Landmark-dependent Navigation Strategy Declines across the Human Life-Span: Evidence from Over 37,000 Participants

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Abstract

■ Humans show a remarkable capacity to navigate various environments using different navigation strategies, and we know that strategy changes across the life span. However, this observation has been based on studies of small sample sizes. To this end, we used a mobile app-based video game (Sea Hero Quest) to test virtual navigation strategies and memory performance within a distinct radial arm maze level in over 37,000 participants. Players were presented with 6 pathways (3 open and 3 closed) and were required to navigate to the 3 open pathways to collect a target. Next, all 6 pathways were made available and the player was required to visit the pathways that were previously unavailable. Both reference memory and working memory errors were calculated. Crucially, at the end of the level, the player was asked a multiple-choice question about how they found the targets (i.e., a counting-dependent strategy vs. a landmark-dependent strategy). As predicted from previous laboratory studies, we found the use of landmarks declined linearly with age. Those using landmark-based strategies also performed better on reference memory than those using a counting-based strategy. These results extend previous observations in the laboratory showing a decreased use of landmark-dependent strategies with age. ■

INTRODUCTION

The human brain changes across the life span—during ageing people experience decreases in executive and memory functions, which are associated with gray matter loss in the frontal cortex and the hippocampus, respectively (Thambisetty et al., 2010; Moffat, Elkins, & Resnick, 2006; Raz, Rodrigue, Head, Kennedy, & Acker, 2004; Small, Tsai, DeLaPaz, Mayeux, & Stern, 2002). The integrity of the hippocampus during ageing is of particular interest to researchers as a decline in behavioral performance supported by this structure, such as wayfinding ability (Mapstone, Steffenella, & Duffy, 2003; Klein et al., 1999; Passini, Rainville, Marchand, & Joanette, 1995) as well as gray matter loss, are an early sign of cognitive decline and Alzheimer's disease (AD; Jessen et al., 2010; Apostolova et al., 2006; Jagust et al., 2006). Changes in hippocampal gray matter during ageing also correlates with changes in behaviors related to other aspects of learning and memory such as navigational strategies used when learning a new environment (West et al., 2018; Bohbot, Lerch, Thorndycraft, Iaria, & Zijdenbos, 2007; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003). The hippocampus is required during navigation when relationships between multiple landmarks in the environment are learned to form a cognitive map, allowing for navigation irrespective of the starting position of the observer and is commonly referred to as *spatial learning* (Ekstrom & Ranganath, 2018; Bohbot et al., 2007; Bohbot, Iaria, & Petrides, 2004; Iaria et al., 2003; Packard, Hirsh, & White, 1989; O'Keefe & Nadel, 1978). In contrast, when a person navigates by using a series of rigid turns from one specific starting point in the environment, stimulus–response associations are formed in the striatum, which includes the caudate nucleus, and this is referred to as *response learning* (Bohbot et al., 2004, 2007; Packard et al., 1989; O'Keefe & Nadel, 1978).

Numerous studies in rodents and humans have demonstrated that spatial learning is supported by the hippocampus while response learning recruits the caudate nucleus (West et al., 2018; Konishi et al., 2013; Konishi & Bohbot, 2013; Lerch et al., 2011; Bohbot et al., 2007; Iaria et al., 2003; Packard & McGaugh, 1992, 1996; McDonald & White, 1993; Packard et al., 1989). For example, when rodents were presented with a dual-solution task that could be completed using spatial or response learning in a plus maze, increased acetylcholine in the hippocampus was

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Journal of Cognitive Neuroscience X:Y, pp. 1–16
https://doi.org/10.1162/jocn_a_01956

measured in rodents that would spontaneously use a spatial strategy, whereas increased acetylcholine was observed in the caudate nucleus of rodents who would spontaneously use a response strategy (Chang & Gold, 2003). Rodents trained on the Morris Water Maze by learning the relationship between visual landmarks (spatial learning) displayed larger hippocampal volume after 5 days of training whereas a separate group trained to solve the maze using a single beacon stimulus while landmarks were hidden with a curtain (response learning) displayed a larger volume in the striatum, which includes the caudate nucleus (Lerch et al., 2011). In humans, hippocampal volume positively correlated with peoples' ability to use a learned cognitive map of a university campus to locate relative building locations (Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013). Furthermore, when people navigated in a dual-solution virtual maze that allowed for the use of both spatial or response navigation learning, people who navigated using spatial strategies showed greater activity in the hippocampus (Iaria et al., 2003) and also greater hippocampal gray matter (Bohbot et al., 2007). In contrast, people who used response strategies showed increased activity (Iaria et al., 2003) and gray matter (Bohbot et al., 2007) in the caudate nucleus. These observations were replicated in older adults where the use of spatial strategies was associated with greater activity (Konishi et al., 2013) and gray matter (Konishi & Bohbot, 2013) in the hippocampus compared with those using response strategies who had more gray matter in the caudate nucleus (Sodums & Bohbot, 2020).

Indeed, many studies have demonstrated a significant relationship between navigational ability and both healthy ageing and neuropathology. For example, older adults display lower route learning and spatial learning during navigation that does not improve to the same degree as younger adults with training (Nemmi, Boccia, & Guariglia, 2017). This is thought to occur in ageing in part because of increased path integration errors that accumulate with travel distance (Stangl, Kanitscheider, Riemer, Fiete, & Wolbers, 2020). When considering early neuropathology associated with AD, asymptomatic preclinical AD patients (biomarkers of beta amyloid and tau protein) show reduced hippocampus-dependent wayfinding ability compared with healthy controls (Allison, Fagan, Morris, & Head, 2016), while these groups have shown no difference when using conventional cognitive tests (Laczo et al., 2022).

Given that atrophy in the hippocampus is associated with age-related cognitive decline (Moffat et al., 2006; Raz et al., 2004; Small et al., 2002; Lupien et al., 1998), it is hypothesized that the use of hippocampus-dependent spatial strategies, previously shown to be associated with higher hippocampal volume, also decline with age. For example, numerous studies have shown that the integrity of the hippocampus is associated with healthy cognition in ageing. Higher volume in the hippocampus is associated with better learning and memory performance in ageing as measured by virtual versions of the Morris Water Maze and Transverse Patterning Discrimination tasks (Driscoll et al., 2003) and higher estimates of global cognition as measured by the Montreal Cognitive Assessment, a test that is sensitive to dementia (Ritter, Hawley, Banks, & Miller, 2017; O'Shea, Cohen, Porges, Nissim, & Woods, 2016). Furthermore, lower gray matter in the hippocampus and the functionally connected entorhinal cortex (EC) are predictors of future diagnosis of AD (Apostolova et al., 2006). Related to this, older adult participants who use hippocampus-dependent spatial strategies had higher scores on the Montreal Cognitive Assessment. These participants also displayed better wayfinding performance and increased hippocampal volume (Konishi, McKenzie, Etchamendy, Roy, & Bohbot, 2017). Moreover, spatial strategies are associated with increased gray matter in the hippocampus, despite the presence of an APOE4 allele. The APOE4 allele, present in approximately 10–15% of people, increases the risk for AD, lowers the age of onset, and is also associated with less gray matter in the hippocampus (O'Dwyer et al., 2012; Pievani et al., 2011) and the EC (Donix et al., 2010). Interestingly, people who are APOE4 carriers that use nonspatial strategies display decreased gray matter in the hippocampus and the EC, whereas in contrast, APOE4 carriers who use spatial strategies have gray matter levels comparable to non-APOE4 carriers (Konishi et al., 2016). Thus, continued experience using spatial strategies is possibly associated with increased gray matter in the hippocampus and EC, which in turn could potentially reduce biological risk factors for developing dementia during ageing. Longitudinal studies examining behavioral and imaging data are needed to confirm the causal relationship between APOE4 status and navigational strategies. Relatedly, it was found that wayfinding performance, which is supported in part by the hippocampus (e.g., Konishi et al., 2017; Guderian et al., 2015; Spiers, Burgess, Hartley, Vargha-Khadem, & O'Keefe, 2001), within the mobile game Sea Hero Quest (SHQ) was lower for APOE4 carriers compared with non-APOE4 carriers (Coughlan et al., 2019).

Spatial strategies are also associated with lower volume in the caudate nucleus, a structure involved in automatization of behavior and reward (West et al., 2018; Bohbot et al., 2007; Iaria et al., 2003). Related to this, young adults who use hippocampus-dependent spatial strategies display lower risk-taking behaviors in the Iowa Gambling Task (Aumont, Blanchette, Bohbot, & West, 2019) and report consuming fewer illicit substances (Bohbot, Del Balso, Conrad, Konishi, & Leyton, 2013). Therefore, hippocampal-dependent spatial strategy use is associated with fewer reward-seeking behaviors.

Crucially, spatial learning, which depends on the use of landmarks, declines throughout the life span. Relative to young adult rodents, senescent rats shift from the use of spatial memory strategies to the use of response strategies to learn the location of a target arm in a plus maze (Barnes, Nadel, & Honig, 1980). Interestingly, when the striatum of older rats was inactivated with lidocaine, they instead favored the use of hippocampus-dependent spatial strategies when tested on a similar task (Gardner, Gold, & Korol, 2020). These results suggest that the down-regulation of striatal processing during ageing can help reinforce the use of hippocampus-dependent strategies. When older mice are given a choice between solving a maze using response or spatial learning, they choose to use response strategies although they demonstrated being capable of using spatial strategies (Nicolle, Prescott, & Bizon, 2003). In humans, older adults tested on a virtual analog of a rodent radial maze displayed decreased spatial strategy use when completing the task (Etchamendy, Konishi, Pike, Marighetto, & Bohbot, 2012). Another study testing younger and older adults in a wayfinding task that allowed participants to use either a flexible spatial strategy involving the use of efficient shortcuts or an inflexible response strategy involving route-following found that older adults consistently used the response strategy. This was in contrast to the younger adults who flexibly switched to the more efficient spatial strategy during the wayfinding task (Harris & Wolbers, 2014). Older adults display impairment when required to revisit locations memorized relative to external landmarks, likely reflecting impairment of relative positional encoding of environmental stimuli (Bates & Wolbers, 2014). Aging has also been associated with a decline in other landmark-dependent navigation processes including impairment in linking directional knowledge to the location of environmental landmarks and decreased memory for the sequence in which landmarks are encountered (Lester, Moffat, Wiener, Barnes, & Wolbers, 2017; Zhong & Moffat, 2016; Head & Isom, 2010). Related to this, a cross sectional study in humans examining the relationship between age and the use of spatial strategies in a radial arm maze found that the proportion of 8-year-old children who were identified as spatial learners was approximately 85%, whereas this proportion decreased to 50% in young adulthood and then continued to decline to only 35% among people over the age of 60 years in favor of the use of more rigid stimulus response strategies (Bohbot et al., 2012). Similarly, among 107 older adults between 55 and 80 years of age, wayfinding performance linearly decreased with age and correlated with a concurrent decrease of gray matter within the hippocampus (Konishi et al., 2017).

The shift away from spatial strategies toward reliance on habit-based response strategies might not simply be because of ageing, but because of experience during young adulthood. For example, action video games (e.g., Call of Duty) require players to perform many rapid stimulus–response actions and navigate by way of the external GPS cues (West et al., 2018). When nonplayers were trained on 90 hr of action video games (e.g., Call of Duty), it was found that the use of environmental landmarks to guide wayfinding decreased and this correlated with gray matter loss in the hippocampus (West et al., 2018). Therefore, this study shows that one's everyday experiences can shape the brain and could even affect how they perceive the world (Cialone, Tenbrink, & Spiers, 2018). Further highlighting this observation, a recent study found that people who rely more on the in-car GPS systems to navigate, over time, displayed a steeper decline in hippocampal-dependent spatial memory performance (Dahmani & Bohbot, 2020). In a longitudinal segment of this study, GPS was found to cause a decrease in the ability to use spatial landmarks years later, independently of participants' awareness of their navigation ability. These results suggest that when people are exposed to tasks or environments that promote response learning, it can reduce the ability to use landmarks, reduce ability to learn the relationships between landmarks, and is associated with a decreased gray matter in the hippocampus, at any age, even in young adults when brain tissue is healthy.

In the current study, we employed a mobile video game designed to measure human spatial navigation ability through gameplay—SHQ—to test if the use of landmark-dependent navigation strategies changes across the life span. SHQ is a VR navigation task for mobile and tablet devices that was funded by T-Mobile owned by Deutsche Telekom and was designed as a possible early diagnostic tool for AD (Spiers, Coutrot, & Hornberger, 2021; Coughlan et al., 2018, 2019, 2020; Coutrot et al., 2018). SHQ was recently further validated using real-world navigation tasks demonstrating that performance in SHQ predicts performance in the real-world (Coutrot et al., 2019). Whereas previous reports using SHQ focused on wayfinding and path integration levels, here we analyze data from the radial maze elements of the game, thereby providing the first summary of this data set. One of the unique elements of the radial maze is that it explores the use of different strategies via direct behavior in the task, thus extending findings on navigation ability beyond those based solely on self-assessment questionnaires not linked to recent experience. The current study aimed to validate and extend findings from radial arm maze tasks found in smaller studies conducted in the laboratory using a larger, more representative worldwide sample. Because landmark use is highly correlated with spatial navigation strategies (Andersen, Dahmani, Konishi, & Bohbot, 2012) and spatial learners display increased visual attention to targets in the environment (Drisdelle et al., 2017), we used this measure as an approximation of the use of spatial strategies within the SHQ Virtual Radial Maze. Using a sample of over 37,000 participants, we examined whether landmark use during the completion of the SHQ Virtual Radial Maze varied across an age range between 19 and 69 years and whether there was an interaction with gender. Spatial memory performance within the SHQ Virtual Radial Maze was also recorded. We predicted that, as in previous studies conducted in the laboratory suggest, navigational strategies that depend on the use of landmarks will decline with age in favor of more rigid stimulus–response strategies. We also predicted that, as demonstrated by previous studies, landmark-dependent navigation will be associated with better cognitive performance within the SHQ Virtual Radial Maze.

METHODS

Game Design

As detailed in Coutrot et al. (2018) and Spiers et al. (2021), SHQ was developed in collaboration with the independent video games design company Glitchers Ltd and used Unity 3D (Unity Technologies) for smart phones and tablets (apple and android devices). "SHQ" (https://www.alzheimersresearchuk.org/research/for-researchers/resources-and-information) was released on May 4, 2016 on the App Store for iOS and on Google Play for Android and was available in 17 languages. Through the game, participants followed a sea captain as he tries to recover his father's lost memories. The player manipulates the game through four controls, (i.e., tap left to turn left, tap right to turn right, swipe up to speed up, and swipe down to halt). Players were asked a set of optional questions, which included their age, gender, and nationality.

SHQ was designed to reproduce classic navigation tasks used in the literature. Players were tasked to complete game levels that tested performance in three different types of tasks found in the literature. The data from the first two task types, wayfinding and path integration, have been described in Coutrot et al. (2018). The third task type, performance in a virtual radial maze (SHQ Virtual Radial Maze), has previously not been examined and is the focus of the current research report. The experimental tasks in SHQ were accessed by unlocking levels sequentially. These levels were grouped into five themed areas, each containing 15 levels that contained the wayfinding and path integration tasks. At the end of each themed area, players were asked to complete a bonus level (five in total), which consisted of the SHQ Virtual Radial Maze, which we focus on in this article. The completion of the bonus SHQ Virtual Radial Maze levels was optional, and players had the option to skip them to progress to the next themed area.

SHQ Virtual Radial Maze Task

The focus of the current article centers around performance in the SHQ Virtual Radial Maze levels based on radial mazes used in the rodent and human literatures (Bohbot et al., 2007; Iaria et al., 2003; Packard et al., 1989; Olton & Papas, 1979). Specifically, the SHQ Virtual Radial Maze task was modeled after the 4 on 8 virtual maze (4/8VM), a computerized behavioral task used in the laboratory to assess learning and memory performance and navigation strategy (Bohbot et al., 2007; Iaria et al., 2003). The player is presented with a novel environment with distinct landmarks in each level. The SHQ Virtual Radial Maze was used to assess the degree to which landmarks were used during navigation. At the beginning of each SHQ Virtual Radial Maze level, the player's boat in which they control begins in the center of a platform surrounded by six radial arms (see Figure 1). The environment that surrounds the radial arms contains both proximal and distal landmarks (e.g., icebergs, animals, volcanoes, mountains). The player is instructed to collect as many stars as possible. In Part 1, three of the six radial arms are blocked and the player's goal is to visit the three available arms. When the player enters an arm, a star appears and is collected. When all three stars are collected, the player moves on to the second part of the level. Players were unable to see the stars from the center; therefore, they had to remember which arms contained stars and which did not to perform the second part of the task without

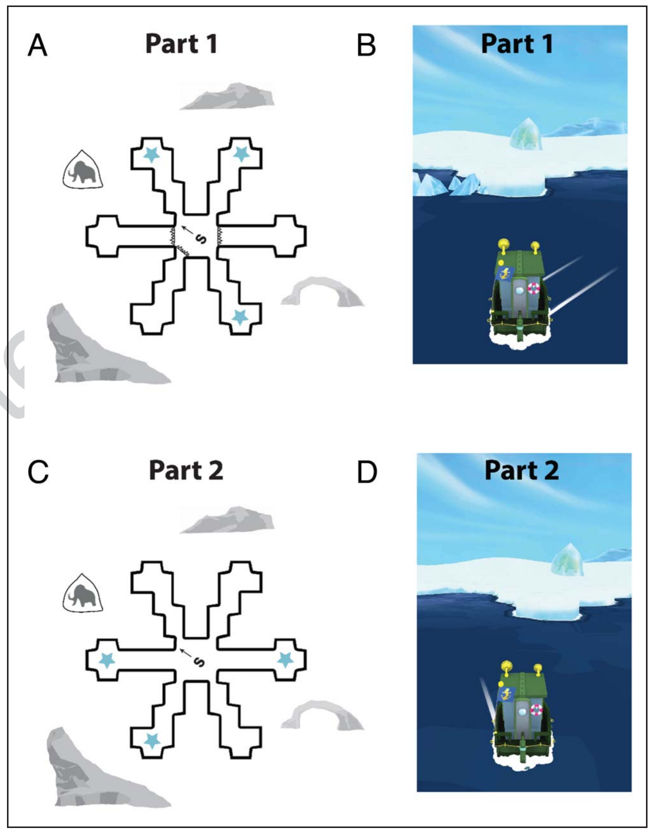

Figure 1. An example of a SHQ Virtual Radial Maze level. The radial maze levels contain six pathways surrounded by proximal and distal landmarks (e.g., ice bergs, mountains) and consist of two parts. Part 1 is shown from both an overview perspective (A) and a third-person perspective. (B) Three of the six pathways are blocked, and the player is required to navigate the boat to visit the three open pathways to collect a star that pops out of the water. Part 2 is shown from both an overview perspective (A) and a third-person perspective. (B) All six pathways are made available, and the player is required to visit the pathways that were unavailable during Part 1 to collect the remaining three stars. Reference memory errors were defined as entering a pathway entered during Part 1 that needed to be avoided during Part 2. Working memory errors were defined as re-entering a pathway in Part 2 that was already entered previously during Part 2. When the radial arm maze level is completed, the player is asked a multiple-choice question about how they found the stars (i.e., a counting-dependent strategy vs. a landmark-dependent strategy).

errors. In Part 2, all six radial arms are now open. The player's goal in Part 2 is to visit the three radial arms that were blocked during Part 1 and collect the remaining three stars. Because 1) the SHQ Virtual Radial Maze levels are very different compared with the standard levels and only begin to be presented to the player after 15 standard levels are completed and 2) no overt instructions are given to the player about the goal of the level, SHQ Virtual Radial Maze Level 1 was counted as a practice trial. It should be noted that this makes the SHQ Virtual Radial Maze different from the 4/8VM because the latter includes detailed instructions to the participants.

Two types of memory errors are recorded during Part 2 of SHQ Virtual Radial Maze levels. First, a "reference memory error" is recorded when a participant visits a radial arm that does not contain an object in Part 2, that is, entering a radial arm that they previously visited in Part 1 of that trial and needed to avoid during Part 2. A "spatial working memory error" is recorded in Part 2 when a participant visits an arm that they had already visited before collecting all three stars, that is, entering a radial arm that they already visited in the same Part 2 of that trial.

While data from these game levels did not provide specific details about navigational strategies used (e.g., did you use the *relationship* between *multiple* landmarks), reports of whether landmarks were used or not to complete the radial maze were obtained. To assess the degree to which landmarks were used, players were presented with a multiple-choice question after each SHQ Virtual Radial Maze level that asked players what they did to remember which radial arms they needed to visit and which ones they needed to avoid: "How did you navigate?" (1) Counted from the start; (2) used multiple landmarks; (3) counted from a landmark. A player was identified as using landmarks or not using landmarks when solving the maze based on their answer to a question after the first experimental level was complete (SHQ Virtual Radial Maze Level 2, which was done after the practice trial in Level 1). If a player answered that they used a landmark to navigate, they were categorized as using a landmark-based strategy (i.e., Answer 2 or 3). In contrast, if the player indicated that they counted the radial arms from the start and did not use any landmarks (i.e., Answer 1), they were categorized as spontaneously using a counting strategy. An option to skip this question was also provided; if this was chosen, their strategy was classified as "none reported" and was not included in the analysis.

There are several important differences between the SHQ Virtual Radial Maze and the 4/8VM that is used in the laboratory. First, a detailed verbal report from the player about how they completed the task was not obtained, as is the case with the 4/8VM, and we therefore could not distinguish between people's strategies that used the relationship between multiple landmarks (spatial strategy) and strategies that used a single landmark or multiple landmarks in conjunction with a rigid pattern or counting (response strategy). Because of this, we combined people into two groups: People reported using a strategy that relied on landmarks and people who reported using a strategy that relied on counting only. Therefore, this task is able to distinguish between people who were inclined to use external landmarks during the resolution of the task and those who were not. However, the current methodology cannot distinguish between more fine-grained strategy differences as done in the past based on data collected in the laboratory (e.g., Aumont, Arguin, Bohbot, & West, 2019; West et al., 2018; Bohbot et al., 2007, 2013; Konishi & Bohbot, 2013; Iaria et al., 2003). Second, because of time constraints, there were six arms in total instead of eight. Third, the SHQ Virtual Radial Maze only presented players with each environment once per level (i.e., one trial), whereas the standard 4/8VM repeats a minimum of three trials in the same environment and required people to learn the environment. Because the SHQ Virtual Radial Maze does not repeat the same environment across multiple trials, we only compared memory errors within Parts 1 and 2 of a single trial. Our operationalization of a reference memory error in the SHQ Virtual Radial Maze therefore differs from previous reports using the 4/8VM: A reference memory error in the SHQ Virtual Radial Maze is recorded when a participant visits a radial arm that does not contain an object in Part 2 of the same trial; in contrast, a reference memory error in the 4/8VM is recorded when a participant visits a radial arm that does not contain an object in Part 2 of multiple trials that repeat the same environment.

Data Collection

Within the opening screen menu, participants were made aware of the purpose of the game. They were then asked to give their consent to share their data. Furthermore, the opt out was always available in the game's settings. Data integrity and data privacy were adhered to according to German data security law. For full details please see Coutrot et al. (2018).

Data Analysis

We did not include data of people who indicated that they were 18 years old as this was the minimum age required to consent to data sharing and likely contained a large number of people who were under the age of 18 years. In other words, people under the age of 18 years who accessed the game more than likely selected the lowest age possible, adding a potential confound. Significantly lower sample sizes were obtained for people older than 69 years, so we chose this age as the higher end cutoff. To analyze the factor of age, we organized the data in bins that ranged 10 years (19–29, 30–39, 40–49, 50–59, 60–69). As stated above, participants completed a first practice level before completing the experimental levels. We chose to focus our analyses on SHQ Virtual Radial Maze Level 2 (i.e., the first experimental level) because (a) this level provided data for the initial measures of spontaneous navigation strategy

Table 1. Participant Breakdown by Age, Sex, and Strategy

	Age				
	19–29	*30–39*	*40–49*	*50–59*	*60–69*
Female					
Counting	n = 3338	n = 1000	n = 506	n = 234	n = 117
Landmark	n = 4742	n = 1215	n = 590	n = 324	n = 128
Male					
Counting	n = 5439	n = 2775	n = 1399	n = 516	n = 154
Landmark	n = 8937	n = 3705	n = 1713	n = 602	n = 151

used and spatial memory performance within the radial maze and, (b) as noted in Coutrot et al. (2018), the sample size falls dramatically the later into the game the sample is taken from (Coutrot et al., 2018). Other demographics included gender and home environment. Home environment was analyzed because of the fact that people who grow up in rural environments are hypothesized to have more opportunity to use distal landmarks during navigation while people who grow up in cities are more reliant on Cartesian coordinates, thereby engaging spatial memory to a significantly lower degree. For simplicity, home environment was collapsed across noncity categories (rural, suburbs, mixed) and was compared with those participants who reported living in cities (Coutrot et al., 2018, 2019, 2022).

Data Analysis and Predictions

Linear and logistic regressions were performed using MATLAB's "fitglm" function (MATLAB and Statistics Toolbox Release 2022b, The MathWorks, Inc.). Odd ratios were calculated by taking the exponential of the model estimate of the relevant variable (e.g., exp(β1)). Follow-up effects sizes ("mes"/"mestab") and two-way ANOVAs ("mes2way") were calculated using Hentschke's effect size toolbox as described in Hentschke H, Stüttgen MC. Computation of measures of effect size for neuroscience data sets (Hentschke & Stuttgen, 2011).

RESULTS

Participants

Participants were included in analyses if they (a) provided their age and gender, (b) completed a minimum of the first two SHQ Virtual Radial Maze levels (i.e., the practice level [SHQ Virtual Radial Maze Level 1] and the first experimental level [SHQ Virtual Radial Maze Level 2]), (c) reported a navigation strategy, and (d) were between the ages of 19 and 69 years. Six thousand thirty-seven did not report a navigation strategy and therefore were not included in the analyses. This resulted in a total N = 37,585 being included for analysis (n = 12,194 female (mean age [*SEM*] = 29.3 [0.09]); n = 25,391 male (mean age [*SEM*] = 30.4 [0.06])). See Table 1 for a total breakdown by age range, gender, and navigational strategy. Planned a priori comparisons were made to examine the factors of age and gender when analyzing the dependent measures of navigational strategy, reference memory errors, and spatial working memory errors.

Navigational Strategy

We first analyzed the spontaneous navigational strategies people used to complete SHQ Virtual Radial Maze Level 2. Overall, 42% of participants reported using a counting-based strategy whereas 58% of participants reported using a landmark-based strategy. We ran a logistic regression to predict navigational strategy, based on age, gender, and home environment. Gender (odds ratio = 1.415, $t(35186) = 4.32$, $p < .001$) and age (odds ratio = 0.9929, $t(35186) = -3.49$, $p < .001$) were both significant predictors, as was the interaction between age and gender (odds ratio = 0.9911, $t(35186) = -3.52$, $p < .001$), chi-square statistic versus constant model: 161, $p < .001$. There was no effect of home environment or any other interactions. To more closely examine these effects, we ran direct comparisons between the predictor variables using the age bins (as described in Methods section) and interpreted the resultant effect sizes. We found that females and males employed a counting-based strategy (female = 43%; male = 40%) and a landmark-based strategy (female = 57%; male = 60%) at similar rates (phi = 0.02, CI [0.01, 0.03]; see Figure 2A). Furthermore, when exploring strategy use differences between genders within age bins, we found negligible effects (all phi < 0.1). Importantly, we did observe that overall landmark-dependent strategy use declined with age (Figure 2B). Because of the significant Age × Gender interaction that predicted navigational strategy, we conducted separate regressions examining changes in strategy with age for both males and females. We found that males showed a stronger decline in landmark-dependent navigation strategy use with age compared with females (odds ratio = 0.865, $t(23766) = -10.32$, $p < .001$; frequency across age bins: Cramer's V = 0.066

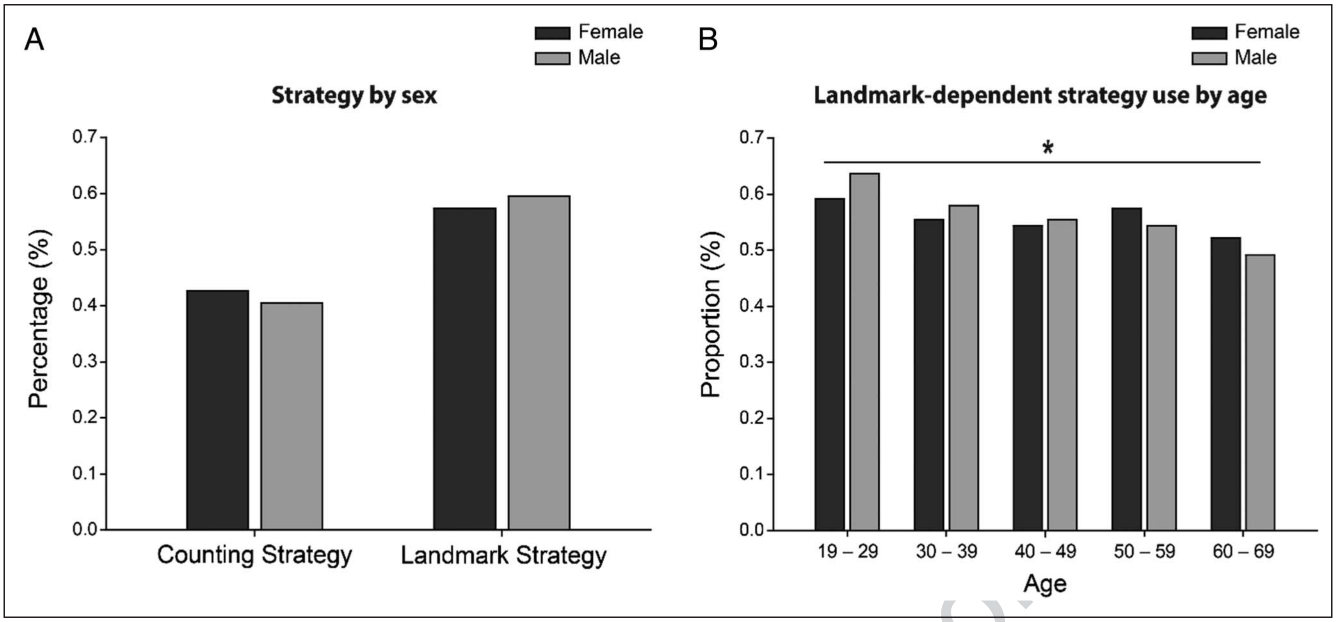

Figure 2. (A) Percentage of players reporting a counting- versus landmark-dependent strategy by sex. (B) Proportion of players reporting a landmark-dependent strategy by sex and by age bin.

[0.05, 0.08], chi-square = 110.1; females: odds ratio = 0.937, $t(11426) = -3.37$, $p < .001$; frequency across age bins: Cramer's $V = 0.04$ [0.03 0.06], chi-square = 19.8) (Figure 2B). Thus, gender and age do seem to be relevant to spontaneous strategy use—however, it should be noted that there are large sample size differences among the age and gender groups (see Table 1).

Spatial Memory Performance

Both reference and spatial working memory errors in SHQ Virtual Radial Maze Level 2 were compared between people who used a landmark-based or counting-based strategy. We first examined reference memory errors that occurred when a participant visited a radial arm that did not contain an object, that is, a radial arm that they previously visited in Part 1 of that trial. People reporting a landmark-dependent strategy made fewer overall reference memory errors ($M = 1.21$, $SEM = 0.007$) compared with those who used a counting-based strategy ($M = 1.58$, $SEM = 0.008$; Figure 3A). We then ran a linear regression model to predict reference memory errors based on age, gender, and navigational strategy. We

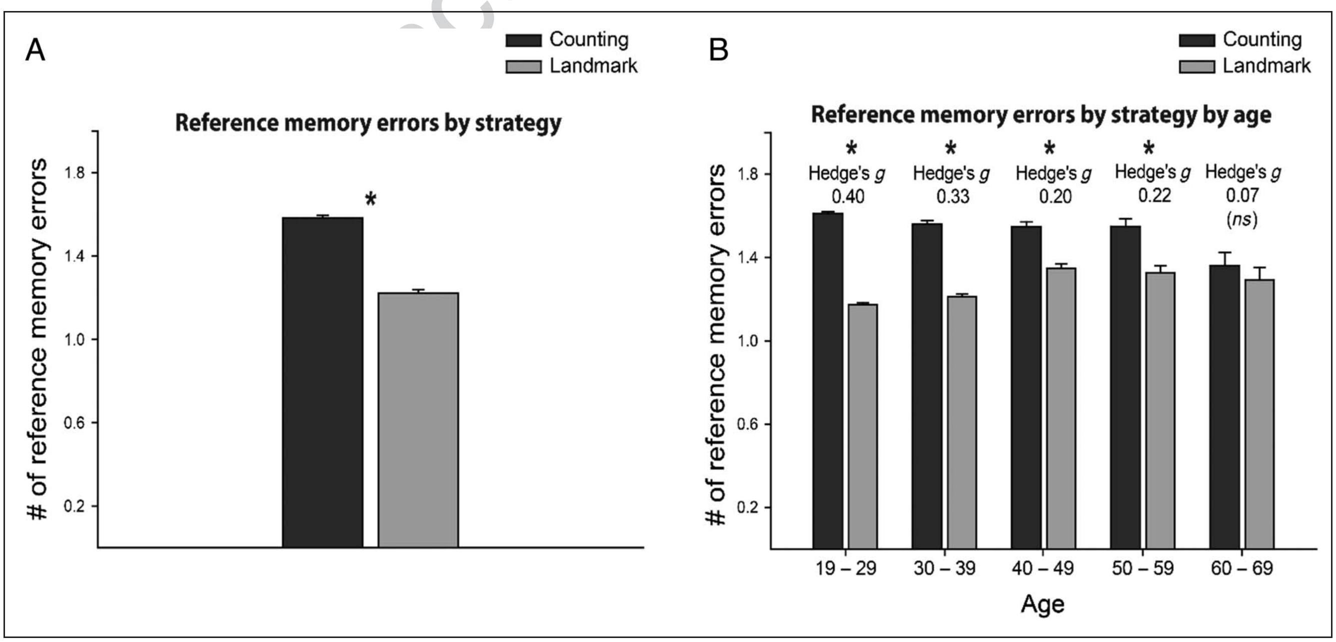

Figure 3. (A) Reference memory errors made by players reporting using a counting versus landmark-dependent strategy. (B) Reference memory errors by players reporting using a counting versus landmark-dependent strategy by age bin.

found a significant effect of strategy (beta [*SD*] = 0.46 [0.06], $t(37577) = 8.12$, $p < .001$), gender (beta [*SD*] = −0.26 [0.05], $t(37577) = -5.50$, $p < .001$), as well as a significant interaction between all factors (Age × Gender: [beta (*SD*) = 0.006 (0.002), $t(37577) = 4.13$, $p = .001$]; Age × Strategy: [beta (*SD*) = −0.005 (0.002), $t(37577) = -2.49$, $p = .013$]; Gender × Strategy: [beta (*SD*) = 0.25 (0.071), $t(37577) = 3.55$, $p < .001$]; Age × Gender × Strategy: [beta (*SD*) = −0.006 (0.002), $t(37577) = -2.62$, $p = .008$], *F*-statistic versus constant model: 173, $p < .001$. Briefly, when including home environment in this model, we found no significant effects of this predictor or interactions with it. To interpret these effects related to reference memory errors, we examined the effect sizes. When we compared reference memory errors within strategy type, males showed a small advantage when using a landmark-dependent strategy (Hedge's g(CI) = 0.06 [0.03 0.09], $t(22105) = 4.32$, $p < .001$) but not when using a counting strategy (Hedge's g(CI) = 0 [−0.03 0.03], $t(15476) = 0.028$, $p > .9$). However, both females and males showed that landmark-dependent strategy use was associated with fewer reference memory errors (females: Hedge's g (CI): 0.31 [0.27 0.34], $t(12192) = 16.7$, $p < .001$; males: Hedge's g (CI): 0.37 [0.34 0.39], $t(25389) = 28.8$, $p < .001$). To look at the effect of age, we first collapsed across gender (based on the above analysis), and found there was a small to medium effect of strategy type across all age bins showing landmark-dependent strategy use was associated with fewer errors, except in the oldest 60–69 age bin (all Hedge's $g > 0.19$, $t(> = 1674) > = 4.44$, $p < .001$; except last age bin: Hedge's $g = 0.07$, $t(548) = 0.81$, $p = .42$; see Figure 3B). However, when looking at males and females separately within each age bin, we observed an effect of strategy use on reference memory errors in the 60–69 age bin (see Figure 4A and 4B). To investigate this further, we ran a factorial analysis (two-way ANOVA) of gender and strategy in the 60–69 age bin, and found a significant effect of gender ($F = 5.7$, $p = .02$, eta-square = .01), with females relying on a landmark-dependent strategy showing better reference memory ($M = 1.10$, $SEM = 0.08$) than their male landmark-dependent counterparts ($M = 1.45$, $SEM = 0.08$; Hedge's g (CI) = 0.34 [0.11 0.58], $t(277) = 2.87$, $p = .004$). These landmark-dependent females also performed better than their female counting counterparts ($M = 1.32$, $SEM = 0.10$; Hedge's g (C)I) = 0.22 [−0.03 0.47], $t(243) = 1.71$, $p = .09$). This confirmed that within the 60–69 age range, females using landmarks displayed better reference memory performance compared with males overall and females who used a counting strategy. Of note, although this age category was the least populated, we have similar participant numbers across the groups compared, and a large sample size compared with laboratory testing (all $116 > n > 155$; see Table 1).

We next examined spatial working memory errors, which were recorded during Part 2 when a participant revisited an arm that they had already visited before collecting all three stars. People reporting a landmark-based strategy made similar working memory errors ($M = 0.18$, $SEM = 0.003$) compared with those who used a counting-based strategy ($M = 0.18$, $SEM = 0.004$). We ran a linear regression model on spatial working memory errors with the same predictors as above and found a significant effect of age (beta [*SD*] = 0.002 [0.001], $t(37577) = 3.06$,$p = .002$), and strategy (beta [*SD*] = 0.058 [0.025], $t(37577) = 2.30$, $p = .02$), and a trend for gender (beta [*SD*] = −0.037 [0.02], $t(37577) = -1.81$, $p = .069$). There was a trend for significant interactions between gender and strategy (beta [*SD*] = −0.054 [0.03], $t(37577) = -1.71$, $p = .09$), and a trend toward a significant interaction between age and strategy (beta [*SD*] = −0.0015 [0.0008], $t(37577) = -1.81$, $p = .07$), *F*-statistic versus constant model: 15.3, $p < .001$. Again, we found no effect of home environment when included in the model.

When examining the effect sizes related to spatial working memory errors (see Figure 4C and D) there was a negligible effect size of gender (Hedge's g = 0.08 [0.06, 0.11], $t(37583) = 7.76$, $p < .001$). There was a negligible effect size of gender within strategy types, but nevertheless, males showed an advantage when using a landmark-dependent strategy (Hedge's g[CI] = 0.06 [0.03, 0.09], $t(22105) = 4.26$, $p < .001$) and when using a counting strategy (Hedge's g[CI] = 0.12 [0.09, 0.15], $t(15476) = 6.9$, $p < .001$). There was no effect of strategy when collapsing across gender (Hedge's g = 0.003 [−0.018, 0.023], $t(37583) = 0.27$, $p = .79$), and this pattern was reflected in every age bin (all Hedge's $g < 0.03$, $t(> = 1674) < = -1.04$, $p > 0.2$) with the exception of people who were 60–69 years old, where there was a small effect of strategy in that both females and males showing fewer errors associated with using the counting strategy ($F = 7.002$, $p = .008$, eta-square = 0.013, Hedge's g = −0.22 [−0.06–0.39], $t(548) = -2.62$, $p = .009$), females: counting: $M = 0.17$, $SEM = 0.04$; landmark: $M = 0.30$, $SEM = 0.05$; Hedge's g = −0.25 [−0.5 0.001], $t(243) = -1.97$, $p = .051$; males: counting: $M = 0.20$, $SEM = 0.04$; landmark: $M = 0.31$, $SEM = 0.05$; Hedge's g = −0.20 [−0.43, 0.03], $t(303) = -1.77$, $p = .078$; see Figure 4C and 4D).

Control for Time to Complete Radial Maze Level

Although there was no time constraint or instruction to complete the radial maze in a certain time limit, we found that there was a general slowing of completion time (for simplicity, we refer to this measure as "RT") with age. Furthermore, based on the diminishing effect sizes with age displayed in Figure 4A and 4B, it appears that the cost of using a counting strategy on reference memory error performance could diminish with age. To account for the slowed RT with age and to explore errors in the context of ageing in more detail, we normalized errors as a function of RT ([RT × error] + error). Thus, errors would be further penalized for slow completion time (for zero errors, we used the value of the raw RT). A regression of the

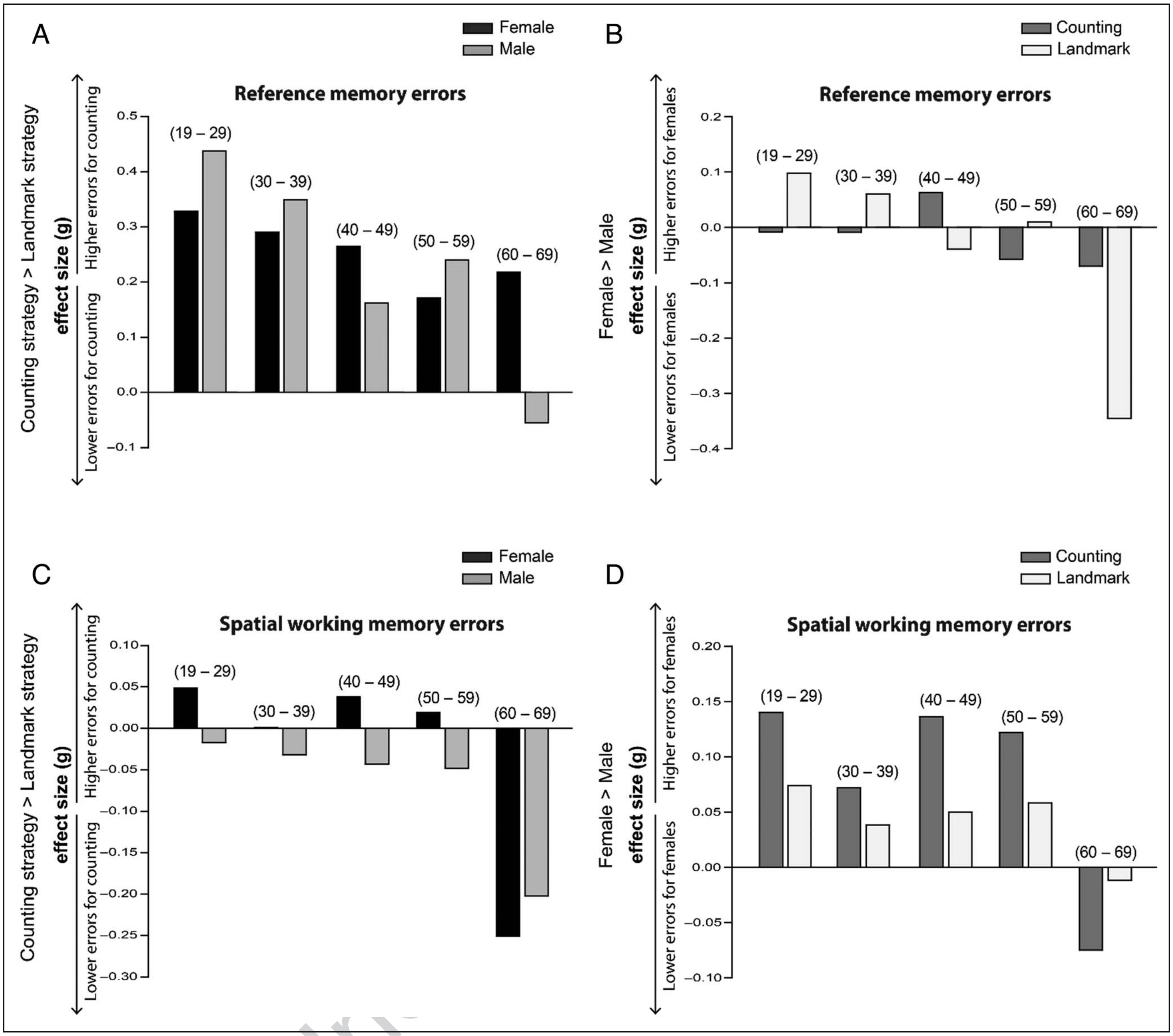

Figure 4. Effect sizes by age bin displayed for both reference memory errors (A and B) and spatial working memory errors (C and D). Age bins are indicated in parentheses. In all figures, higher effect sizes represent higher error levels. Separate comparisons were made for navigation strategy and gender. For navigation strategy (A and C), a higher effect size represents more errors for people using the counting strategy compared with the landmark strategy (effect sizes for males and females are plotted separately). For gender (B and D), a higher effect size represents more errors for females compared with males (effect sizes for the counting groups and landmark groups are plotted separately). Within the 60–69 age range, females using the landmark strategy displayed better reference memory performance compared with males overall and females who used a counting strategy (A and B). In parallel, 60- to 69-year-olds who used the counting strategy displayed fewer spatial working memory errors overall (C and D).

normalized reference memory errors showed a significant effect of age (beta [*SD*] = 0.014 [0.003], $t(37577) = 5.42$, $p < .001$), gender (beta [*SD*] = −0.34 [0.10], $t(37577) = -3.37$, $p < .001$) and strategy (beta [*SD*] = 0.76 [0.12], $t(37577) = 6.17$, $p < .001$) and an interaction between Age × Strategy (beta [*SD*] = −0.011 [0.004], $t(37577) = -2.81$, $p = .005$). See Figure 5A and 5B for effect sizes. Overall, the pattern of results was very similar to the previous reference memory error analysis; however, those employing a counting strategy no longer showed an age-related decline in errors when RT is taken into consideration.

A regression of the normalized spatial working memory errors showed a significant effect of strategy (beta [*SD*] = 0.13 [0.06], $t(37577) = 2.40$, $p = .02$), and age (beta [*SD*] = 0.012 [0.001], $t(37577) = 9.95$, $p < .001$), as well as a significant interaction between all factors (Age × Gender: (beta [*SD*] = −0.005 [0.001], $t(37577) = -3.36$, $p < .001$); Age × Strategy: (beta [*SD*] = −0.006 [0.002], $t(37577) = -3.21$, $p = .001$); Gender × Strategy: (beta [*SD*] = −0.21 [0.070], $t(37577) = -2.97$, $p = .003$); Age × Gender × Strategy: (beta [*SD*] = 0.006 [0.002], $t(37577) = 2.53$, $p = .01$). See Figure 5C and 5D for effect sizes. Overall, the pattern was similar to the previous

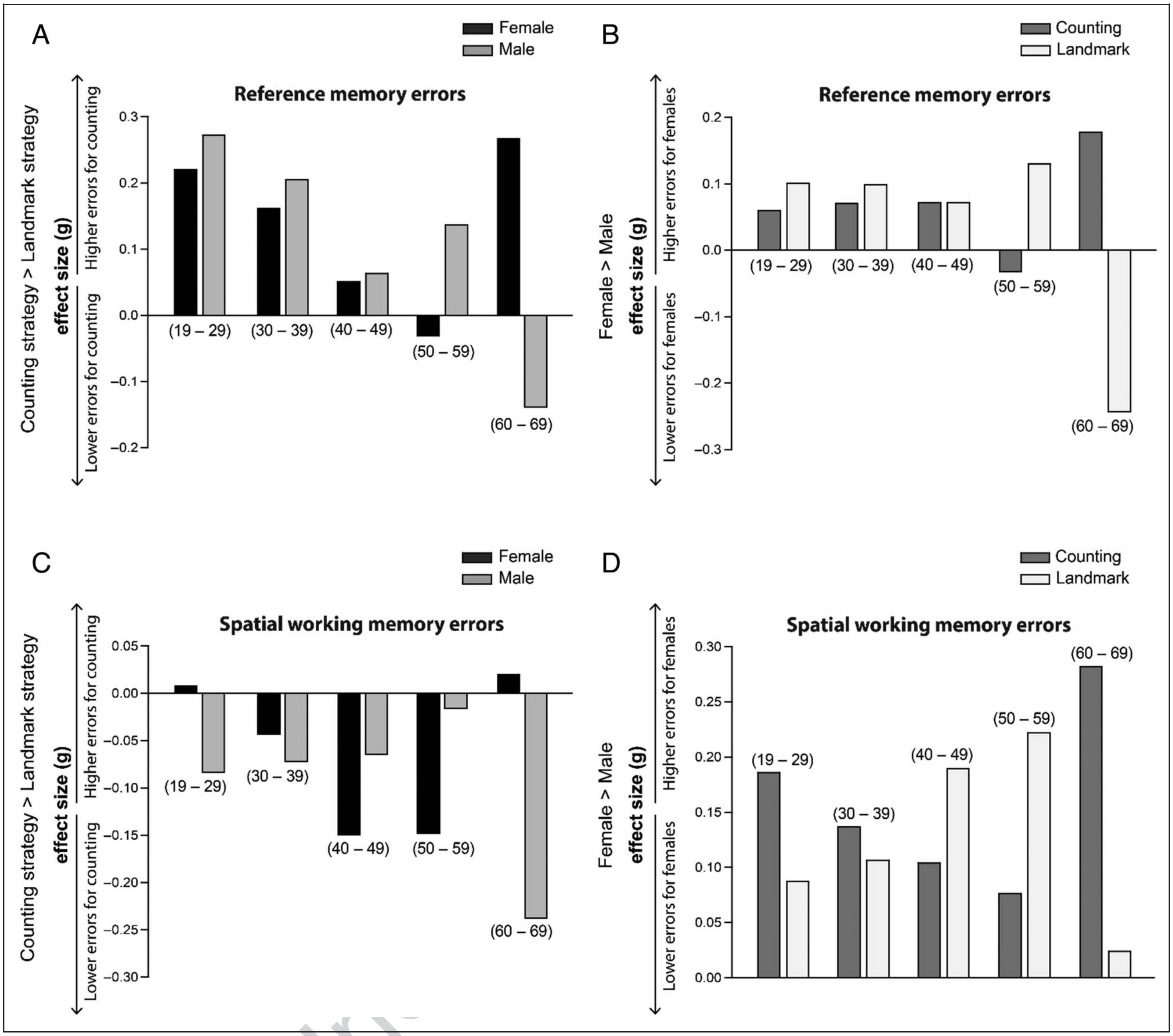

Figure 5. Normalized errors accounting for variations in RT with age. Effect sizes by age bin displayed for both normalized reference memory errors (A and B) and normalized spatial working memory errors (C and D). Age bins are indicated in parentheses. In all figures, higher effect sizes represent higher error levels. Separate comparisons were made for navigation strategy and gender. For navigation strategy (A and C), a higher effect size represents more errors for people using the counting strategy compared with the landmark strategy (effect sizes for males and females are plotted separately). For gender (B and D), a higher effect size represents more errors for females compared to males (effect sizes for the counting groups and landmark groups are plotted separately). When RT is included in the model, there are no declines in errors associated with age. Furthermore, within the 60–69 age range, females using the landmark strategy again display better reference memory performance compared with males overall and females who used a counting strategy (A and B). In parallel, within the 60- to 69-year-old range, only males who use the counting strategy displayed fewer spatial working memory errors (C and D).

spatial working memory error analysis; however, females showed worse performance overall, and the advantage seen in the counting group in the 60–69 age range was restricted to males when RT is taken into consideration.

Radial Maze Errors in Relation to Wayfinding Ability

We obtained wayfinding ability scores for our participants from the larger pool of data reported in Coutrot et al. (2018), which is a video-gaming-skill corrected value for overall spatial navigation abilities (reported as "OPcorr"). We compared wayfinding ability between those using a landmark (M = 141.8, SEM = 1.42) and a counting-based (M = 134.9, SEM = 1.71) strategy and found no difference (Hedge's g = 0.04 [0.01, 0.06])—the same held when comparing within gender or across age groups. We also found no correlation between wayfinding ability and the number of reference or spatial working memory errors (all $r < -.05$).

Table 2. Proportion of Players Who Reported Using a Landmark-dependent Strategy in Each Country Who Had at Least 500 Players Completed the First Two SHQ Virtual Radial Maze Levels

Country	*% of Participants Reporting a Landmark-dependent Strategy*	*N*
France	69%	919
Spain	67%	614
Greece	67%	2600
Poland	66%	1511
Brazil	66%	576
Hungary	64%	1471
Slovakia	61%	881
Czechia	61%	2869
Italy	59%	1326
Canada	59%	1133
Netherlands	57%	2626
China	57%	817
United States	57%	8579
Australia	56%	794
Germany	55%	3537
United Kingdom	51%	5593

Country and Navigational Strategy

We conducted an exploratory analysis examining by country the proportion of people who used a counting versus landmark-based strategy. We reported the country data if they had at least 500 participants. The data are shown in Table 2 and reflect that there is variability among countries with respect to the proportion of participants who completed the SHQ Virtual Radial Maze using a counting versus landmark-based strategy. No evident pattern was observed in this sample of countries.

DISCUSSION

In the current study, we examined data collected from a radial arm maze (SHQ Virtual Radial Maze) contained in the SHQ mobile video game. The SHQ Virtual Radial Maze was designed after radial arm mazes used in the human and rodent literatures (Bohbot et al., 2007; Iaria et al., 2003; Packard & McGaugh, 1992; Packard et al., 1989; Olton & Papas, 1979), and allowed for the testing of our hypotheses generated from these previous smaller studies with a significantly larger, diverse sample of the world population normally inaccessible to researchers. Our results support previous findings showing that, during ageing, people shift away from landmark-dependent navigational strategies, which previous studies have shown is supported by the hippocampus, during early adulthood in favor of stimulus–response navigational strategies later in life (Bohbot et al., 2012). This reveals that the decreased reliance on landmarks during ageing is not simply present with late-life ageing, but is rather progressive from ~30 years of age onward, similar to the general overall decline in spatial ability previously observed with the wayfinding task in SHQ (Coutrot et al., 2018). Previous, smaller sample studies have found no significant overall gender difference with respect to the use of landmark-dependent or stimulus–response navigation strategies (Konishi & Bohbot, 2013; Konishi et al., 2013; Bohbot et al., 2007; Iaria et al., 2003). This stands in contrast to the robust differences in gender observed in the wayfinding task in SHQ (Coutrot et al., 2018). It suggests that the difference between men and women in wayfinding may not be driven by differences in landmark or stimulus–response strategies, as we found no relationship between strategy use and wayfinding performance.

In relation to errors committed on the radial maze, we found a more complex relationship of strategy. Reference memory was better for people using landmark-dependent navigation strategies overall, even in older age ranges up until 50–59. Importantly, the females in the 60–69 age group using landmark-based strategies outperformed their male counterparts as well as their female counting counterparts on reference memory. In contrast, more spatial working memory errors were committed by the same 60–69 age group relying on landmark-based strategies. What might cause this discrepancy between reference and working memory errors? When there are no delays or reorientation of view, as is the case for spatial working memory during Part 2 of the SHQ radial maze, using a counting strategy might be more efficient while at the same time less flexible, as are stimulus–response strategies in general. This could in turn result in fewer errors. Indeed, response learners make fewer non-hippocampus-dependent working memory errors in the laboratory (Blanchette et al., 2020; Aumont, Blanchette, et al., 2019; Bohbot et al., 2007; Iaria et al., 2003).

Our finding supports previous observations from smaller studies that show that hippocampus-dependent spatial learning, which relies on landmarks during navigation, declines with age. The present findings could point to a relationship between increased landmark use (i.e., spatial strategies) and preserved spatial memory performance during ageing (Konishi et al., 2017). This might be especially important in women because compared with men overall and women who use spatial strategies, women who use stimulus–response strategies display the lowest amount of gray matter in the hippocampus and the highest amount of gray matter in the caudate-nucleus (Sodums & Bohbot, 2020), which is associated with greater risk of developing AD (Persson, 2018; Apostolova et al., 2006).

Finally, we did not find any notable effects of home environment on strategy use or errors committed. As mentioned above, there was no effect of strategy use on wayfinding ability, nor any relationship between wayfinding and reference or spatial working memory errors. This suggests that these tasks within SHQ (radial maze vs. wayfinding) measure separate skills. Note, however, that for comparability with existing reports on SHQ, only a basic measure wayfinding ability, that is, trajectory length, of a few select levels was included in our analyses. This parameter may not be the most relevant to correlate with radial maze performance, and future studies that focus on more sophisticated features from the trajectories during wayfinding might be more sensitive to differences between people using different navigation strategies.

There were limitations contained in the current study. First, there was a degree of bias selecting for those who completed the SHQ Virtual Radial Maze because of the fact these radial arm maze game levels were nonmandatory (i.e., they could be skipped) and were offered as a bonus level between each of the main parts of the game that included the wayfinding and path integration tasks (reported in Coutrot, 2018). Furthermore, people had to progress beyond the first 30 levels of the game to complete the first two SHQ Virtual Radial Maze levels (i.e., the practice level and the first experimental level) and be included in our analysis. This likely resulted in selecting for higher performing individuals in our analyses. Even with this limitation, we observed significant declines in landmark-dependent navigation strategy use with age, which was associated with lower spatial memory performance. Another limitation was, unlike the 4/8VM, there was a lack of one-on-one testing and specific instruction about how to complete the task to ensure that the participant paid attention, understood the task, and did not simply enter the pathways randomly without any thought about how to properly complete the task. Indeed, it is possible that that the differences we report could reflect those between people who chose to complete the task in an effortful fashion compared with those who did not. For example, we cannot exclude the possibility that people who reported using landmarks tended to be those who pay attention to the task and notice the environment compared with those who reported using a counting-only strategy. We should, however, also consider the fact that 1) the SHQ Virtual Radial Maze levels were completely optional, 2) participants had to complete 30 standard levels before completing the experimental SHQ virtual maze level where we ascertained whether or not people used landmarks, and 3) people had the option to not answer the question asking about landmark use if they wished, in which case their data were not included in our analyses. Therefore, we can infer that the sample of people for which we do have complete data to include in the current analyses were fairly motivated and likely represent behavioral differences between people who were inclined to use landmarks in some form to complete the task compared with those who did not use landmarks and used a counting strategy. This is especially relevant for the findings in the oldest age group. Another important limitation is that our assessment of navigational strategies in the SHQ Virtual Radial Maze could not distinguish between more granular navigational strategies that are able to be identified in the laboratory. In the original 4/8VM, experimenters undergo a thorough training procedure to properly administer standardized interviews to ascertain a participant's navigational strategy without introducing bias (see Sodums & Bohbot, 2020, for a full description), which was not possible within SHQ. Specifically, using the 4/8VM people have previously been categorized into distinct groups with biological differences based on navigation strategy. People categorized as response learners included those who used no landmarks (i.e., response-start position), those who used a single landmark in conjunction with a full sequence counting strategy (response-landmark), and those who include two or more landmarks but also in conjunction with a full sequence counting strategy from a single starting point (response-landmarks). On the other hand, if multiple landmarks were used, and a full sequence was not used, then people could be categorized as a spatial strategy user (Blanchette et al., 2020; Aumont, Arguin, et al., 2019; Aumont, Blanchette, et al., 2019; Blanchette, Amirova, Bohbot, & West, 2019; West et al., 2015, 2018; Drisdelle et al., 2017; Bohbot, Konishi, Sodums, Dahmani, & Bherer, 2015; Bohbot et al., 2007, 2013; Andersen et al., 2012; Bohbot, Gupta, Banner, & Dahmani, 2011; Iaria et al., 2003). We consider response and spatial learners as distinct groups because of the fact that there are multiple biological differences between them including basal cortisol levels (Blanchette et al., 2020; Hussain, Hanafi, Konishi, Brake, & Bohbot, 2016; Bohbot et al., 2011), volume of the hippocampus and caudate nucleus (West et al., 2018; Bohbot et al., 2007; Iaria et al., 2003), and genetics (Konishi et al., 2016; Banner, Bhat, Etchamendy, Joober, & Bohbot, 2011). Furthermore, our experiments in the laboratory are able to detect if a participant shifts their strategy during the radial arm maze task; however, this process required a detailed interview by a trained experiment and is therefore not possible in the SHQ version of the task. Another interesting avenue for future research would be to include a non-self-report measure of navigational strategy that could be based on, for example, dwell time that includes landmarks in the direct field of view. This could then be used to further evaluate the accuracy of the self-report measures used in the current study.

Despite these observed biological differences when comparing spatial and response learners globally as two groups, differences in wayfinding performance between the subcategories of response learners have also been observed. People categorized as response-landmarks (one or more landmarks but also in conjunction with a full sequence counting strategy) perform better than people who used a counting strategy from a single starting position on a wayfinding task (Etchamendy & Bohbot, 2007). Because of this previously identified behavioral distinction between people categorized as using a response landmarks and response start position strategy and our inability to categorized a more specific response learning strategy, we combined people who reported using "Used multiple landmarks" and "Counted from a landmark," and recognize that we were not able to distinguish more specific navigation strategies that we are able to ascertain using the 4/8VM. We, however, do observe that landmark use of some kind is associated with better memory performance and this does significantly decline with age, which is consistent with previous smaller studies. In fitting with the current data, spatial use in the laboratory is associated with increased landmark use, response-landmark strategies are associated with a moderate amount of landmark use, and people who use a counting-only strategy display the lowest landmark use (Andersen et al., 2012).

Altogether, the results of the current study provided a unique opportunity to validate with a very large data set previous studies that have demonstrated reduced landmark-dependent navigational strategy use in ageing. Furthermore, although overall memory performance was lower for those using non-landmark-dependent strategies, memory performance depended on the memory tested and showed a complex interaction among people in older age ranges. Although we were not in a position to ascertain more specific navigation strategies as we have done previously in the laboratory, our current findings extend previous studies that have shown a decline in landmark-dependent spatial strategy use in ageing that is associated with decreased hippocampal gray matter and cognitive performance. Finally, this study contributes to the mounting evidence in favor of mobile and out-of-lab testing, offering larger and more diverse samples, easier access to patients, and the continuity of research despite mobility limitations (as exemplified by COVID-19).

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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