmark*) of increasing familiarity. In the most unusual, spherical environment without landmarks, performance was bimodally distributed, indicating individual differences rather than sex-dependent patterns. With the introduction of traditional landmarks, the distributions became more multimodal, and in the *Flat Sparse* condition the distributions were roughly normal. The *Flat Landmark* condition also approached a normal form, however, with a rightward shift of the peak, suggesting that the increased plausibility of the environment may have enabled participants to activate more pre-existing spatial knowledge that enhanced their performance. Interestingly, while the form of the distributions evolved across conditions of increased familiarity, average Sequential Recall scores remained similar across environments.

Notably, familiar spatial structure alone did not support female Sequential Recall in the *Flat Sparse* condition, although it substantially influenced strategy use. In the *Spherical*

Landmark condition, on the other hand, despite the presence of traditional landmarks, females still exhibited a roughly equal preference for spatial and non-spatial strategies. In contrast to these two previous conditions, in the *Flat Landmark* condition, 80% of female participants employed a spatial strategy, primarily guided by the traditional landmarks.

We hypothesised that males would outperform females in the *Flat Landmark* condition, as their typical preference for spatial strategies aligned with the experimental condition (i.e., availability of familiar spatial cues). Indeed, strategy reports confirmed that roughly 90% of males relied on a spatial strategy, predominantly using the landmarks. However, despite this consistency in strategy use, male performance was highly variable, more so than that of females. This variability may stem from the increased familiarity of the environment, which likely triggered pre-existing behavioural tendencies and amplified individual differences. Such pattern aligns with the Greater Male Variability Hypothesis, which suggests that males typically show a wider distribution of cognitive abilities, including spatial skills, with more individuals represented at both the high and low ends of performance (Ceci et al., 2009; Lakin, 2013; Feingold, 1992). Alternatively, the greater familiarity may have meant less motivation, for all subjects and in particular for males, to express in full their spatial memory abilities in the task. This is apparent in the left skewed distribution, where a group of participants were clustering at the lower end of Sequential Recall.

Despite previously observed positive associations between Object and Spatial Imagery and Sequential Recall, the *Flat Landmark* condition showed no such trend. Regardless of sex, higher Object Imagery was associated with lower Sequential Recall scores, and a similar (non-significant) tendency was observed for Verbal scores. Spatial Imagery scores showed no association with Sequential Recall. For both sexes, the fitted lines were essentially horizontal, the most striking feature of this condition.

5.7 Conclusion

These findings suggest that once the sequential recall task was adapted into the most familiar and plausible environment, it may have lost the novelty that made earlier conditions particularly revealing. Although the *Flat Landmark* condition confirmed shifts in distributions and changes in strategy use, it led to fewer distinct effects on performance, sex and individual differences, implying that the paradigm's ability to reveal meaningful differences was strongest under less familiar spatial circumstances.

General discussions, conclusions and future directions

6.1 General discussion and conclusion

Across a series of tasks, this thesis demonstrated that sex differences in spatial memory are not universal but emerge selectively, depending on environmental context.

In the opening of this thesis, we proposed to address the challenge of untangling the complexity underlying spatial abilities by introducing an environment designed to minimise reliance on prior experience, biases, and cultural factors: a spatial memory paradigm containing only the bare minimum information needed to navigate and find one's way.

When space is highly unusual and lacks familiar spatial cues, sex differences tend to diminish and individual differences become more apparent, as seen in the spherical sparse condition. Introducing traditional landmarks into this space sustains overall, and across-sex performance, but gives rise to sex-dependent strategy preferences, with spatial strategies dominating among males, as expected. We proposed that the flat space without landmarks would increase spatial plausibility, and indeed, sequential recall distributions shifted from multimodal to roughly Gaussian. In this context, the much anticipated sex difference emerged: males outperformed females. So far, this pattern points to a view that sex-differences are context-dependent and, more precisely, strongly modulated by familiarity.

Hormonal influences likely contribute to these dynamics. Estradiol, progesterone, and testosterone have all been shown to modulate navigation strategies and spatial memory performance in both animals and humans. In rodents and in women, cycle-dependent fluctuations in hormone levels have been associated with variability in spatial memory. In humans, estradiol in particular has been linked to shifts in hippocampal–striatal balance during navigation. Although hormonal status was not measured in the present studies, its potential

role should be acknowledged, not only in the appearance or disappearance of sex differences across contexts, but also in contributing to the substantial variability observed within each sex.

These results also resonate with rodent studies showing sex-dependent reliance on distinct neural circuits during memory consolidation, such as differential engagement of the dorsal hippocampus versus the nucleus reuniens, as demonstrated by Torromino and colleagues (2021). While my paradigm did not include neural measures, their findings highlight that sex differences in performance can arise from differential circuit-level contributions to memory processes. In rodents, causal manipulations of these regions were able to reverse the sex difference, suggesting that what appears behaviourally as a "capacity limit" may reflect underlying neural specialisation, rather than fixed ability differences.

Next, we extended our paradigm with incidental learning to offer a parallel view on sex differences. While participants engaged in the spatial memory task, they were also exposed to task-irrelevant faces or objects, later tested for face/object recognition. Here, too, sex differences appeared selective rather than universal: males occasionally outperformed females, particularly when recognition relied on visual cues, whereas no differences were observed when retrieval depended on verbal descriptions, even though a reverse pattern might have been expected. Similarly, socially salient stimuli, especially famous faces, also had a stronger impact on males than on females.

We then added another layer by considering cognitive styles. Here, sex differences became even more nuanced: they affected not just how strongly imagery abilities related to strategy use, but also the direction of this relationship. Such divergent patterns point to deeper cognitive or even motivational differences in the way males and females approach imagery and spatial reasoning.

The final piece broke our expectations and reintroduced a touch of chaos. We had anticipated that the flat landmark condition would produce the strongest sex differences in this paradigm, with clear links between sequential recall and imagery styles, especially spatial imagery. Instead, males and females performed much the same, they relied on spatial and non-spatial strategies with equal frequency, and spatial imagery scores were entirely unrelated to sequential recall: a perfectly flat line. Has the task lost its charm, and with it, the motivation of the participants?

Thus, as we reintroduced more elements and examined additional perspectives, departing from minimalism just to return back to complexity. Perhaps, we are left with even more questions than at the outset of this thesis.

6.2 From navigation to rotation: a novel mental rotation task

Mental rotation has been demonstrated to show the largest and most consistent sex differences in spatial cognition (Voyer et al., 1995; Linn and Petersen, 1985; Lauer et al., 2015; Collins and Kimura, 1997). While the tasks in this thesis primarily examined spatial memory during navigation, a mental rotation version would allow us to test whether the context-dependent nature of sex differences observed here extends to mental rotation.

Similarly to our original task, the proposed mental rotation paradigm would be based on coloured Platonic solids such as a cube or dodecahedron, with increased symmetry and difficulty for additional cognitive challenge. Here, participant would still rely on the relative positions of the coloured planes as reference points.

The task could be implemented in two forms:

Small-scale, object-based version: participants manipulate and rotate a handheld platonic solid in three dimensions, uncovering coloured faces in a specific sequence. Here, the task resembles a traditional mental rotation problem, but with the added demand of spatial sequential recall of surface colours.

Mid-scale, navigable version: participants navigate directly on the surface of the solid (e.g., jumping across the cube's faces). This would offer a middle ground, between our original task, and a traditional mental rotation task.

In both implementations, after a familiarisation phase, participants would be required to reproduce sequences by moving from one coloured face to another, with each transition between faces counting as a single step. Participants must mentally rotate and align the structure to plan efficient paths across the coloured surfaces, integrating object-based mental rotation with spatial memory for relative positions.

Besides the number of available colours (Cube vs. Dodecahedron), and the length of the sequences, the visibility of the coloured plane that remains constant throughout the task, can further manipulate cognitive demand. For example, in the simple draft (Figure 6.1), two coloured faces remain visible at all times, providing more stable source of spatial information compared to a perspective where only one face is visible at a time.

Based on previous findings, we would expect sex differences to emerge in the small-scale, handheld version, which most closely resembles classical mental rotation tests. By contrast, in the mid-scale navigable version, the presence of embodied, egocentric navigation may attenuate these differences, or even favour females.

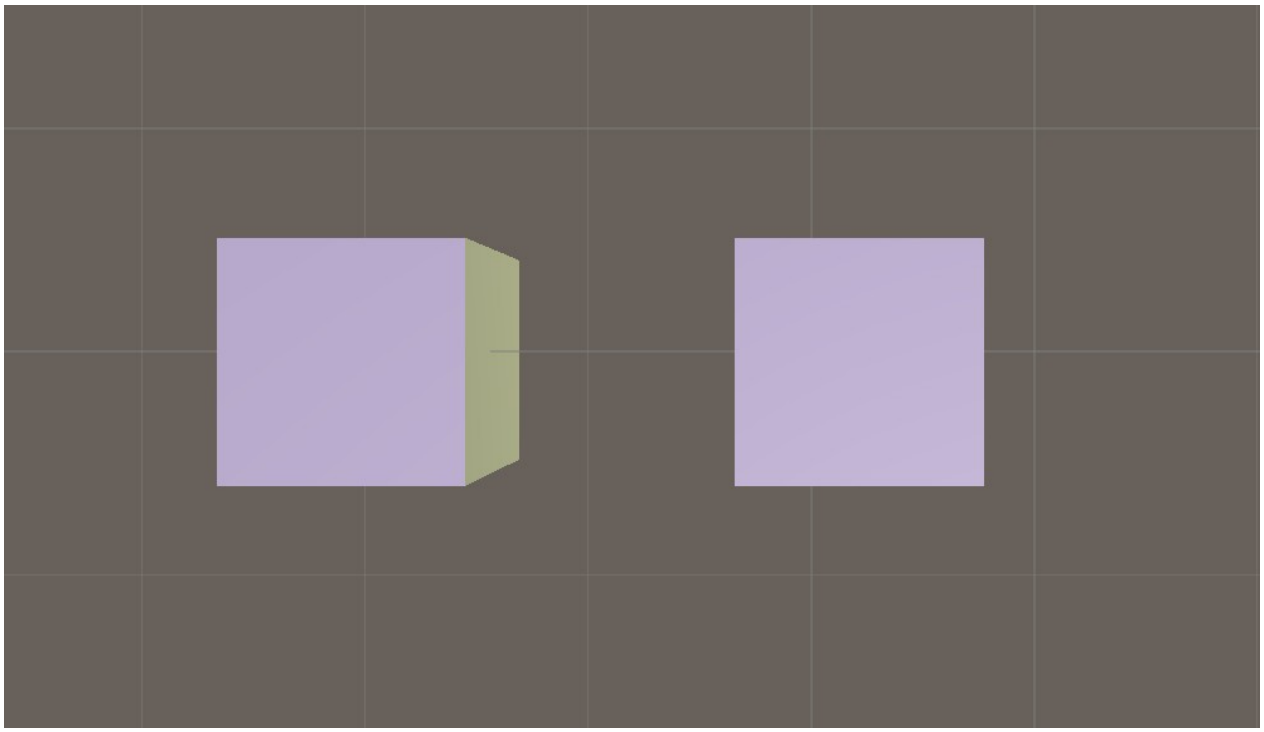


Figure 6.1: Visual manipulation of the cube as basis of the proposed mental rotation task. Depending on perspective, either two plane (left) or one adjacent planes (right) remain visible, altering the availability of spatial reference cues.

Acknowledgements

I would like to express my deepest gratitude to my supervisor, Alessandro Treves, for his patience, support, and understanding throughout my PhD journey. His guidance has been invaluable not only academically but also personally, especially during significant life events. I truly could not have asked for a better supervisor, his mentorship, wisdom, humanity, and humour, make him exceptional in every sense, and I am eternally grateful.

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On that note, I also would like to thank all my little colleagues from the SISSA nursery.

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Above all, I thank my daughter, Ivy, who has been both my anchor and my inspiration. She has given me strength in difficult times, joy in everyday moments, and it is to her that I dedicate this thesis.

Supplementary material for Chapter 2

Table A.1: Regression Results for Sequential Recall from Condition (*Sparse* vs. *Landmark* vs. *Flat*) and Sex in Experiments 1–3.

Condition	**N**	**Estimate (b)**	**SE**	**t-value**	**p-value**
Intercept (Spherical Sparse + Female)	48	19.85	1.26	15.73	$< .001$
Spherical Sparse + Male	48	0.46	1.79	0.26	.798
Spherical Landmark + Female	34	-1.00	1.96	-0.51	.610
Spherical Landmark + Male	34	-0.38	1.96	-0.20	.845
Flat Sparse + Female	34	-3.12	1.92	-1.62	.106
Flat Sparse + Male	34	1.00	1.92	0.52	.604

Note. Regression coefficients (b) represent estimated differences in Sequential Recall scores relative to the reference group (Spherical Sparse + Female). Standard errors (SE), t-values, and p-values are reported. None of the condition comparisons were statistically significant.

Base Strategy Categorization Guidelines

Landmark Any explicit mention of using landmarks qualifies as a Landmark strategy, regardless of additional strategies reported (e.g., "I have used sometimes colours, sometimes the little objects").

Rehearsal Classified as a rehearsal strategy if participants explicitly state they repeated the colours (e.g., "I kept repeating the colours to remember them"). Also included if the participant mentions focusing on colours without specifying repetition or any other strategy (e.g., "I just tried to remember the colours where the balls were"). Not considered rehearsal if the use of colour is mentioned alongside another strategy (e.g., "Memorized the colours on the first one, then the directions, like up, left, diagonal"), since some use of colour is inherent to the task.

Association Includes responses where participants assigned meaning or labels to colour combinations (e.g., "I called white, brown and red 'ice cream cone'—vanilla, chocolate, strawberry") or linked them to familiar concepts (e.g., "I gave names to each set of three colours").

Spatial Any report indicating spatial reasoning, such as turns, angles, direction, or relational cues (e.g., "I tried to remember my starting point and which path I followed," or "I focused on the spatial relation between colours or their pattern").

Table A.2: Regression Results for Sequential Recall of participants who employed a spatial strategy, from Condition (*Sparse* vs. *Landmark* vs. *Flat*) and Sex in Experiment 1, 2 & 3.

Condition	**N**	**Estimate (b)**	**SE**	**t-value**	**p-value**
Intercept (Spherical Sparse + Female)	18	19.50	1.88	10.36	$< .001$
Spherical Sparse + Male	22	-2.59	2.54	-1.02	.310
Spherical Landmark + Female	18	0.67	2.66	0.25	.803
Spherical Landmark + Male	27	0.54	2.43	0.22	.825
Flat Sparse + Female	13	-4.50	2.91	-1.55	.124
Flat Sparse + Male	16	1.88	2.74	0.68	.496

Note. Regression coefficients (b) represent estimated differences in Sequential Recall scores relative to the reference group (Spherical Sparse + Female). Standard errors (SE), t-values, and p-values ($Pr > |t|$) are reported for each condition. None of the condition comparisons were statistically significant.

Table A.3: Regression Results for Sequential Recall of participants who employed a non-spatial strategy, from Condition (*Sparse* vs. *Landmark* vs. *Flat*) and Sex in Experiment 1, 2 & 3.

Condition	**N**	**Estimate (b)**	**SE**	**t-value**	**p-value**
Intercept (Spherical Sparse + Female)	26	20.07	1.64	12.20	$< .001$
Spherical Sparse + Male	30	3.13	2.41	1.30	.198
Spherical Landmark + Female	16	-2.69	2.79	-0.97	.336
Spherical Landmark + Male	7	-2.78	3.78	-0.74	.463
Flat Sparse + Female	21	-2.26	2.56	-0.88	.380
Flat Sparse + Male	18	0.32	2.68	0.12	.905

Note. Regression coefficients (b) represent estimated differences in Sequential Recall scores relative to the reference group (Spherical Sparse + Female). Standard errors (SE), t-values, and p-values ($Pr > |t|$) are reported for each condition. None of the condition comparisons were statistically significant.

Supplementary material for Chapter 3

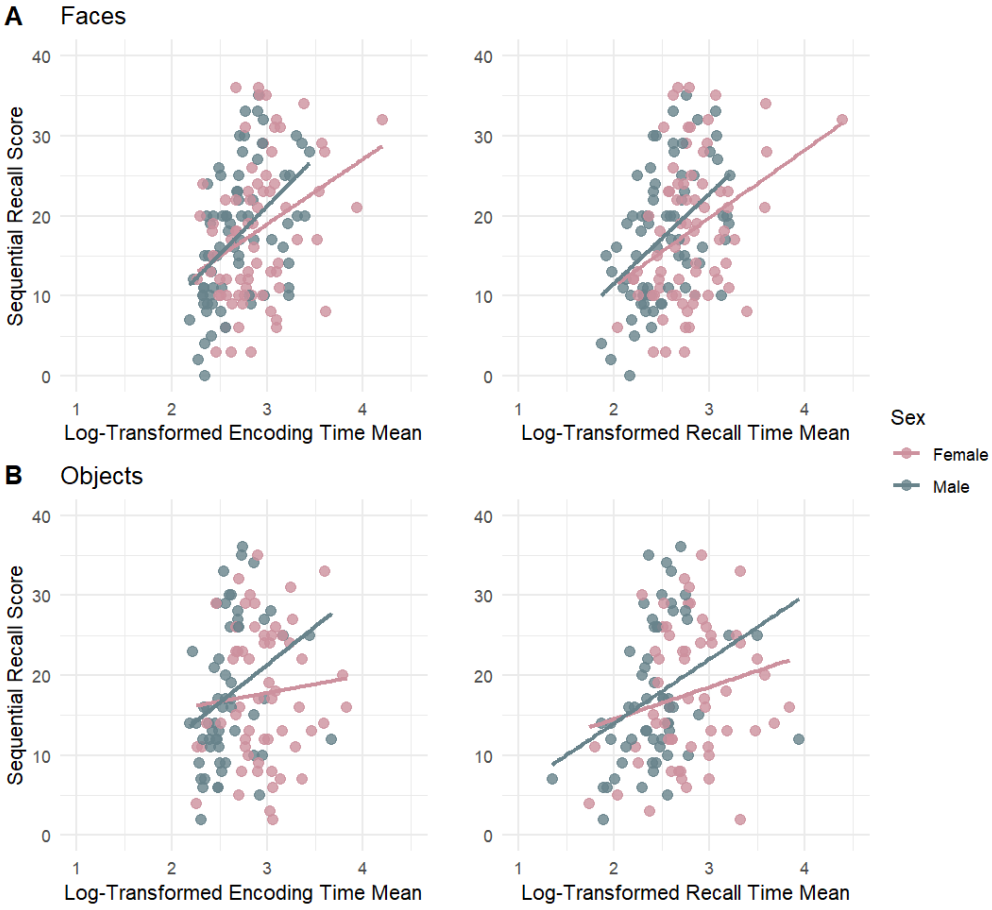


Figure A.1: Correlations between encoding means and Sequential Recall, and between recall means and Sequential Recall, across conditions (*Face*, *Object*) and for males and females.

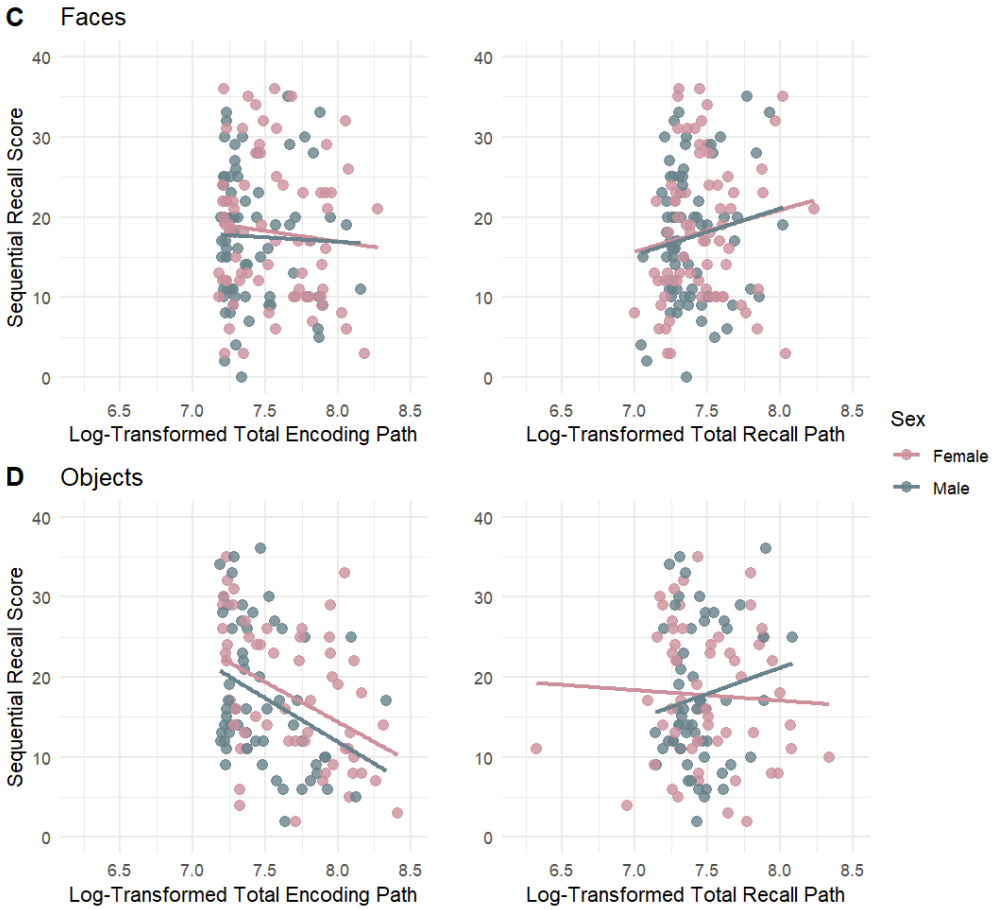


Figure A.2: Correlations between total encoding path and Sequential Recall, and between total recall path and Sequential Recall, across conditions (*Face*, *Object*) and for males and females.

Supplementary material for Chapter 4

A.0.1 Exploratory correlations

Exploratory Pearson correlations between the three cognitive styles (Object Imagery, Spatial Imagery, and Verbal scores) and performance measures from the original memory for trajectories task (Sequential Recall, Encoding Mean, Recall Mean, Total Encoding Path, and Total Recall Path), and sensory sensitivity measures (Sensory Sensitivity, Other Sensitivity), by Condition and by Sex, are presented in Figure A.1 for the *Spherical Landmark* condition and in Figure A.2for the *Flat Sparse* condition.

Exploratory Pearson correlations between cognitive styles, performance measures from the original memory for trajectories task, sensory sensitivity measures, and performance in the incidental learning paradigm, as measured by Recognition and Rejection accuracy scores, are displayed in Figure A.3 for the *Famous Face* condition and in Figure A.4for the *Object (Verbal)* condition.

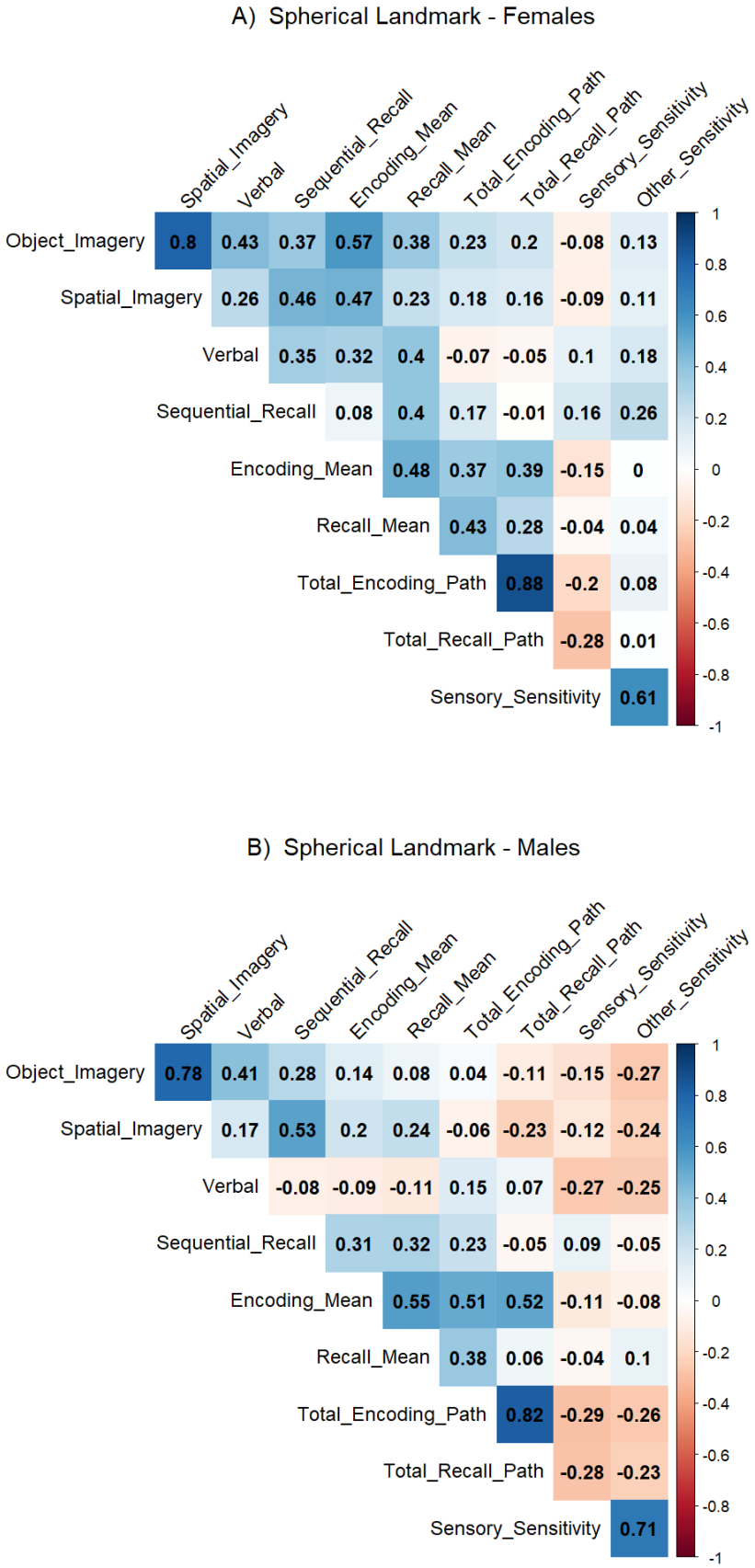


Figure A.1: Exploratory Pearson correlation matrices for the *Spherical Landmark* condition, by A) females and B) males.

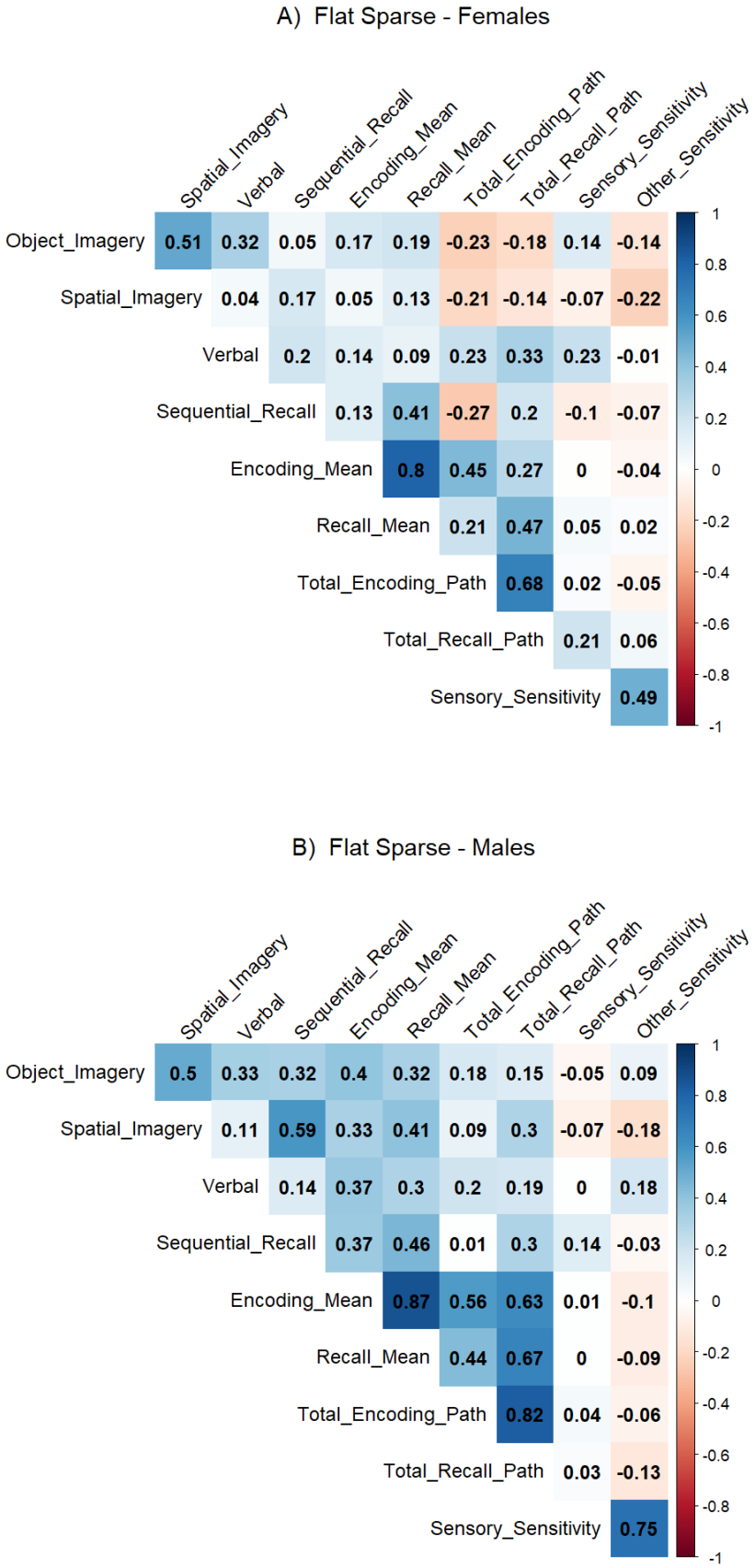


Figure A.2: Exploratory Pearson correlation matrices for the *Flat Sparse* condition, by A) females and B) males.

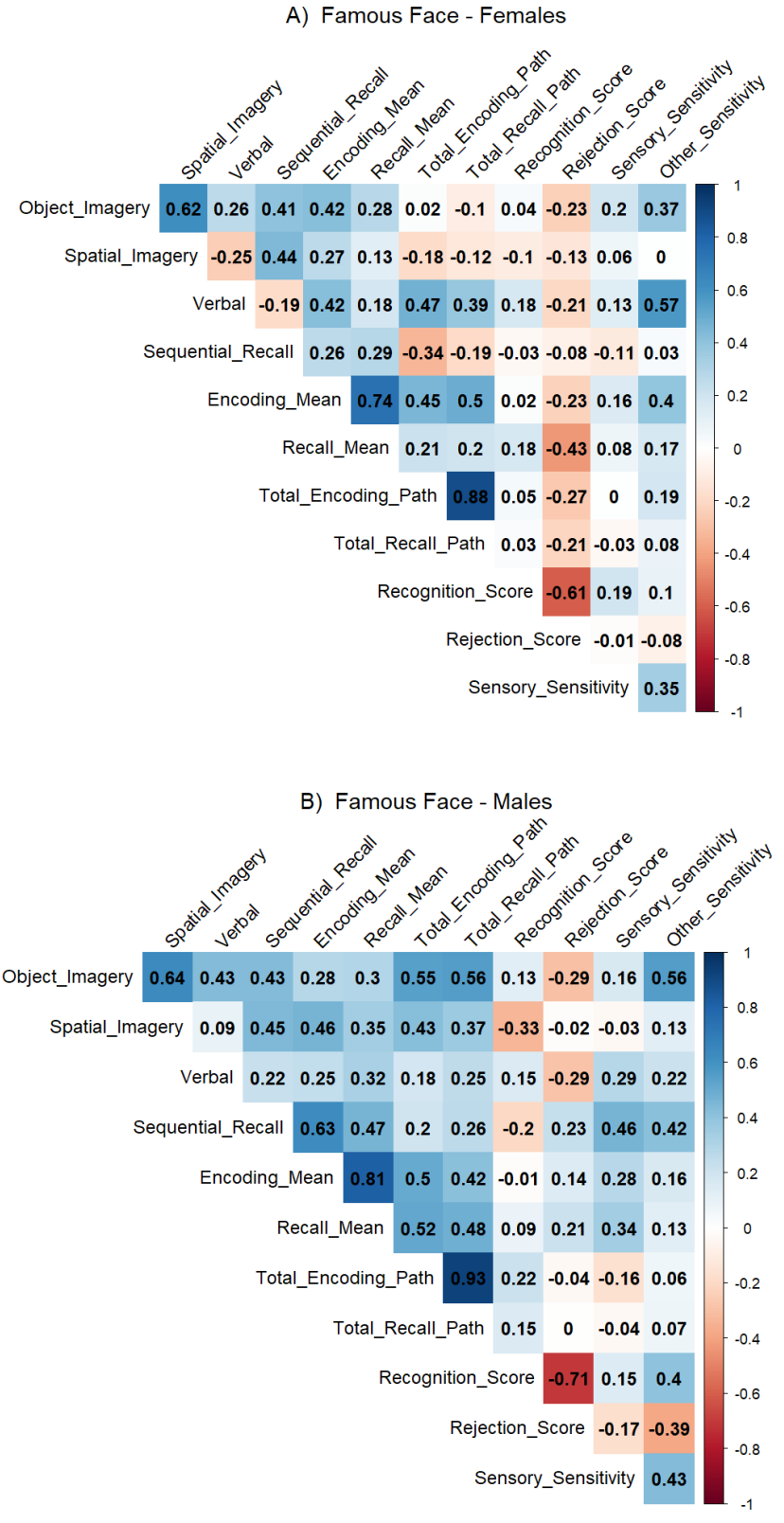


Figure A.3: Exploratory Pearson correlation matrices for the *Famous Face* condition, by A) females (n = 27) and B) males (n = 23).

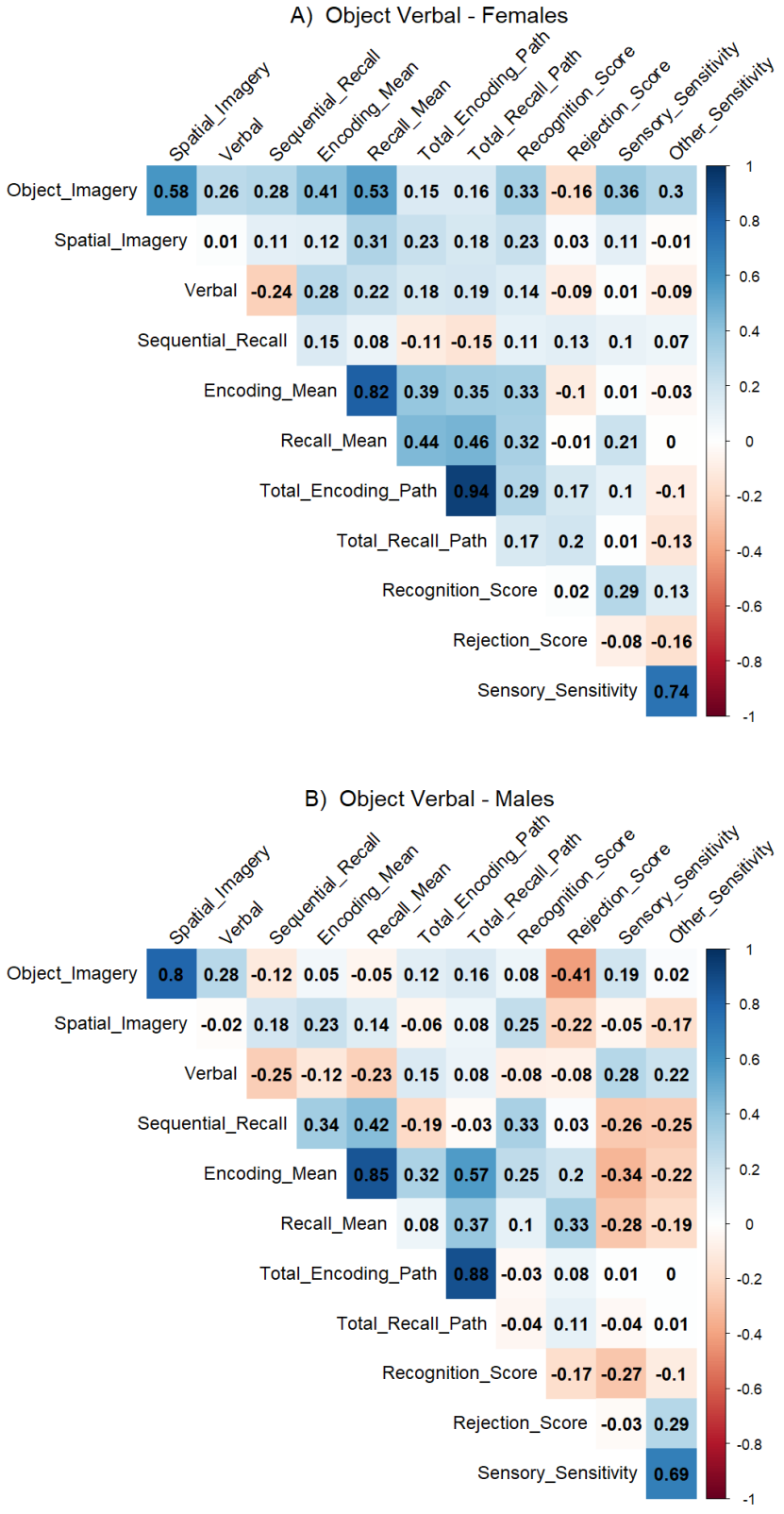


Figure A.4: Exploratory Pearson correlation matrices for the *Object (Verbal)* condition, by A) females and B) males.

A.0.2 Cognitive styles by condition and sex

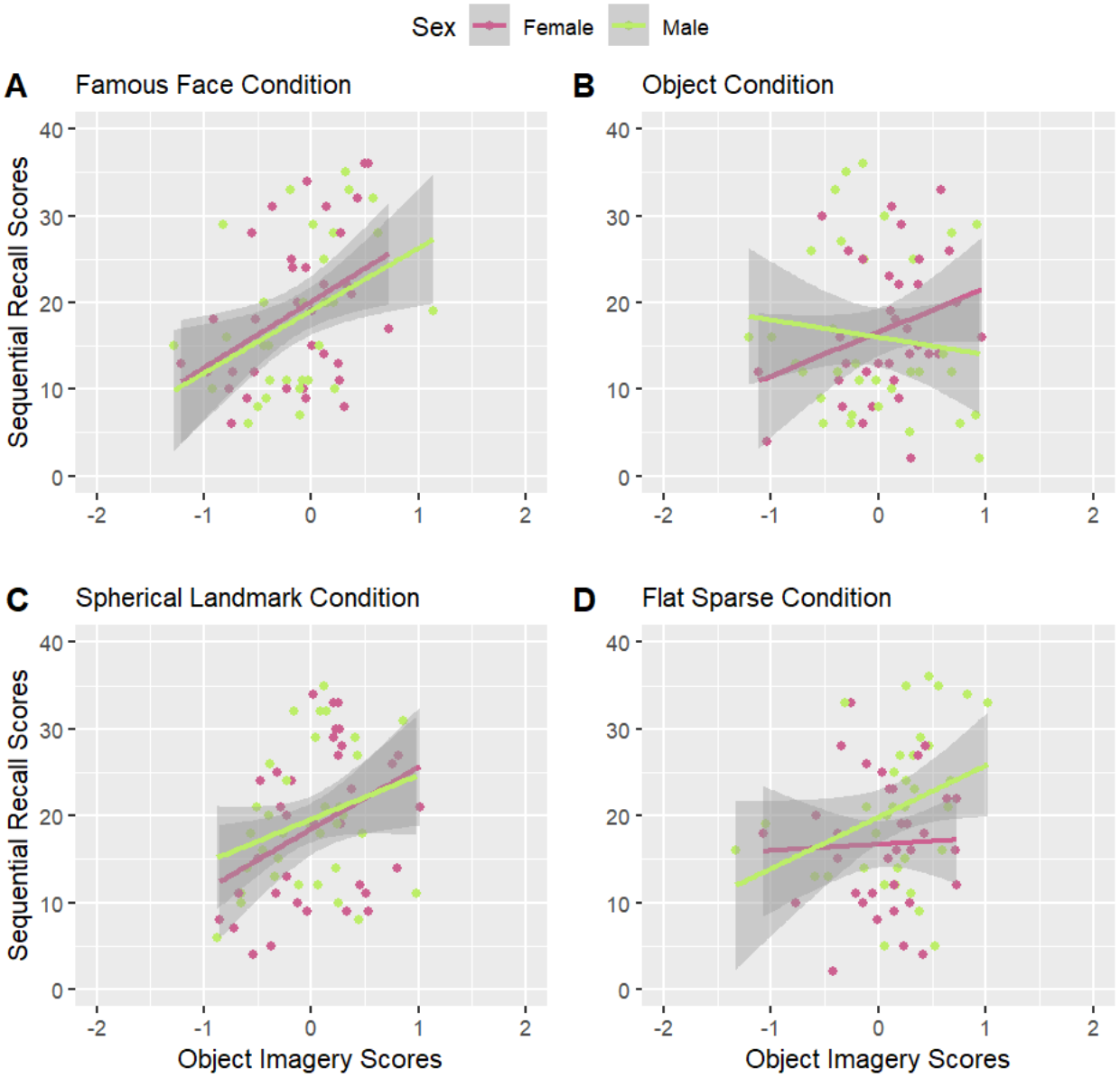


Figure A.5: Scatterplot displaying the relationship between Object Imagery scores and Sequential Recall performance, split by sex and condition. Here and in similar plots, linear regression lines were fitted within each subgroup to visualise trends.

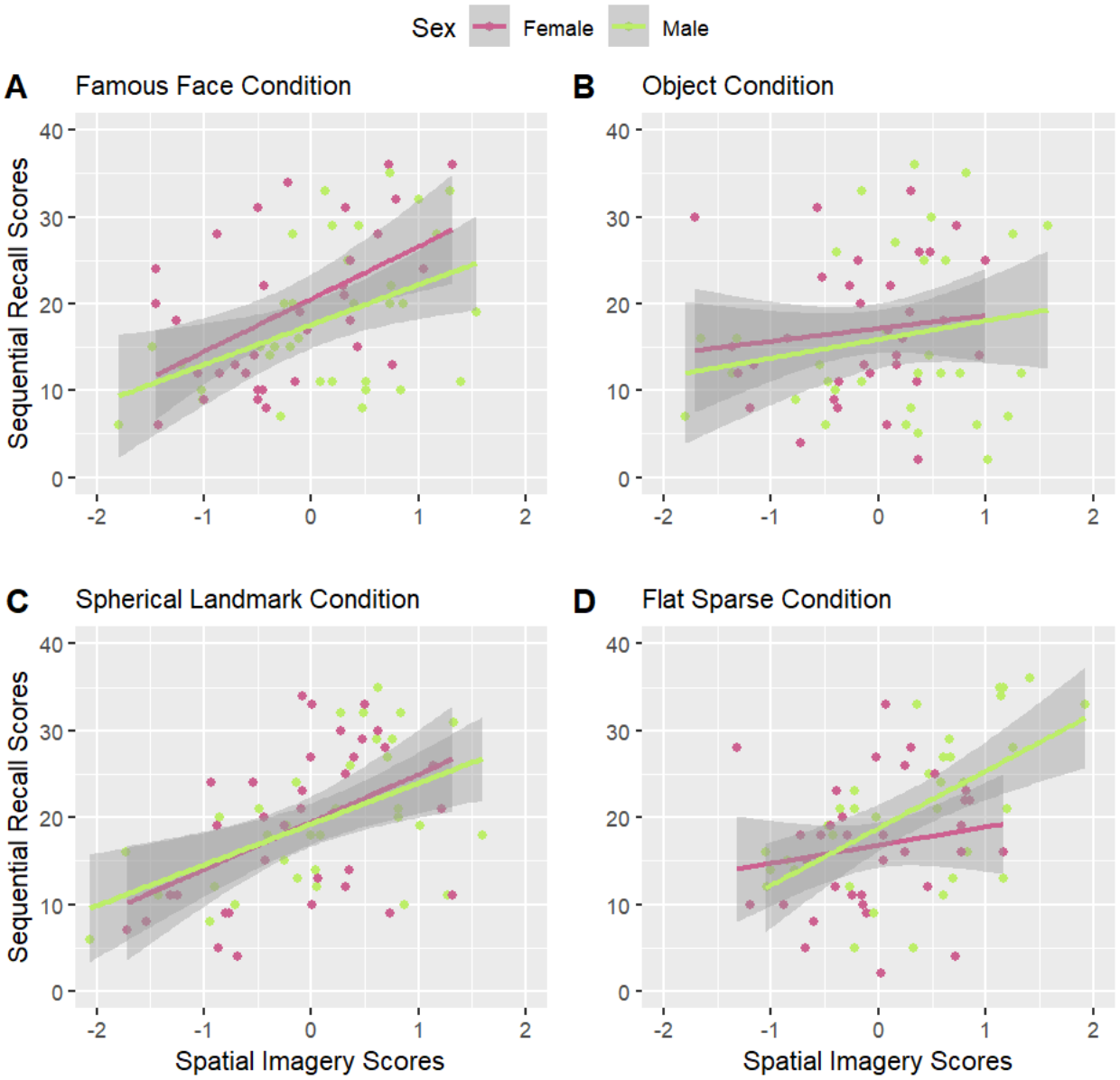


Figure A.6: Scatterplot displaying the relationship between Spatial Imagery scores and Sequential Recall performance, split by sex and condition.

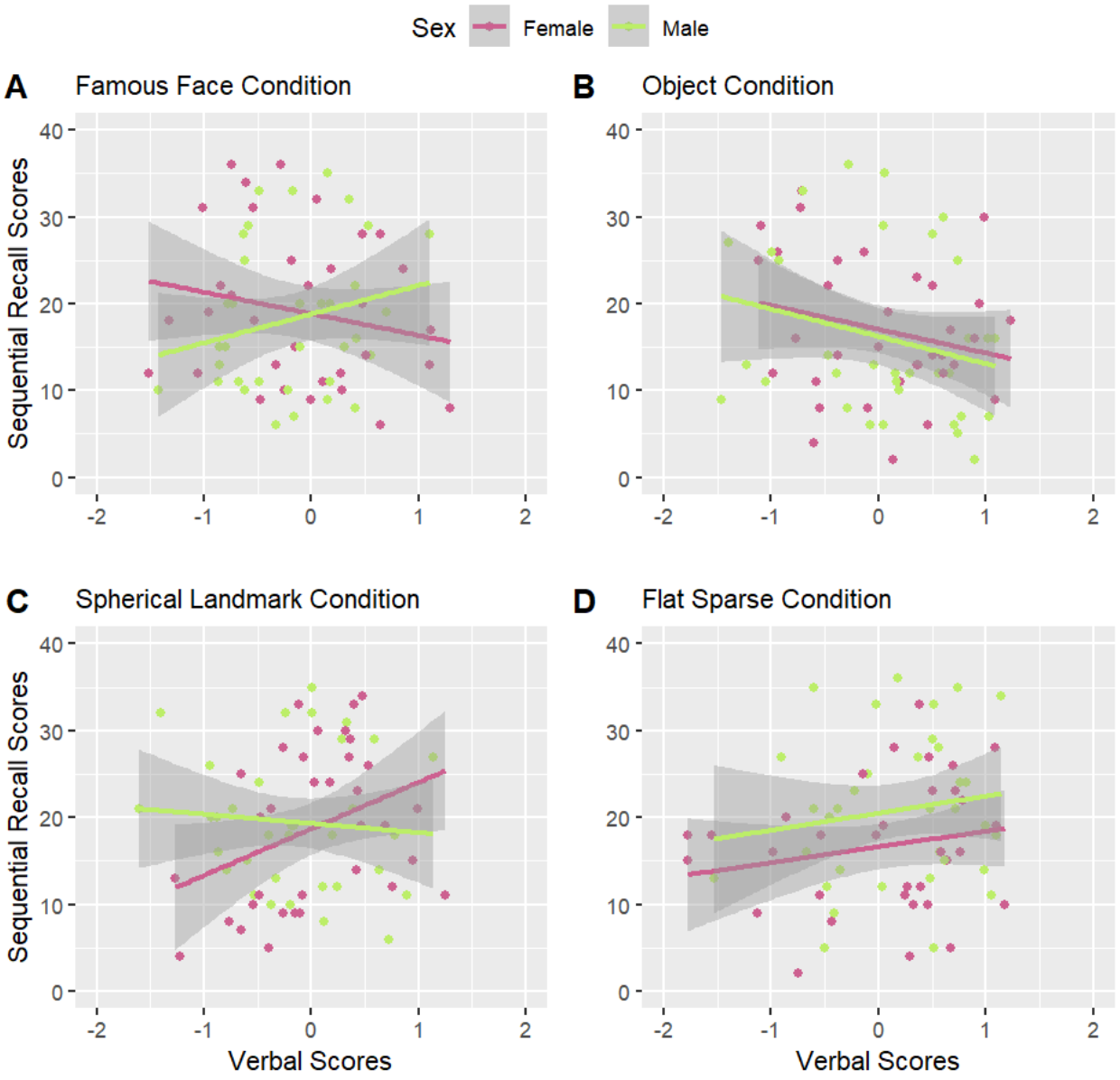


Figure A.7: Scatterplot displaying the relationship between Verbal scores and Sequential Recall performance, split by sex and condition.

A.0.3 Cognitive styles by condition, sex, and strategy preference

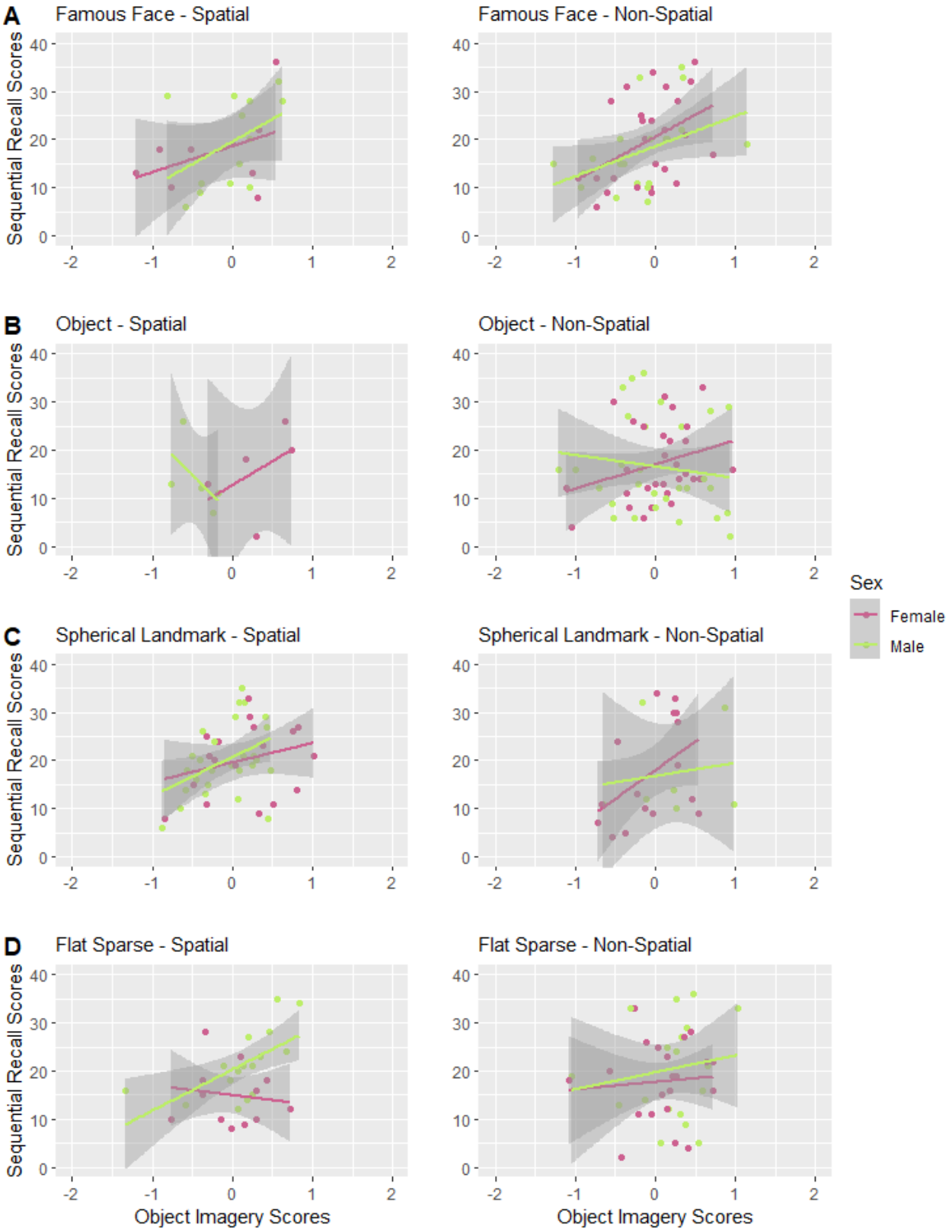


Figure A.8: Exploratory scatterplot illustrating the relationship between Object Imagery scores and Sequential Recall performance, split by sex, condition, and strategy preference

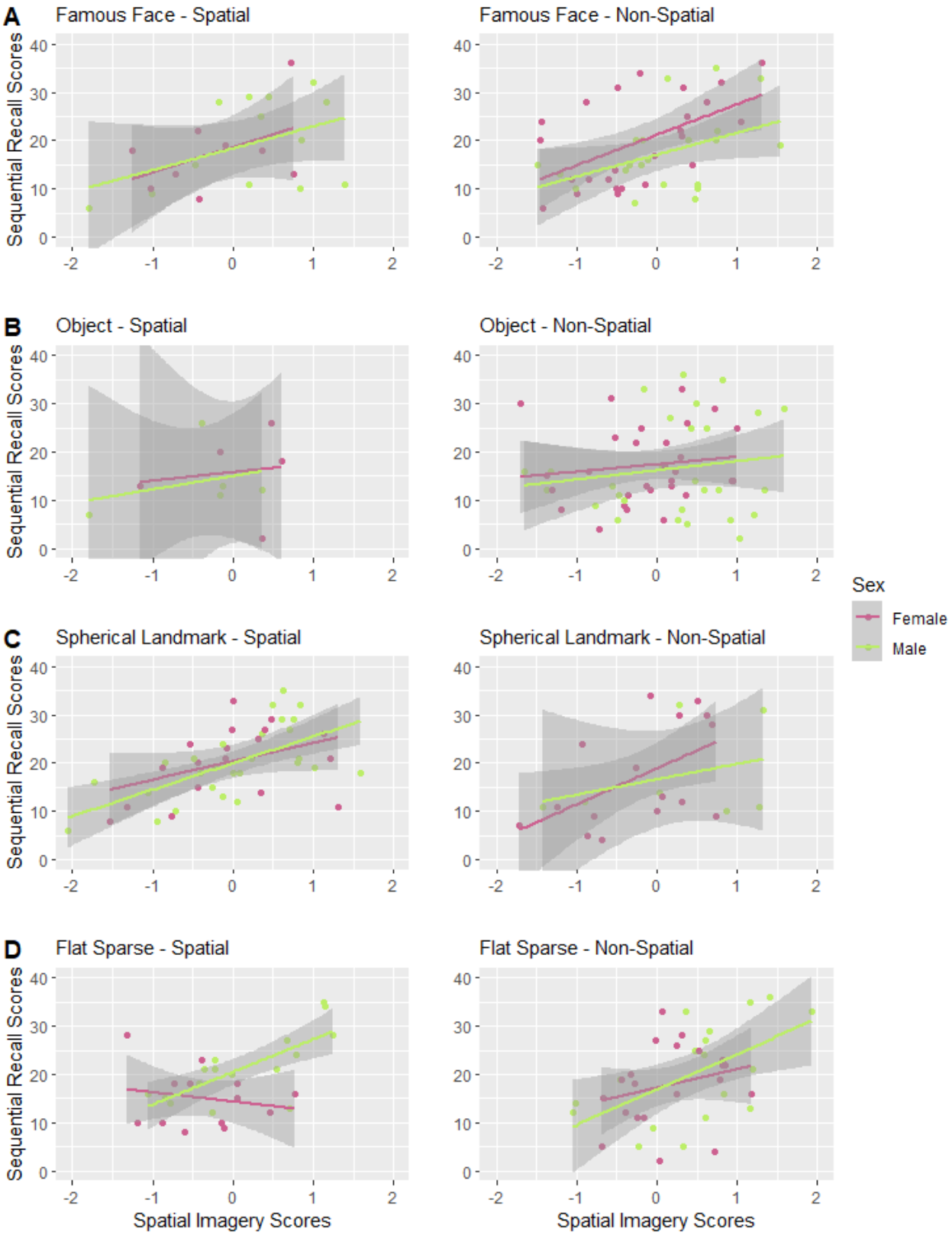


Figure A.9: Exploratory scatterplot illustrating the relationship between Spatial Imagery scores and Sequential Recall performance, split by sex, condition, and strategy preference (spatial vs. non-spatial).

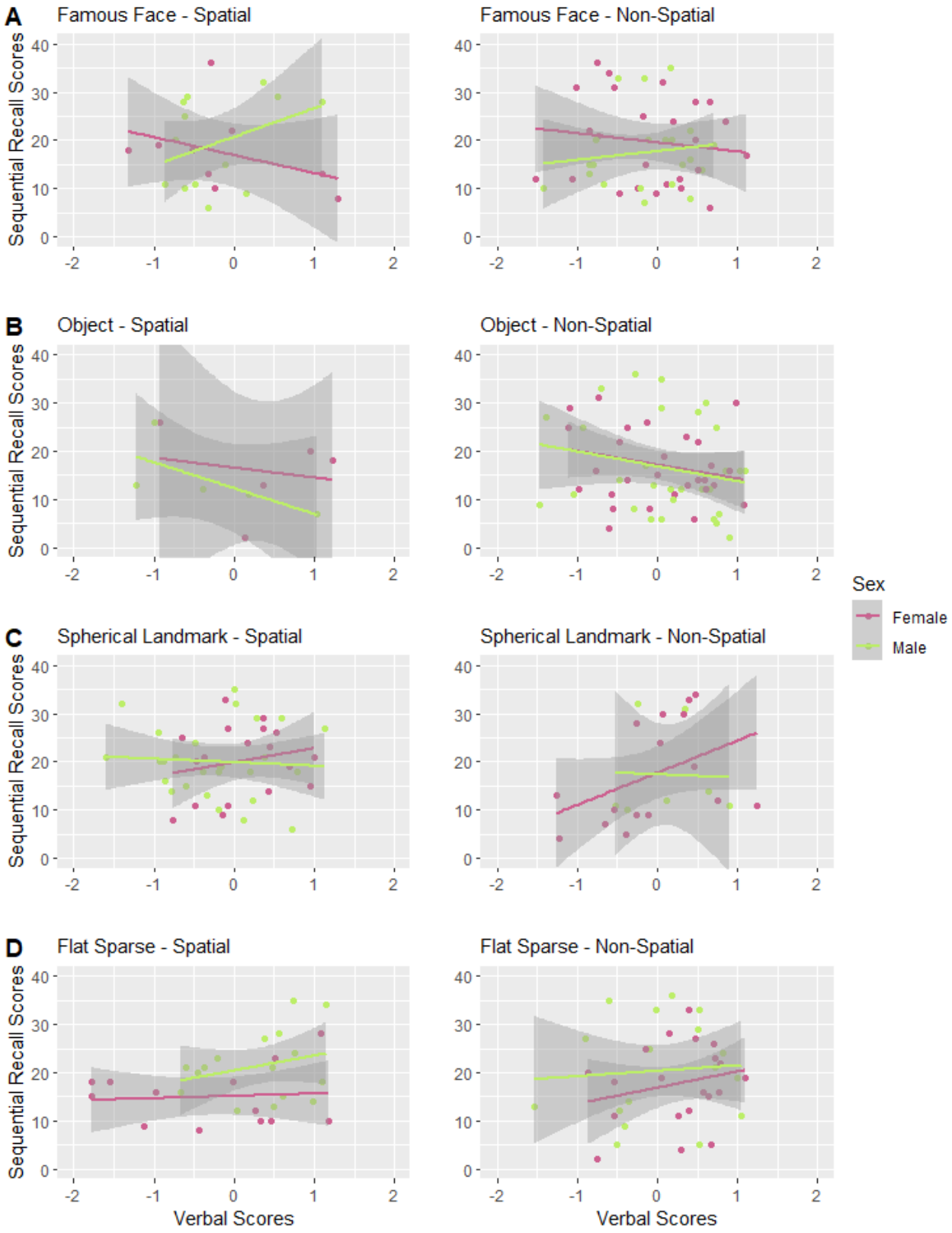


Figure A.10: Exploratory scatterplot illustrating the relationship between Verbal scores and Sequential Recall performance, split by sex, condition, and strategy preference (spatial vs. non-spatial).

A.0.4 Sequential Recall and sensory sensitivity by condition and sex

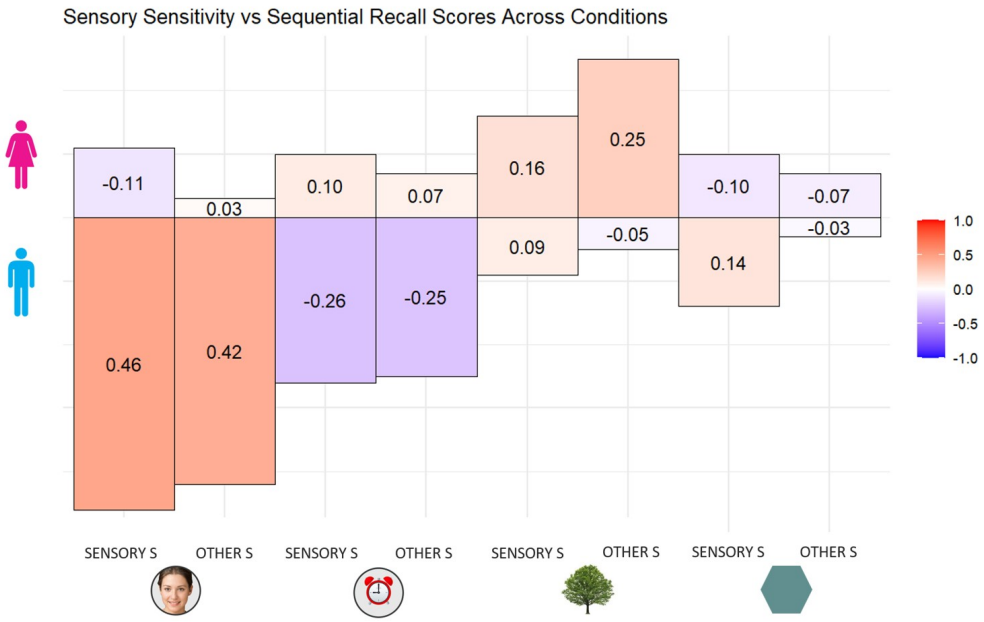


Figure A.11: Exploratory correlations of sensory sensitivity measures with Sequential Recall, shown separately for each condition (*Face*, *Object*, *Spherical Landmark*, *Flat Sparse*) and for males and females.

Supplementary material for Chapter 5

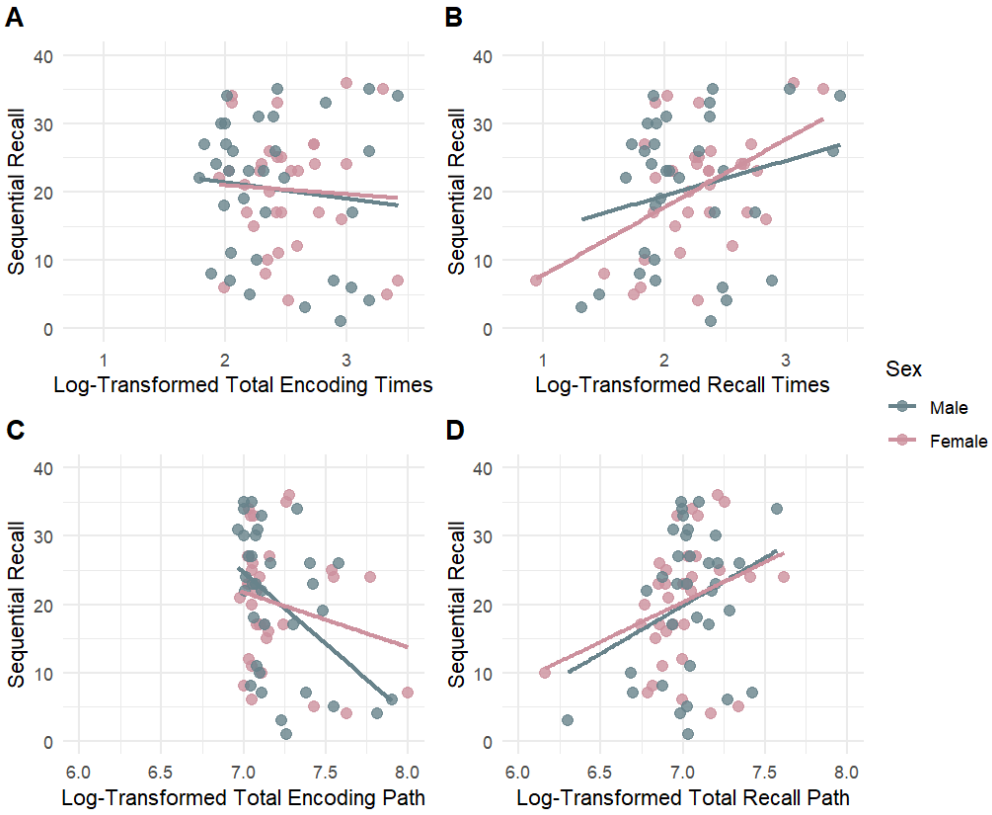


Figure A.1: Correlations between encoding and recall means and Sequential Recall, and between total encoding and recall paths and Sequential Recall, for males and females in the *Flat Landmark* condition.

Bibliography

E.M. Aminoff, S. Freeman, D. Clewett, C. Tipper, A. Frithsen, A. Johnson, S.T. Grafton, and M.B. Miller. Maintaining a cautious state of mind during a recognition test: A large-scale fmri study. *Neuropsychologia*, 67:132–147, 2015. ISSN 0028-3932. doi: https://doi.org/10.1016/j.neuropsychologia.2014.12.011. URL https://www.sciencedirect.com/science/article/pii/S0028393214004655.

Nicolas E. Andersen, Louisa Dahmani, Kyoko Konishi, and Véronique D. Bohbot. Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory*, 97(1):81–89, January 2012. ISSN 1074-7427. doi: 10.1016/j.nlm.2011.09.007. URL http://dx.doi.org/10.1016/j.nlm.2011.09.007.

Sebastian O. Andersson, Edvard I. Moser, and May-Britt Moser. Visual stimulus features that elicit activity in object-vector cells. *Communications Biology*, 4(1), October 2021. ISSN 2399-3642. doi: 10.1038/s42003-021-02727-5. URL http://dx.doi.org/10.1038/s42003-021-02727-5.

Joseph M. Andreano and Larry Cahill. Sex influences on the neurobiology of learning and memory. *Learning amp; Memory*, 16(4):248–266, March 2009. ISSN 1549-5485. doi: 10.1101/lm.918309. URL http://dx.doi.org/10.1101/lm.918309.

Elaine N. Aron and Arthur Aron. Sensory-processing sensitivity and its relation to introversion and emotionality. *Journal of Personality and Social Psychology*, 73(2):345–368, 1997. ISSN 0022-3514. doi: 10.1037/0022-3514.73.2.345. URL http://dx.doi.org/10.1037/0022-3514.73.2.345.

Robert S Astur, Maria L Ortiz, and Robert J Sutherland. A characterization of performance by men and women in a virtual morris water task:. *Behavioural Brain Research*, 93(1–2):185–190, June 1998. ISSN 0166-4328. doi: 10.1016/s0166-4328(98)00019-9. URL http://dx.doi.org/10.1016/s0166-4328(98)00019-9.

Alan Baddeley, Michael W. Eysenck, and Michael C. Anderson. *Memory*. Psychology Press, Hove, UK, 2nd edition, 2014. ISBN 978-1-84872-183-0.

C. Barry, C. Lever, R. Hayman, T. Hartley, S. Burton, J. O'Keefe, K. Jeffery, and . Burgess. The boundary vector cell model of place cell firing and spatial memory. *Reviews in the Neurosciences*, 17(1–2), January 2006. ISSN 0334-1763. doi: 10.1515/revneuro.2006.17.1-2.71. URL http://dx.doi.org/10.1515/revneuro.2006.17.1-2.71.

Caswell Barry, Robin Hayman, Neil Burgess, and Kathryn J Jeffery. Experience-dependent rescaling of entorhinal grids. *Nature Neuroscience*, 10(6):682–684, May 2007. ISSN 1546-1726. doi: 10.1038/nn1905. URL http://dx.doi.org/10.1038/nn1905.

Tristan Baumann and Hanspeter A. Mallot. Metric information in cognitive maps: Euclidean embedding of non-euclidean environments. *PLOS Computational Biology*, 19(12):e1011748, December 2023. ISSN 1553-7358. doi: 10.1371/journal.pcbi.1011748. URL http://dx.doi.org/10.1371/journal.pcbi.1011748.

John W. Berry. Temne and eskimo perceptual skills. *International Journal of Psychology*, 1(3):207–229, January 1966. ISSN 1464-066X. doi: 10.1080/00207596608247156. URL http://dx.doi.org/10.1080/00207596608247156.

Chris M. Bird and Neil Burgess. The hippocampus and memory: insights from spatial processing. *Nature Reviews Neuroscience*, 9(3):182–194, March 2008. ISSN 1471-0048. doi: 10.1038/nrn2335. URL http://dx.doi.org/10.1038/nrn2335.

T. L. Bjerknes, E. I. Moser, and M.-B. Moser. Representation of geometric borders in the developing rat. *Neuron*, 82(1):71–78, 2014. doi: 10.1016/j.neuron.2014.02.010.

Torill L. Bjerknes, Rosamund F. Langston, Ingrid U. Kruge, Edvard I. Moser, and May-Britt Moser. Coherence among head direction cells before eye opening in rat pups. *Current Biology*, 25(1):103–108, 2015. doi: 10.1016/j.cub.2014.11.009. URL https://doi.org/10.1016/j.cub.2014.11.009.

Olesya Blazhenkova and Maria Kozhevnikov. The new object-spatial-verbal cognitive style model: Theory and measurement. *Applied Cognitive Psychology*, 23(5):638–663, May 2008. ISSN 1099-0720. doi: 10.1002/acp.1473. URL http://dx.doi.org/10.1002/acp.1473.

Charlotte N Boccara, Francesca Sargolini, Veslemøy Hult Thoresen, Trygve Solstad, Menno P Witter, Edvard I Moser, and May-Britt Moser. Grid cells in pre- and parasubiculum. *Nature Neuroscience*, 13(8):987–994, July 2010. ISSN 1546-1726. doi: 10.1038/nn.2602. URL http://dx.doi.org/10.1038/nn.2602.

Charlotte N. Boccara, Michele Nardin, Federico Stella, Joseph O'Neill, and Jozsef Csicsvari. The entorhinal cognitive map is attracted to goals. *Science*, 363(6434):1443–1447, March 2019. ISSN 1095-9203. doi: 10.1126/science.aav4837. URL `http://dx.doi.org/10.1126/science.aav4837`.

A. Mike Burton and Rob Jenkins. Unfamiliar face perception. In Andrew Calder, Gillian Rhodes, Mark Johnson, and James Haxby, editors, *The Oxford Handbook of Face Perception*, pages 287–306. Oxford University Press, Oxford, UK, 2011. ISBN 978-0-19-955905-3.

Elizabeth Cashdan and Steven J. C. Gaulin. Why go there? evolution of mobility and spatial cognition in women and men: An introduction to the special issue. *Human Nature*, 27(1):1–15, January 2016. ISSN 1936-4776. doi: 10.1007/s12110-015-9253-4. URL `http://dx.doi.org/10.1007/s12110-015-9253-4`.

Elizabeth Cashdan, Frank W. Marlowe, Alyssa Crittenden, Claire Porter, and Brian M. Wood. Sex differences in spatial cognition among hadza foragers. *Evolution and Human Behavior*, 33(4):274–284, July 2012. ISSN 1090-5138. doi: 10.1016/j.evolhumbehav.2011.10.005. URL `http://dx.doi.org/10.1016/j.evolhumbehav.2011.10.005`.

Daniel A. Casiere and Nancy L. Ashton. Eyewitness accuracy and gender. *Perceptual and Motor Skills*, 83(3):914–914, December 1996. ISSN 1558-688X. doi: 10.2466/pms.1996.83.3.914. URL `http://dx.doi.org/10.2466/pms.1996.83.3.914`.

Stephen J. Ceci, Wendy M. Williams, and Susan M. Barnett. Women's underrepresentation in science: Sociocultural and biological considerations. *Psychological Bulletin*, 135(2):218–261, 2009. ISSN 0033-2909. doi: 10.1037/a0014412. URL `http://dx.doi.org/10.1037/a0014412`.

Christopher F. Chabris, Trond E. Jerde, Anita W. Woolley, Margaret E. Gerbasi, Jon P. Schuldt, Sarah L. Bennett, J. Richard Hackmann, and Stephen M. Kosslyn. Spatial and object visualization cognitive styles: Validation studies in 3800 individuals. Technical Report Technical Report #2, Group Brain Project, 2006. URL `http://chabris.com/Chabris2006d.pdf`.

Karen Chipman and Doreen Kimura. An investigation of sex differences on incidental memory for verbal and pictorial material. *Learning and Individual Differences*, 10(4):259–272, January 1998. ISSN 1041-6080. doi: 10.1016/s1041-6080(99)80122-8. URL `http://dx.doi.org/10.1016/S1041-6080(99)80122-8`.

Elizabeth R. Chrastil and William H. Warren. From cognitive maps to cognitive graphs. *PLoS ONE*, 9(11):e112544, November 2014. ISSN 1932-6203. doi: 10.1371/journal.pone.0112544. URL http://dx.doi.org/10.1371/journal.pone.0112544.

Elisa Ciaramelli, Rosapia Lauro-Grotto, and Alessandro Treves. Dissociating episodic from semantic access mode by mutual information measures: Evidence from aging and alzheimer's disease. *Journal of Physiology-Paris*, 100(1–3):142–153, July 2006. ISSN 0928-4257. doi: 10.1016/j.jphysparis.2006.09.008. URL http://dx.doi.org/10.1016/j.jphysparis.2006.09.008.

Elisa Ciaramelli, R. Shayna Rosenbaum, Stephanie Solcz, Brian Levine, and Morris Moscovitch. Mental space travel: Damage to posterior parietal cortex prevents egocentric navigation and reexperiencing of remote spatial memories. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 36(3):619–634, May 2010. ISSN 0278-7393. doi: 10.1037/a0019181. URL http://dx.doi.org/10.1037/a0019181.

Edward K. Clint, Elliott Sober, Theodore Garland, and Justin S. Rhodes. Male superiority in spatial navigation: Adaptation or side effect? *The Quarterly Review of Biology*, 87(4): 289–313, December 2012. ISSN 1539-7718. doi: 10.1086/668168. URL http://dx.doi.org/10.1086/668168.

Jacob Cohen. *Statistical Power Analysis for the Behavioral Sciences*. Routledge, May 2013. ISBN 9781134742707. doi: 10.4324/9780203771587. URL http://dx.doi.org/10.4324/9780203771587.

David W. Collins and Doreen Kimura. A large sex difference on a two-dimensional mental rotation task. *Behavioral Neuroscience*, 111(4):845–849, August 1997. ISSN 0735-7044. doi: 10.1037/0735-7044.111.4.845. URL http://dx.doi.org/10.1037/0735-7044.111.4.845.

Nelson Cowan. The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, 24(1):87–114, February 2001. ISSN 1469-1825. doi: 10.1017/s0140525x01003922. URL http://dx.doi.org/10.1017/S0140525X01003922.

Jesse D. Cushman, Daniel B. Aharoni, Bernard Willers, Pascal Ravassard, Ashley Kees, Cliff Vuong, Briana Popeney, Katsushi Arisaka, and Mayank R. Mehta. Multisensory control of multimodal behavior: Do the legs know what the tongue is doing? *PLoS ONE*, 8 (11):e80465, November 2013. ISSN 1932-6203. doi: 10.1371/journal.pone.0080465. URL http://dx.doi.org/10.1371/journal.pone.0080465.

Louisa Dahmani, Miryam Idriss, Kyoko Konishi, Greg L West, and Veronique D Bohbot. Sex differences in spatial tasks: Considering environmental factors, navigation strategies, and age. *Front. Virtual Real.*, 4(1166364), September 2023.

Helen E. Davis, Jonathan Stack, and Elizabeth Cashdan. Cultural change reduces gender differences in mobility and spatial ability among seminomadic pastoralist-forager children in northern namibia. *Human Nature*, 32(1):178–206, March 2021. ISSN 1936-4776. doi: 10.1007/s12110-021-09388-7. URL http://dx.doi.org/10.1007/s12110-021-09388-7.

Helen Elizabeth Davis and Elizabeth Cashdan. *You Don't Have to Know Where Your Kids Are, Just Where They Aren't: Exploring Free-Range Parenting in the Bolivian Amazon*, page 59–74. Springer International Publishing, 2020. ISBN 9783030355906. doi: 10.1007/978-3-030-35590-6_5. URL http://dx.doi.org/10.1007/978-3-030-35590-6_5.

Sachin S. Deshmukh and James J. Knierim. Influence of local objects on hippocampal representations: Landmark vectors and memory. *Hippocampus*, 23(4):253–267, February 2013. ISSN 1098-1063. doi: 10.1002/hipo.22101. URL http://dx.doi.org/10.1002/hipo.22101.

Howard Eichenbaum. Hippocampus. *Neuron*, 44(1):109–120, September 2004. ISSN 0896-6273. doi: 10.1016/j.neuron.2004.08.028. URL http://dx.doi.org/10.1016/j.neuron.2004.08.028.

Alan Feingold. Sex differences in variability in intellectual abilities: A new look at an old controversy. *Review of Educational Research*, 62(1):61, 1992. ISSN 0034-6543. doi: 10.2307/1170716. URL http://dx.doi.org/10.2307/1170716.

Marianne Fyhn, Torkel Hafting, Alessandro Treves, May-Britt Moser, and Edvard I. Moser. Hippocampal remapping and grid realignment in entorhinal cortex. *Nature*, 446(7132):190–194, February 2007. ISSN 1476-4687. doi: 10.1038/nature05601. URL http://dx.doi.org/10.1038/nature05601.

Sandrine Gallois, Romain Duda, Barry Hewlett, and Victoria Reyes-García. Children's daily activities and knowledge acquisition: A case study among the baka from south-eastern cameroon. *Journal of Ethnobiology and Ethnomedicine*, 11(1), December 2015. ISSN 1746-4269. doi: 10.1186/s13002-015-0072-9. URL http://dx.doi.org/10.1186/s13002-015-0072-9.

Klara Gerlei, Jessica Passlack, Ian Hawes, Brianna Vandrey, Holly Stevens, Ioannis Papastathopoulos, and Matthew F. Nolan. Grid cells are modulated by local head di-

rection. *Nature Communications*, 11(1), August 2020. ISSN 2041-1723. doi: 10.1038/s41467-020-17500-1. URL http://dx.doi.org/10.1038/s41467-020-17500-1.

Asaf Gilboa and Hannah Marlatte. Neurobiology of schemas and schema-mediated memory. *Trends in Cognitive Sciences*, 21(8):618–631, August 2017. ISSN 1364-6613. doi: 10.1016/j.tics.2017.04.013. URL http://dx.doi.org/10.1016/j.tics.2017.04.013.

Johannes Golchert, Susanne Roehr, Tobias Luck, Michael Wagner, Angela Fuchs, Birgitt Wiese, Hendrik van den Bussche, Christian Brettschneider, Jochen Werle, Horst Bickel, Michael Pentzek, Anke Oey, Marion Eisele, Hans-Helmut König, Siegfried Weyerer, Edelgard Mösch, Wolfgang Maier, Martin Scherer, Kathrin Heser, and Steffi G. Riedel-Heller. Women outperform men in verbal episodic memory even in oldest-old age: 13-year longitudinal results of the agecode/agequalide study. *Journal of Alzheimer's Disease*, 69(3):857–869, June 2019. ISSN 1875-8908. doi: 10.3233/jad-180949. URL http://dx.doi.org/10.3233/JAD-180949.

KM Gothard, WE Skaggs, KM Moore, and BL McNaughton. Binding of hippocampal ca1 neural activity to multiple reference frames in a landmark-based navigation task. *The Journal of Neuroscience*, 16(2):823–835, January 1996. ISSN 1529-2401. doi: 10.1523/jneurosci.16-02-00823.1996. URL http://dx.doi.org/10.1523/JNEUROSCI.16-02-00823.1996.

David M. Green and John A. Swets. *Signal Detection Theory and Psychophysics*. John Wiley & Sons, New York, 1966. Contains introductions to probability theory, statistical decision theory, waveform analysis, and experimental techniques; reviews the basic experiments supporting detection theory in psychophysics; describes applications across psychology.

Corina U. Greven, Francesca Lionetti, Charlotte Booth, Elaine N. Aron, Elaine Fox, Haline E. Schendan, Michael Pluess, Hilgo Bruining, Bianca Acevedo, Patricia Bijttebier, and Judith Homberg. Sensory processing sensitivity in the context of environmental sensitivity: A critical review and development of research agenda. *Neuroscience amp; Biobehavioral Reviews*, 98:287–305, March 2019. ISSN 0149-7634. doi: 10.1016/j.neubiorev.2019.01.009. URL http://dx.doi.org/10.1016/j.neubiorev.2019.01.009.

G. Grön, A. P. Wunderlich, M. Spitzer, R. Tomczak, and M. W. Riepe. Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nature Neuroscience*, 3(4):404–408, 2000. ISSN 1546-1726. doi: 10.1038/73980. URL https://doi.org/10.1038/73980.

Erhan Selcuk Haciomeroglu and Mark LaVenia. Object-spatial imagery and verbal cognitive styles in high school students. *Perceptual and Motor Skills*, 124(3):689–702, March 2017.

ISSN 1558-688X. doi: 10.1177/0031512517698555. URL http://dx.doi.org/10.1177/0031512517698555.

Torkel Hafting, Marianne Fyhn, Sturla Molden, May-Britt Moser, and Edvard I. Moser. Microstructure of a spatial map in the entorhinal cortex. *Nature*, 436(7052):801–806, June 2005. ISSN 1476-4687. doi: 10.1038/nature03721. URL http://dx.doi.org/10.1038/nature03721.

J. A. Hartigan and P. M. Hartigan. The dip test of unimodality. *The Annals of Statistics*, 13 (1), March 1985. ISSN 0090-5364. doi: 10.1214/aos/1176346577. URL http://dx.doi.org/10.1214/aos/1176346577.

Tom Hartley, N. Burgess, C. Lever, F. Cacucci, and J. O'Keefe. Modeling place fields in terms of the cortical inputs to the hippocampus. *Hippocampus*, 10(4):369–379, 2000. ISSN 1098-1063. doi: 10.1002/1098-1063(2000)10:4<369::aid-hipo3>3.0.co;2-0. URL http://dx.doi.org/10.1002/1098-1063(2000)10:4<369::AID-HIPO3>3.0.CO;2-0.

M Hegarty. Development of a self-report measure of environmental spatial ability. *Intelligence*, 30(5):425–447, October 2002. ISSN 0160-2896. doi: 10.1016/s0160-2896(02)00116-2. URL http://dx.doi.org/10.1016/S0160-2896(02)00116-2.

Agneta Herlitz, Eija Airaksinen, and Eva Nordström. Sex differences in episodic memory: The impact of verbal and visuospatial ability. *Neuropsychology*, 13(4):590–597, 1999. ISSN 0894-4105. doi: 10.1037/0894-4105.13.4.590. URL http://dx.doi.org/10.1037/0894-4105.13.4.590.

Marco Hirnstein, Josephine Stuebs, Angelica Moè, and Markus Hausmann. Sex/gender differences in verbal fluency and verbal-episodic memory: A meta-analysis. *Perspectives on Psychological Science*, 18(1):67–90, July 2022. ISSN 1745-6924. doi: 10.1177/17456916221082116. URL http://dx.doi.org/10.1177/17456916221082116.

Tim N. Höffler, Marta Koć-Januchta, and Detlev Leutner. More evidence for three types of cognitive style: Validating the object-spatial imagery and verbal questionnaire using eye tracking when learning with texts and pictures. *Applied Cognitive Psychology*, 31(1):109–115, 2017. ISSN 1099-0720. doi: 10.1002/acp.3300. URL https://doi.org/10.1002/acp.3300.

Terrence G. Horgan, Marianne Schmid Mast, Judith A. Hall, and Jason D. Carter. Gender differences in memory for the appearance of others. *Personality and Social Psychology*

Bulletin, 30(2):185–196, February 2004. ISSN 1552-7433. doi: 10.1177/0146167203259928. URL http://dx.doi.org/10.1177/0146167203259928.

Kenneth Hugdahl, Tormod Thomsen, and Lars Ersland. Sex differences in visuo-spatial processing: An fmri study of mental rotation. *Neuropsychologia*, 44(9):1575–1583, January 2006. ISSN 0028-3932. doi: 10.1016/j.neuropsychologia.2006.01.026. URL http://dx.doi.org/10.1016/j.neuropsychologia.2006.01.026.

Connor M. Hults, Richard C. Francis, Edward K. Clint, Winter Smith, Elliott R. Sober, Theodore Garland, and Justin S. Rhodes. Still little evidence sex differences in spatial navigation are evolutionary adaptations. *Royal Society Open Science*, 11(1), January 2024. ISSN 2054-5703. doi: 10.1098/rsos.231532. URL http://dx.doi.org/10.1098/rsos.231532.

Øyvind A. Høydal, Erlend R. Skytøen, Sturla O. Andersson, May-Britt Moser, and Edvard I. Moser. Object-vector coding in the medial entorhinal cortex. *Nature*, 568(7752):400–404, 2019. doi: 10.1038/s41586-019-1077-7.

T Ishikawa and D Montello. Spatial knowledge acquisition from direct experience in the environment: Individual differences in the development of metric knowledge and the integration of separately learned places. *Cognitive Psychology*, 52(2):93–129, March 2006. ISSN 0010-0285. doi: 10.1016/j.cogpsych.2005.08.003. URL http://dx.doi.org/10.1016/j.cogpsych.2005.08.003.

Toru Ishikawa. Satellite navigation and geospatial awareness: Long-term effects of using navigation tools on wayfinding and spatial orientation. *The Professional Geographer*, 71 (2):197–209, October 2018. ISSN 1467-9272. doi: 10.1080/00330124.2018.1479970. URL http://dx.doi.org/10.1080/00330124.2018.1479970.

Revekka Ismakov, Omri Barak, Kate Jeffery, and Dori Derdikman. Grid cells encode local positional information. *Current Biology*, 27(15):2337–2343.e3, August 2017. ISSN 0960-9822. doi: 10.1016/j.cub.2017.06.034. URL http://dx.doi.org/10.1016/j.cub.2017.06.034.

Hyun Jang, Christophe Boesch, Roger Mundry, Véronique Kandza, and Karline R. L. Janmaat. Sun, age and test location affect spatial orientation in human foragers in rainforests. *Proceedings of the Royal Society B: Biological Sciences*, 286(1907):20190934, 2019. ISSN 1471-2954. doi: 10.1098/rspb.2019.0934. URL https://doi.org/10.1098/rspb.2019.0934.

Petra Jansen and Martin Heil. Gender differences in mental rotation across adulthood. *Experimental Aging Research*, 36(1):94–104, December 2009. ISSN 1096-4657. doi: 10.1080/03610730903422762. URL http://dx.doi.org/10.1080/03610730903422762.

Petra Jansen-Osmann and Gunnar Wiedenbauer. The representation of landmarks and routes in children and adults: A study in a virtual environment. *Journal of Environmental Psychology*, 24(3):347–357, 2004. doi: 10.1016/j.jenvp.2004.08.003. URL https://doi.org/10.1016/j.jenvp.2004.08.003.

Gabriele Janzen and Miranda van Turennout. Selective neural representation of objects relevant for navigation. *Nature Neuroscience*, 7(6):673–677, May 2004. ISSN 1546-1726. doi: 10.1038/nn1257. URL http://dx.doi.org/10.1038/nn1257.

David H. Jonassen and Barbara L. Grabowski. *Handbook of Individual Differences, Learning, and Instruction.* Routledge, New York, NY, 1993. ISBN 9780203052860. doi: 10.4324/9780203052860. URL https://www.taylorfrancis.com/books/mono/10.4324/9780203052860/handbook-individual-differences-learning-instruction-david-jonassen-barbara-grabowski.

Catherine M Jones and Susan D Healy. Differences in cue use and spatial memory in men and women. *Proceedings of the Royal Society B: Biological Sciences*, 273(1598):2241–2247, May 2006. ISSN 1471-2954. doi: 10.1098/rspb.2006.3572. URL http://dx.doi.org/10.1098/rspb.2006.3572.

Catherine M. Jones, Victoria A. Braithwaite, and Susan D. Healy. The evolution of sex differences in spatial ability. *Behavioral Neuroscience*, 117(3):403–411, 2003. ISSN 0735-7044. doi: 10.1037/0735-7044.117.3.403. URL http://dx.doi.org/10.1037/0735-7044.117.3.403.

Alexandra T Keinath, Russell A Epstein, and Vijay Balasubramanian. Environmental deformations dynamically shift the grid cell spatial metric. *eLife*, 7, October 2018. ISSN 2050-084X. doi: 10.7554/elife.38169. URL http://dx.doi.org/10.7554/eLife.38169.

Misun Kim and Christian F. Doeller. Cognitive maps for a non-euclidean environment: Path integration and spatial memory on a sphere. *Psychological Science*, 35(11):1217–1230, October 2024. ISSN 1467-9280. doi: 10.1177/09567976241279291. URL http://dx.doi.org/10.1177/09567976241279291.

Takashi Kitamura and Kaoru Inokuchi. Role of adult neurogenesis in hippocampal-cortical memory consolidation. *Molecular Brain*, 7(1):13, 2014. ISSN 1756-6606. doi: 10.1186/1756-6606-7-13. URL http://dx.doi.org/10.1186/1756-6606-7-13.

George S. Klein. *The personal world through perception.*, page 328–355. Ronald Press Company, 1951. doi: 10.1037/11505-012. URL http://dx.doi.org/10.1037/11505-012.

Dionysia Kontaxopoulou, Ion N. Beratis, Stella Fragkiadaki, Dimosthenis Pavlou, George Yannis, Alexandra Economou, Andrew C. Papanicolaou, and Sokratis G. Papageorgiou. Incidental and intentional memory: Their relation with attention and executive functions. *Archives of Clinical Neuropsychology*, 32(5):519–532, April 2017. ISSN 1873-5843. doi: 10.1093/arclin/acx027. URL http://dx.doi.org/10.1093/arclin/acx027.

Wendy A. Koss and Karyn M. Frick. Sex differences in hippocampal function. *Journal of Neuroscience Research*, 95(1–2):539–562, November 2016. ISSN 1097-4547. doi: 10.1002/jnr.23864. URL http://dx.doi.org/10.1002/jnr.23864.

Maria Kozhevnikov, Stephen Kosslyn, and Jennifer Shephard. Spatial versus object visualizers: A new characterization of visual cognitive style. *Memory amp; Cognition*, 33(4):710–726, June 2005. ISSN 1532-5946. doi: 10.3758/bf03195337. URL http://dx.doi.org/10.3758/BF03195337.

David J. M. Kraemer, Lauren M. Rosenberg, and Sharon L. Thompson-Schill. The neural correlates of visual and verbal cognitive styles. *The Journal of Neuroscience*, 29(12):3792–3798, March 2009. ISSN 1529-2401. doi: 10.1523/jneurosci.4635-08.2009. URL http://dx.doi.org/10.1523/JNEUROSCI.4635-08.2009.

Emilio Kropff, James E. Carmichael, May-Britt Moser, and Edvard I. Moser. Speed cells in the medial entorhinal cortex. *Nature*, 523(7561):419–424, July 2015. ISSN 1476-4687. doi: 10.1038/nature14622. URL http://dx.doi.org/10.1038/nature14622.

Julija Krupic, Marius Bauza, Stephen Burton, Caswell Barry, and John O'Keefe. Grid cell symmetry is shaped by environmental geometry. *Nature*, 518(7538):232–235, February 2015. ISSN 1476-4687. doi: 10.1038/nature14153. URL http://dx.doi.org/10.1038/nature14153.

Joni M. Lakin. Sex differences in reasoning abilities: Surprising evidence that male–female ratios in the tails of the quantitative reasoning distribution have increased. *Intelligence*, 41(4):263–274, July 2013. ISSN 0160-2896. doi: 10.1016/j.intell.2013.04.004. URL http://dx.doi.org/10.1016/j.intell.2013.04.004.

Rosamund F. Langston, James A. Ainge, Jonathan J. Couey, Cathrin B. Canto, Tale L. Bjerknes, Menno P. Witter, Edvard I. Moser, and May-Britt Moser. Development of the spatial representation system in the rat. *Science*, 328(5985):1576–1580, June 2010. ISSN

1095-9203. doi: 10.1126/science.1188210. URL http://dx.doi.org/10.1126/science.1188210.

Jillian E. Lauer, Hallie B. Udelson, Sung O. Jeon, and Stella F. Lourenco. An early sex difference in the relation between mental rotation and object preference. *Frontiers in Psychology*, 6, May 2015. ISSN 1664-1078. doi: 10.3389/fpsyg.2015.00558. URL http://dx.doi.org/10.3389/fpsyg.2015.00558.

Carol A. Lawton. Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. *Sex Roles*, 30(11–12):765–779, June 1994. ISSN 1573-2762. doi: 10.1007/bf01544230. URL http://dx.doi.org/10.1007/BF01544230.

Shang Lin Tommy Lee, Brian Timmerman, Riley Pflomm, Nikita Roy, Mahathi Kumar, and Etan J. Markus. Sequential order spatial memory in male rats: Characteristics and impact of medial prefrontal cortex and hippocampus disruption. *Neurobiology of Learning and Memory*, 200:107739, April 2023. ISSN 1074-7427. doi: 10.1016/j.nlm.2023.107739. URL http://dx.doi.org/10.1016/j.nlm.2023.107739.

Colin Lever, Stephen Burton, Ali Jeewajee, John O'Keefe, and Neil Burgess. Boundary vector cells in the subiculum of the hippocampal formation. *The Journal of Neuroscience*, 29(31):9771–9777, August 2009. ISSN 1529-2401. doi: 10.1523/jneurosci.1319-09.2009. URL http://dx.doi.org/10.1523/JNEUROSCI.1319-09.2009.

Marcia C. Linn and Anne C. Petersen. Emergence and characterization of sex differences in spatial ability: A meta-analysis. *Child Development*, 56(6):1479, December 1985. ISSN 0009-3920. doi: 10.2307/1130467. URL http://dx.doi.org/10.2307/1130467.

Francesca Lionetti, Massimiliano Pastore, Ughetta Moscardino, Annalaura Nocentini, Karen Pluess, and Michael Pluess. Sensory processing sensitivity and its association with personality traits and affect: A meta-analysis. *Journal of Research in Personality*, 81: 138–152, August 2019. ISSN 0092-6566. doi: 10.1016/j.jrp.2019.05.013. URL http://dx.doi.org/10.1016/j.jrp.2019.05.013.

Yifan Luo, Matteo Toso, Bailu Si, Federico Stella, and Alessandro Treves. *Grid Cells Lose Coherence in Realistic Environments*. IntechOpen, January 2022. ISBN 9781839699122. doi: 10.5772/intechopen.100310. URL http://dx.doi.org/10.5772/intechopen.100310.

Neil A. Macmillan and C. Douglas Creelman. *Detection Theory: A User's Guide*. Lawrence Erlbaum Associates, Mahwah, NJ, 2 edition, 2005. ISBN 978-0-8058-3831-0.

Yukiko Maeda and So Yoon Yoon. A meta-analysis on gender differences in mental rotation ability measured by the purdue spatial visualization tests: Visualization of rotations (psvt:r). *Educational Psychology Review*, 25(1):69–94, December 2012. ISSN 1573-336X. doi: 10.1007/s10648-012-9215-x. URL http://dx.doi.org/10.1007/s10648-012-9215-x.

David J.-N. Maisson, Andrew Wikenheiser, Jean-Paul G. Noel, and Alexandra T. Keinath. Making sense of the multiplicity and dynamics of navigational codes in the brain. *The Journal of Neuroscience*, 42(45):8450–8459, November 2022. ISSN 1529-2401. doi: 10.1523/jneurosci.1124-22.2022. URL http://dx.doi.org/10.1523/JNEUROSCI.1124-22.2022.

Klara Malinakova, Lukas Novak, Radek Trnka, and Peter Tavel. Sensory processing sensitivity questionnaire: A psychometric evaluation and associations with experiencing the covid-19 pandemic. *International Journal of Environmental Research and Public Health*, 18(24):12962, December 2021. ISSN 1660-4601. doi: 10.3390/ijerph182412962. URL http://dx.doi.org/10.3390/ijerph182412962.

Caitlin S. Mallory, Kiah Hardcastle, Jason S. Bant, and Lisa M. Giocomo. Grid scale drives the scale and long-term stability of place maps. *Nature Neuroscience*, 21(2):270–282, January 2018. ISSN 1546-1726. doi: 10.1038/s41593-017-0055-3. URL http://dx.doi.org/10.1038/s41593-017-0055-3.

Hans A. Mallot. *From Geometry to Behavior: An Introduction to Spatial Cognition*. The MIT Press, Cambridge, MA, 2023. ISBN 9780262546684.

Marianne Schmid Mast and Judith A. Hall. Women's advantage at remembering others' appearance: A systematic look at the why and when of a gender difference. *Personality and Social Psychology Bulletin*, 32(3):353–364, March 2006. ISSN 1552-7433. doi: 10.1177/0146167205282150. URL http://dx.doi.org/10.1177/0146167205282150.

Robert F. McGivern, Kandis L. Mutter, Julie Anderson, Graham Wideman, Mark Bodnar, and Patrick J. Huston. Gender differences in incidental learning and visual recognition memory: support for a sex difference in unconscious environmental awareness. *Personality and Individual Differences*, 25(2):223–232, August 1998. ISSN 0191-8869. doi: 10.1016/s0191-8869(98)00017-8. URL http://dx.doi.org/10.1016/S0191-8869(98)00017-8.

Elinor McKone, Nancy Kanwisher, and Bradley C. Duchaine. Can generic expertise explain special processing for faces? *Trends in Cognitive Sciences*, 11(1):8–15, January 2007. ISSN 1364-6613. doi: 10.1016/j.tics.2006.11.002. URL http://dx.doi.org/10.1016/j.tics.2006.11.002.

Jacqueline Metzler and Roger N. Shepard. Transformational studies of the internal representation of three-dimensional objects. In Robert L. Solso, editor, *Theories in Cognitive Psychology: The Loyola Symposium*, pages 147–201. Lawrence Erlbaum Associates, Hillsdale, NJ, 1974.

George A. Miller. The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, 63(2):81–97, 1956. doi: 10.1037/0033-295X.63.2.81. URL https://doi.org/10.1037/0033-295X.63.2.81.

Emily J. Miner, Michael Gurven, Hillard Kaplan, and Steven J. C. Gaulin. Sex difference in travel is concentrated in adolescence and tracks reproductive interests. *Proceedings of the Royal Society B: Biological Sciences*, 281(1796):20141476, December 2014. ISSN 1471-2954. doi: 10.1098/rspb.2014.1476. URL http://dx.doi.org/10.1098/rspb.2014.1476.

Laura Miola, Veronica Muffato, Enrico Sella, Chiara Meneghetti, and Francesca Pazzaglia. Gps use and navigation ability: A systematic review and meta-analysis. *Journal of Environmental Psychology*, 99:102417, November 2024. ISSN 0272-4944. doi: 10.1016/j.jenvp.2024.102417. URL http://dx.doi.org/10.1016/j.jenvp.2024.102417.

M. L. Mittelstaedt and H. Mittelstaedt. Homing by path integration in a mammal. *Naturwissenschaften*, 67:566–567, 1980. doi: 10.1007/BF00450672. In German.

Daniel R. Montello, Kristin L. Lovelace, Reginald G. Golledge, and Carole M. Self. Sex-related differences and similarities in geographic and environmental spatial abilities. *Annals of the Association of American Geographers*, 89(3):515–534, September 1999. ISSN 1467-8306. doi: 10.1111/0004-5608.00160. URL http://dx.doi.org/10.1111/0004-5608.00160.

Morris Moscovitch, Roberto Cabeza, Gordon Winocur, and Lynn Nadel. Episodic memory and beyond: The hippocampus and neocortex in transformation. *Annual Review of Psychology*, 67(1):105–134, January 2016. ISSN 1545-2085. doi: 10.1146/annurev-psych-113011-143733. URL http://dx.doi.org/10.1146/annurev-psych-113011-143733.

May-Britt Moser, David C. Rowland, and Edvard I. Moser. Place cells, grid cells, and memory. *Cold Spring Harbor Perspectives in Biology*, 7(2):a021808, February 2015. ISSN 1943-0264. doi: 10.1101/cshperspect.a021808. URL http://dx.doi.org/10.1101/cshperspect.a021808.

Michael A. Motes, Rafael Malach, and Maria Kozhevnikov. Object-processing neural efficiency differentiates object from spatial visualizers. *NeuroReport*, 19(17):1727–1731, November 2008. ISSN 0959-4965. doi: 10.1097/wnr.0b013e328317f3e2. URL http://dx.doi.org/10.1097/WNR.0b013e328317f3e2.

D. W. Müller and G. Sawitzki. Excess mass estimates and tests for multimodality. *Journal of the American Statistical Association*, 86(415):738–746, September 1991. ISSN 1537-274X. doi: 10.1080/01621459.1991.10475103. URL http://dx.doi.org/10.1080/01621459.1991.10475103.

RU Muller and JL Kubie. The effects of changes in the environment on the spatial firing of hippocampal complex-spike cells. *The Journal of Neuroscience*, 7(7):1951–1968, July 1987. ISSN 1529-2401. doi: 10.1523/jneurosci.07-07-01951.1987. URL http://dx.doi.org/10.1523/JNEUROSCI.07-07-01951.1987.

Alina Nazareth, Xing Huang, Daniel Voyer, and Nora Newcombe. A meta-analysis of sex differences in human navigation skills. *Psychonomic Bulletin amp; Review*, 26 (5):1503–1528, July 2019. ISSN 1531-5320. doi: 10.3758/s13423-019-01633-6. URL http://dx.doi.org/10.3758/s13423-019-01633-6.

Stephanie Noble, Nick Dalton, Michael Hornberger, and Hugo Spiers. Redefining global and local landmarks: When does a landmark stop being local and become a global one? In Stefan Hundt, Christian Freksa, and Timo Tikkanen, editors, *Spatial Cognition XII: 12th International Conference, Spatial Cognition 2020, Proceedings*, volume 12162 of *Lecture Notes in Computer Science*, pages 111–124. Springer Nature, 2020. doi: 10.1007/978-3-030-57983-8_9. URL https://doi.org/10.1007/978-3-030-57983-8_9.

John O'Keefe. Biographical. https://www.nobelprize.org/prizes/medicine/2014/okeefe/biographical/, 2014a. Nobel Prize website, accessed 2025-08-18.

John O'Keefe. Spatial cells in the hippocampal formation. https://www.nobelprize.org/uploads/2018/06/okeefe-lecture.pdf, 2014b. Nobel Prize in Physiology or Medicine 2014, Nobel Lecture, accessed 2025-08-18.

John O'Keefe and Lynn Nadel. *The Hippocampus as a Cognitive Map*. Oxford University Press, Oxford, UK, 1978.

J. O'Keefe and J. Dostrovsky. The hippocampus as a spatial map. preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, 34(1):171–175, November

1971. ISSN 0006-8993. doi: 10.1016/0006-8993(71)90358-1. URL http://dx.doi.org/10.1016/0006-8993(71)90358-1.

Hector J. I. Page and Kate J. Jeffery. Landmark-based updating of the head direction system by retrosplenial cortex: A computational model. *Frontiers in Cellular Neuroscience*, 12, July 2018. ISSN 1662-5102. doi: 10.3389/fncel.2018.00191. URL http://dx.doi.org/10.3389/fncel.2018.00191.

Michael Peer, Iva K. Brunec, Nora S. Newcombe, and Russell A. Epstein. Structuring knowledge with cognitive maps and cognitive graphs. *Trends in Cognitive Sciences*, 25(1):37–54, January 2021. ISSN 1364-6613. doi: 10.1016/j.tics.2020.10.004. URL http://dx.doi.org/10.1016/j.tics.2020.10.004.

Yoni Pertzov, Sanjay Manohar, and Masud Husain. Rapid forgetting results from competition over time between items in visual working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 43(4):528–536, April 2017. ISSN 0278-7393. doi: 10.1037/xlm0000328. URL http://dx.doi.org/10.1037/xlm0000328.

Adrien Peyrache, Nicolás Schieferstein, and György Buzsáki. Transformation of the head-direction signal into a spatial code. *Nature Communications*, 8(1):1752, 2017. doi: 10.1038/s41467-017-01908-3. URL https://doi.org/10.1038/s41467-017-01908-3.

Praveen K. Pilly and Stephen Grossberg. How does the modular organization of entorhinal grid cells develop? *Frontiers in Human Neuroscience*, 8, June 2014. ISSN 1662-5161. doi: 10.3389/fnhum.2014.00337. URL http://dx.doi.org/10.3389/fnhum.2014.00337.

Belinda Pletzer. Sex-specific strategy use and global-local processing: a perspective toward integrating sex differences in cognition. *Frontiers in Neuroscience*, Volume 8 - 2014, 2014. ISSN 1662-453X. doi: 10.3389/fnins.2014.00425. URL https://www.frontiersin.org/journals/neuroscience/articles/10.3389/fnins.2014.00425.

Belinda Pletzer, Andrea Scheuringer, and Thomas Scherndl. Global-local processing relates to spatial and verbal processing: implications for sex differences in cognition. *Scientific Reports*, 7(1), September 2017. ISSN 2045-2322. doi: 10.1038/s41598-017-11013-6. URL http://dx.doi.org/10.1038/s41598-017-11013-6.

Alison R. Preston and Howard Eichenbaum. Interplay of hippocampus and prefrontal cortex in memory. *Current Biology*, 23(17):R764–R773, 2013. doi: 10.1016/j.cub.2013.05.041. URL https://doi.org/10.1016/j.cub.2013.05.041.

Bruno Rivard, Yu Li, Pierre-Pascal Lenck-Santini, Bruno Poucet, and Robert U. Muller. Representation of objects in space by two classes of hippocampal pyramidal cells. *The Journal of General Physiology*, 124(1):9–25, June 2004. ISSN 0022-1295. doi: 10.1085/jgp.200409015. URL http://dx.doi.org/10.1085/jgp.200409015.

Edmund T. Rolls. *Brain Computations and Connectivity*. Oxford University Press, Oxford, 2023. doi: 10.1093/oso/9780198877075.001.0001. URL https://doi.org/10.1093/oso/9780198877075.001.0001. Open Access.

Deborah M Saucier, Sheryl M Green, Jennifer Leason, Alastair MacFadden, Scott Bell, and Lorin J Elias. Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behav. Neurosci.*, 116(3):403–410, 2002.

Bailu Si, Emilio Kropff, and Alessandro Treves. Grid alignment in entorhinal cortex. *Biological Cybernetics*, 106(8–9):483–506, August 2012. ISSN 1432-0770. doi: 10.1007/s00422-012-0513-7. URL http://dx.doi.org/10.1007/s00422-012-0513-7.

Alexander W. Siegel and Sheldon H. White. *The Development of Spatial Representations of Large-Scale Environments*, page 9–55. Elsevier, 1975. doi: 10.1016/s0065-2407(08)60007-5. URL http://dx.doi.org/10.1016/S0065-2407(08)60007-5.

Davide Spalla, Alessandro Treves, and Charlotte N. Boccara. Angular and linear speed cells in the parahippocampal circuits. *Nature Communications*, 13(1), April 2022. ISSN 2041-1723. doi: 10.1038/s41467-022-29583-z. URL http://dx.doi.org/10.1038/s41467-022-29583-z.

Dylan S. Spets and Scott D. Slotnick. Are there sex differences in brain activity during long-term memory? a systematic review and fmri activation likelihood estimation meta-analysis. *Cognitive Neuroscience*, 12(3–4):163–173, August 2020. ISSN 1758-8936. doi: 10.1080/17588928.2020.1806810. URL http://dx.doi.org/10.1080/17588928.2020.1806810.

Hugo J Spiers and Eleanor A Maguire. A "landmark" study on the neural basis of navigation. *Nature Neuroscience*, 7(6):572–574, June 2004. ISSN 1546-1726. doi: 10.1038/nn0604-572. URL http://dx.doi.org/10.1038/nn0604-572.

Larry R. Squire, Craig E. Stark, and Robert E. Clark. The medial temporal lobe. *Annual Review of Neuroscience*, 27:279–306, 2004. doi: 10.1146/annurev.neuro.27.070203.144130. URL https://doi.org/10.1146/annurev.neuro.27.070203.144130.

Larry R. Squire, Lisa Genzel, John T. Wixted, and Richard G. Morris. Memory consolidation. *Cold Spring Harbor Perspectives in Biology*, 7(8):a021766, 2015. ISSN 1943-0264. doi: 10.1101/cshperspect.a021766. URL https://doi.org/10.1101/cshperspect.a021766.

Federico Stella, Eugenio Urdapilleta, Yifan Luo, and Alessandro Treves. Partial coherence and frustration in self-organizing spherical grids. *Hippocampus*, 30(4):302–313, July 2019. ISSN 1098-1063. doi: 10.1002/hipo.23144. URL http://dx.doi.org/10.1002/hipo.23144.

Hanne Stensola, Tor Stensola, Trygve Solstad, Kristian Frøland, May-Britt Moser, and Edvard I. Moser. The entorhinal grid map is discretized. *Nature*, 492(7427):72–78, December 2012. ISSN 1476-4687. doi: 10.1038/nature11649. URL http://dx.doi.org/10.1038/nature11649.

Hui Min Tan, Joshua Pope Bassett, John O'Keefe, Francesca Cacucci, and Thomas Joseph Wills. The development of the head direction system before eye opening in the rat. *Current Biology*, 25(4):479–483, February 2015. ISSN 0960-9822. doi: 10.1016/j.cub.2014.12.030. URL http://dx.doi.org/10.1016/j.cub.2014.12.030.

Laura Tascón, Carmen Di Cicco, Laura Piccardi, Massimiliano Palmiero, Alessia Bocchi, and José Manuel Cimadevilla. Sex differences in spatial memory: Comparison of three tasks using the same virtual context. *Brain Sciences*, 11(6):757, June 2021. ISSN 2076-3425. doi: 10.3390/brainsci11060757. URL http://dx.doi.org/10.3390/brainsci11060757.

Jeffrey S Taube. New building blocks for navigation. *Nature Neuroscience*, 20(2):131–133, January 2017. ISSN 1546-1726. doi: 10.1038/nn.4480. URL http://dx.doi.org/10.1038/nn.4480.

Edward C. Tolman. Cognitive maps in rats and men. *Psychological Review*, 55(4):189–208, 1948. ISSN 0033-295X. doi: 10.1037/h0061626. URL http://dx.doi.org/10.1037/h0061626.

G. Torromino, V. Loffredo, D. Cavezza, G. Sonsini, F. Esposito, A. H. Crevenna, M. Gioffrè, M. De Risi, A. Treves, M. Griguoli, and E. De Leonibus. Thalamo-hippocampal pathway regulates incidental memory load in mice. August 2021. doi: 10.1101/2021.08.07.453742. URL http://dx.doi.org/10.1101/2021.08.07.453742.

M. E. Tresselt and M. S. Mayzner. A study of incidental learning. *The Journal of Psychology*, 50(2):339–347, October 1960. ISSN 1940-1019. doi: 10.1080/00223980.1960.9916451. URL http://dx.doi.org/10.1080/00223980.1960.9916451.

Benjamin C. Trumble, Steven J. C. Gaulin, Matt D. Dunbar, Hillard Kaplan, and Michael Gurven. No sex or age difference in dead-reckoning ability among tsimane forager-horticulturalists. *Human Nature*, 27(1):51–67, November 2015. ISSN 1936-4776. doi: 10.1007/s12110-015-9246-3. URL http://dx.doi.org/10.1007/s12110-015-9246-3.

Benjamin C. Trumble, Steven J. C. Gaulin, Mhairi D. Dunbar, Hillard Kaplan, and Michael Gurven. No sex or age difference in dead-reckoning ability among tsimane forager-horticulturalists. *Human Nature*, 27(1):51–67, 2016. ISSN 1936-4776. doi: 10.1007/s12110-015-9246-3. URL https://doi.org/10.1007/s12110-015-9246-3.

Doris Y. Tsao and Margaret S. Livingstone. Mechanisms of face perception. *Annual Review of Neuroscience*, 31(1):411–437, July 2008. ISSN 1545-4126. doi: 10.1146/annurev.neuro.30.051606.094238. URL http://dx.doi.org/10.1146/annurev.neuro.30.051606.094238.

Nicholas B. Turk-Browne. The hippocampus as a visual area organized by space and time: A spatiotemporal similarity hypothesis. *Vision Research*, 165:123–130, December 2019. ISSN 0042-6989. doi: 10.1016/j.visres.2019.10.007. URL http://dx.doi.org/10.1016/j.visres.2019.10.007.

Ingvild Ulsaker-Janke, Torgeir Waaga, Tanja Waaga, Edvard I. Moser, and May-Britt Moser. Grid cells in rats deprived of geometric experience during development. *Proceedings of the National Academy of Sciences*, 120(41), October 2023. ISSN 1091-6490. doi: 10.1073/pnas.2310820120. URL http://dx.doi.org/10.1073/pnas.2310820120.

Yash S. Vakilna, William C. Tang, Bruce C. Wheeler, and Gregory J. Brewer. The flow of axonal information among hippocampal subregions: 1. feed-forward and feedback network spatial dynamics underpinning emergent information processing. *Frontiers in Neural Circuits*, 15, August 2021. ISSN 1662-5110. doi: 10.3389/fncir.2021.660837. URL http://dx.doi.org/10.3389/fncir.2021.660837.

Steven G. Vandenberg and Allan R. Kuse. Mental rotations, a group test of three-dimensional spatial visualization. *Perceptual and Motor Skills*, 47(2):599–604, December 1978. ISSN 1558-688X. doi: 10.2466/pms.1978.47.2.599. URL http://dx.doi.org/10.2466/pms.1978.47.2.599.

Daniel Voyer, Susan Voyer, and M. Philip Bryden. Magnitude of sex differences in spatial abilities: A meta-analysis and consideration of critical variables. *Psychological Bulletin*, 117(2):250–270, 1995. ISSN 0033-2909. doi: 10.1037/0033-2909.117.2.250. URL http://dx.doi.org/10.1037/0033-2909.117.2.250.

Daniel Voyer, Jean Saint Aubin, Katelyn Altman, and Genevieve Gallant. Sex differences in verbal working memory: A systematic review and meta-analysis. *Psychological Bulletin*, 147(4):352–398, April 2021. ISSN 0033-2909. doi: 10.1037/bul0000320. URL http://dx.doi.org/10.1037/bul0000320.

Carole C. Wagnon, Katharina Wehrmann, Stefan Klöppel, and Jessica Peter. Incidental learning: A systematic review of its effect on episodic memory performance in older age. *Frontiers in Aging Neuroscience*, 11, July 2019. ISSN 1663-4365. doi: 10.3389/fnagi.2019.00173. URL http://dx.doi.org/10.3389/fnagi.2019.00173.

Paul Webley. Sex differences in home range and cognitive maps in eight-year old children. *Journal of Environmental Psychology*, 1(4):293–302, December 1981. ISSN 0272-4944. doi: 10.1016/s0272-4944(81)80027-8. URL http://dx.doi.org/10.1016/S0272-4944(81)80027-8.

Tanja Wernle, Torgeir Waaga, Maria Mørreaunet, Alessandro Treves, May-Britt Moser, and Edvard I. Moser. Integration of grid maps in merged environments. *Nature Neuroscience*, 21(1):92–101, December 2017. ISSN 1546-1726. doi: 10.1038/s41593-017-0036-6. URL http://dx.doi.org/10.1038/s41593-017-0036-6.

Christopher Widdowson and Ranxiao Frances Wang. Human navigation in curved spaces. *Cognition*, 218:104923, January 2022. ISSN 0010-0277. doi: 10.1016/j.cognition.2021.104923. URL http://dx.doi.org/10.1016/j.cognition.2021.104923.

Shawn S. Winter, Benjamin J. Clark, and Jeffrey S. Taube. Disruption of the head direction cell network impairs the parahippocampal grid cell signal. *Science*, 347(6224):870–874, February 2015. ISSN 1095-9203. doi: 10.1126/science.1259591. URL http://dx.doi.org/10.1126/science.1259591.

Menno P. Witter. *The perforant path: projections from the entorhinal cortex to the dentate gyrus*, page 43–61. Elsevier, 2007. ISBN 9780444530158. doi: 10.1016/s0079-6123(07)63003-9. URL http://dx.doi.org/10.1016/s0079-6123(07)63003-9.

Shunya Yagi and Liisa A. M. Galea. Sex differences in hippocampal cognition and neurogenesis. *Neuropsychopharmacology*, 44(1):200–213, September 2018. ISSN 1740-634X. doi: 10.1038/s41386-018-0208-4. URL http://dx.doi.org/10.1038/s41386-018-0208-4.

Andrew Yonelinas, Chris Hawkins, Ani Abovian, and Mariam Aly. The role of recollection, familiarity, and the hippocampus in episodic and working memory. *Neuropsychologia*, 193:

108777, January 2024. ISSN 0028-3932. doi: 10.1016/j.neuropsychologia.2023.108777. URL http://dx.doi.org/10.1016/j.neuropsychologia.2023.108777.

Andrew P Yonelinas. The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, 46(3):441–517, April 2002. ISSN 0749-596X. doi: 10.1006/jmla.2002.2864. URL http://dx.doi.org/10.1006/jmla.2002.2864.

Ruohan Zhang, Edmund T. Rolls, Wei Cheng, and Jianfeng Feng. Different cortical connectivities in human females and males relate to differences in strength and body composition, reward and emotional systems, and memory. *Brain Structure and Function*, 229(1):47–61, October 2023. ISSN 1863-2661. doi: 10.1007/s00429-023-02720-0. URL http://dx.doi.org/10.1007/s00429-023-02720-0.