This article is part of the topic "Individual Differences in Spatial Navigation: Building a Cognitive Science of Human Variation," Nora S. Newcombe, Mary Hegarty and David Uttal (Topic Editors).

Understanding Differences in Wayfinding Strategies

Mary Hegarty,[a] Chuanxiuyue He,[a] Alexander P. Boone,[a] Shuying Yu,[a] Emily G. Jacobs,[a] Elizabeth R. Chrastil[b]

[a]*Department of Psychological & Brain Sciences, University of California*
[b]*Department of Neurobiology and Behavior, University of California*

Abstract

Navigating to goal locations in a known environment (wayfinding) can be accomplished by different strategies, notably by taking habitual, well-learned routes (response strategy) or by inferring novel paths, such as shortcuts, from spatial knowledge of the environment's layout (place strategy). Human and animal neuroscience studies reveal that these strategies reflect different brain systems, with response strategies relying more on activation of the striatum and place strategies associated with activation of the hippocampus. In addition to individual differences in strategy, recent behavioral studies show sex differences such that men use place strategies more than women, and age differences such that older adults use more response strategies than younger adults. This paper takes a comprehensive multilevel approach to understanding these differences, characterizing wayfinding as a complex information processing task. This analysis reveals factors that affect navigation strategy, including availability of the relevant type of environmental knowledge, momentary access to this knowledge, trade-offs between physical and mental effort in different navigation contexts, and risk taking. We consider how strategies are influenced by the computational demands of a navigation task and by factors that affect the neural circuits underlying navigation. We also discuss limitations of laboratory studies to date and outline priorities for future research, including relating wayfinding strategies to independent measures of spatial knowledge, and studying wayfinding strategies in naturalistic environments.

Keywords: Navigation; Wayfinding; Strategy; Cognitive map; Virtual environments; Individual differences

Correspondence should be sent to Mary Hegarty, Department of Psychological & Brain Sciences, University of California, Santa Barbara, Santa Barbara, CA 93106-9660, USA. E-mail: hegarty@ucsb.edu

1. Introduction

The ability to learn the layout of a new space, maintain a sense of direction and location while moving around an environment, and make our way to places we need to visit, are fundamental cognitive functions. Spatial navigation is an essential competence for humans and animals alike. For humans, it includes planning routes to locations of interest, finding our way as we take those routes, and returning home safely. Despite the importance of navigation in everyday life, there are large individual differences in navigation ability (Wolbers & Hegarty, 2010). To date, research on individual differences in navigation has focused primarily on the ability to learn spatial layout from a controlled amount of navigation experience (Hegarty, Montello, Richardson, Ishikawa & Lovelace, 2006; Ishikawa & Montello, 2006; Weisberg & Newcombe, 2018). However, environmental learning is just one aspect of navigation. Here, we focus on individual differences in wayfinding, that is, how we ***use*** our spatial knowledge to navigate to goal locations. Wayfinding is an ecologically valid task, as everyday navigation frequently involves finding our way to specific locations in the environment. Moreover, individual differences in wayfinding include not only differences in *ability*, that is, in how well we navigate, but also in *strategy*, or the nature of the routes we choose to take when we navigate.

Wayfinding involves planning and executing paths to goal locations, based on spatial knowledge and perceptual cues, which enable us to update our position and orientation in space as we travel. Wayfinding can be accomplished by different strategies, notably by taking well-learned routes (referred to as response strategies) or by finding novel paths, such as shortcuts (Hartley, Maguire, Spiers, & Burgess, 2003), referred to as place strategies and assumed to depend on a flexible representation of the configuration of the environment such as a cognitive map. These different "strategies" are not necessarily conscious. They are best thought of as different algorithms, or processes, operating on different mental representations (cf. Marr, 1982). We first summarize the research on strategy differences in wayfinding from animal and human studies, and then interpret this research from a broad cognitive science perspective, discuss strengths and limitations of research to date, and finally, identify priorities for future research.

1.1. Wayfinding strategies: Evidence from animal studies

Research in psychology on navigation strategies can be traced back to the classic studies of learning by Tolman (1948). Tolman taught rodents to follow a designated path through an apparatus with a circular arena leading to a singular path to the end goal. At test, the circular arena was fitted with radial arms arranged in a semicircle. The learned path was blocked, and the rat had to choose which arm led to the goal. Surprisingly, rats tended to take the arm corresponding to a most direct path to the goal, rather than probing arms at either side of the learned path. This result indicated that the rats had learned more than a chain of stimulus response relations (i.e., a route representation). They had a representation of the food location that was independent of the route taken—Tolman labeled this a "cognitive map"—which enabled the rats to take a direct route to the food (i.e., use a place strategy rather than

a response strategy). This was one of the first demonstrations that animals can develop and use a mental representation to guide behavior. This important finding challenged behaviorism and inspired the cognitive revolution.

In the 1970s, specialized "place" cells were found in the rodent hippocampus that fired only when physically situated at particular locations within a familiar environment, regardless of the animal's orientation in space (O'Keefe & Dostrovsky, 1971; O'Keefe and Nadel, 1978). These cells, along with head-direction cells (Taube, Muller, & Ranck, 1990), grid cells (Hafting, Fyhn, Molden, Moser, & Moser, 2005; Moser, Kropff, & Moser, 2008), and boundary cells (Lever, Burton, Jeewajee, O'Keefe, & Burgess, 2009), are elements in the neural representation of a cognitive map and implicated in *place-based* navigation, that is, flexible navigation strategies that depend on configural knowledge of an environment. In contrast, habit forming striatal regions of the brain (Chorover & Gross, 1963), including the caudate-putamen, give rise to more habit-based navigation based on familiar routes, which is known as *response-based* navigation. Packard and McGaugh (1996) found that temporary deactivation of the rodent hippocampus led to less place-based navigation and more learned route usage, whereas deactivation of the caudate led to more place-based navigation. This result supports a functional distinction between these strategies and the brain regions that support them. However, other research has suggested a more nuanced characterization of these brain regions, with areas of the striatum also implicated in flexible navigation, and evidence that these systems interact synergistically (Devan & White, 1999; Ferbinteanu, 2016, 2020; Gahnstrom & Spiers, 2020). On the basis of such evidence, Chersi and Burgess (2015) have proposed a model of spatial navigation in which the prefrontal cortex plays a role in integrating outputs from the striatal and hippocampal systems to control navigation behavior.

Navigation strategies can also be affected by hormonal mechanisms. The mammalian brain is densely populated with sex hormone receptors, with enriched expression of estrogen receptors in the hippocampus (Taxier, Gross & Frick, 2020). Rodent (Woolley & McEwen, 1992), non-human primate (Hao et al., 2003, 2007), and human studies (Mueller et al., 2021; Pritschet et al., 2020; Taylor et al., 2020) have established sex steroid hormones as powerful neuromodulators that regulate hippocampal morphology (Rossetti et al., 2016) and function. For example, estrogen fluctuations over the 4–5 day rodent estrous cycle induce a 30% increase in dendritic spines in hippocampal neurons (Woolley & McEwan, 1992), which increases the connections between neurons that support the likelihood of hippocampal-mediated place strategies and behaviors. In turn, these fluctuations impact rodents' preferred spatial navigation strategy (Brake & Lacasse, 2018; Hussain et al., 2014; Quinlan et al., 2008). For example, Korol, Malin, Borden, Busby, and Couper-Leo (2004) tested female rats on a task that allowed the animals to freely choose between a response-based versus place-based strategy and found that the animals were more likely to use a response-based learning strategy when estrogen concentrations were low, but shifted their preference to a flexible place-based learning strategy when estrogen concentrations were naturally elevated.

Similarly, rodents that have undergone surgical removal of the ovaries tend to use response-based strategies, while estrogen replacement biases rats toward place-based strategies (Hussain et al., 2014). Strategy choice is also influenced by testosterone. Castration decreases place strategy preference in males and replacement with high concentrations of
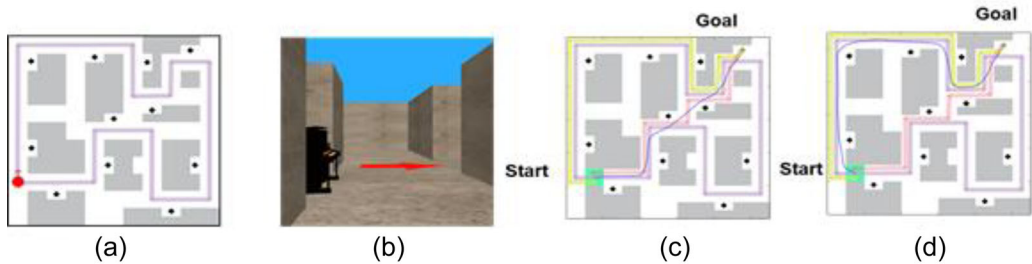
Fig 1. The dual solution paradigm tests participants' use of a place-based and response-based strategy. (a) Map of the DSP virtual environment used by Boone et al. (2018), (b) participant view of the environment, (c) example of a trial on which the participant took a shortcut, and (d) the learned route to navigate to a goal.

testosterone increased rats preference for a place strategy in a dual-solution water maze task (Yagi & Galea, 2019). Together, these findings suggest that sex steroid hormones influence which strategy is evoked to solve a wayfinding task and may contribute to intraindividual differences in strategy use over time. Hippocampal-dependent place-based strategies are enhanced under high estrogen or testosterone conditions, while striatal-dependent response-based strategies are favored under low estrogen or testosterone conditions.

1.2. Wayfinding strategies: Evidence from human studies

The *Dual Solution Paradigm* (DSP; Marchette et al., 2011) was developed to examine differences in place versus response strategies in humans. In this task, participants are first transported on a prescribed path through a novel desktop virtual environment with salient landmarks (see Fig. 1). After following this path several times, participants perform a series of trials in which they are placed at a location in the environment and asked to travel to one of the landmarks. Each participant's strategy on each trial is categorized as either following the learned route or taking a shortcut and a place/response index is computed for each participant, equal to the number of trials on which they successfully took a shortcut divided by the number of trials on which they successfully navigated to the goal. The results indicate a continuum of strategies: some participants always take the learned route, some always take a shortcut, and most use a mix of strategies. Those who take more shortcuts show greater activation in the hippocampus during encoding (Marchette et al., 2011), consistent with the role of the hippocampus in the neural representation of cognitive maps. Those who tend to follow the learned route show more activation of the caudate nucleus during encoding. Moreover, the relative activation of the hippocampus and caudate during the test phase shows the same pattern as at learning, and correlates with the place/response index (Furman et al., 2014). Other tasks, such as the radial arm maze, have also revealed differences in place and response learning, particularly with regard to distal landmarks (Iaria et al., 2003). Moreover, similar individual differences in spontaneous navigation strategies have been found in animals, and are associated with distinct patterns of neural activity between the striatum and hippocampus (Goldenberg, Lentzou, Ackert-Smith, Knowlton, & Dash, 2020).
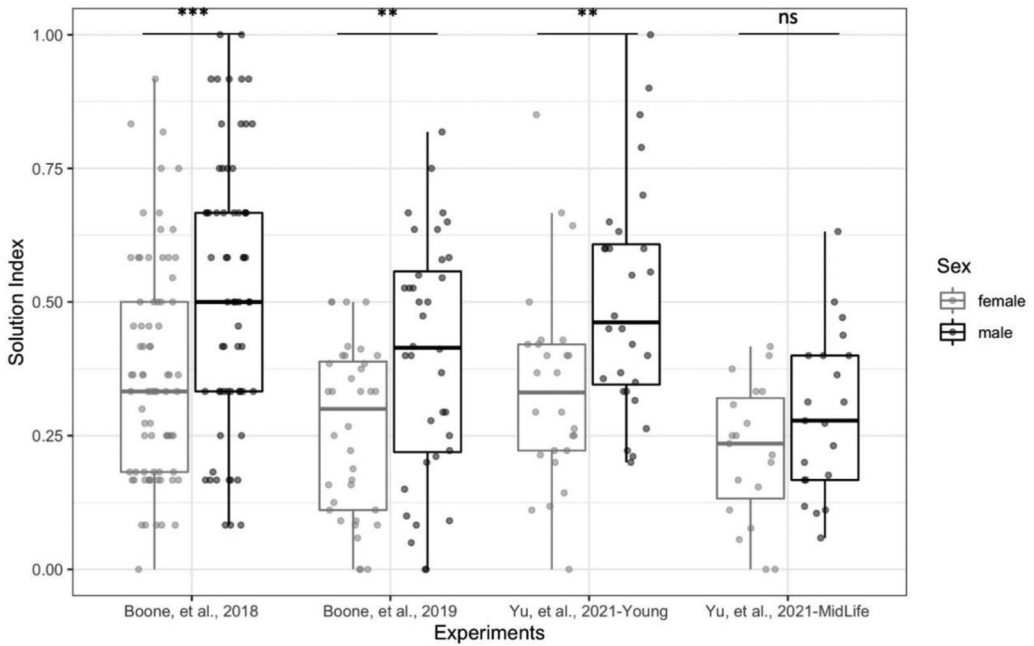
Fig 2. Navigation strategy differs by sex and age. The tendency to take shortcuts in the DSP, quantified here as the Solution Index (number of shortcuts/number of successful trials), was greater for young adults relative to midlife adults. Men overall took more shortcuts than women. Boone et al. (2018) (college students, male: $n = 64$; female: $n = 76$) used a different set of trials, which leads to a different range of Solution Index. Data from Boone et al. (2019) (college students, male: $n = 36$; female: $n = 35$) include data from both Experiment 1 and Experiment 2 for those who were instructed to "go to goal" in the first session. The Yu et al. (2021) study includes young and midlife men and women (young male: $n = 28$; young female: $n = 26$; midlife men: $n = 21$; midlife female: $n = 19$).

Boone, Gong, and Hegarty (2018) found sex differences in navigation strategies, such that men were more likely to use place-based (shortcut) strategies in the DSP, while women more often used the response-based strategy of following the learned route, as illustrated in Fig. 2. These results are consistent with sex differences in self-reported navigation strategies (Lawton, 1994, 1996). More recently, Yu et al. (2021) examined sex differences in navigation strategy in both young- and middle-aged adults and replicated sex differences in this task in young (college-aged) students with a different set of test trials (also used by Boone, Maghen, & Hegarty, 2019; see Fig. 2). However, by mid-life, this sex difference was no longer evident. Young men tended to take more shortcuts in the DSP (place strategy) through the center of the maze, as shown in Fig. 3, while young women, midlife women, and midlife men preferred to take learned routes (response strategy).

More generally, aging affects navigational strategy, such that older adults shift to an increased reliance on the response strategy while younger adults show less preference between place and response strategies (Rodgers et al., 2012; Zhong & Moffat, 2018). Notably, this shift is observed in animals as well as humans, and might be due to structural and
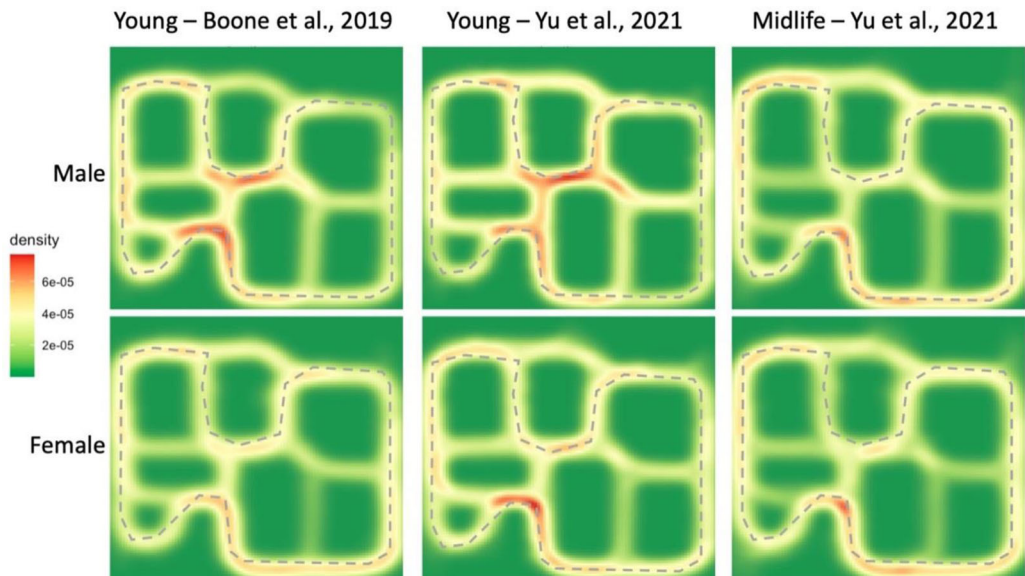
Fig 3. Heatmaps illustrate participants' tendency to take shortcuts through the center of a maze. Gray dash lines illustrate the learned route. In both Boone et al. (2019) (Experiment 2: go-to-goal condition and first session data only) and Yu et al. (2021), young men ($n = 10$; $n = 28$) tend to take more shortcuts (as indicated by paths taken through the center of the maze), while young women ($n = 10$; $n = 26$), midlife men ($n = 21$), and midlife women ($n = 19$) favor the learned route around the periphery.

functional changes in the regions that support the place strategy (for a comprehensive discussion of effects of aging on navigation, see Lester, Moffat, Wiener, Barnes, & Wolbers, 2017). In addition, older adults have difficulty switching from response to place strategies, for example, when a task requires them to take a shortcut (Harris, Wiener, & Wolbers, 2012; Harris & Wolbers, 2014). These results suggest that changes in navigation strategies may also be due, in part, to decreased functional connectivity between the hippocampus and prefrontal cortex, which is implicated in task switching and navigation strategy selection specifically (Chersi & Burgess, 2015; Zhong & Moffat, 2018).

Effects of sex and age on navigation strategy raise questions about the role of sex hormones in choice of navigation strategy in humans. Some evidence suggests that changes in sex hormones across the menstrual cycle influence participants' use of place-based versus response-based strategies in young women (Hussain et al., 2016). Questions also arise regarding aging influences on human spatial navigation in the context of menopause. Sex hormone production declines by 90% during the menopausal transition (ages 45–55), which could further impact the neural circuitry that supports navigation strategies (Jacobs & Goldstein, 2018; Jacobs et al., 2016; Taylor et al., 2019). Most studies of aging to date compare younger adults to older adults (over 65). Considering the dynamics of endocrine changes and how they interact with the aging process could lead to better understanding of how sex hormones regulate individual differences in spatial memory and wayfinding strategies. At the other end of the

age range, it is notable that sex differences are much smaller before age 13 (i.e., pre-puberty) than at other age ranges (Nazareth, Huang, Voyer, & Newcombe, 2019).

Transient changes in hormones due to stress can also alter neural circuitry underlying navigation. The stress response stimulates the release of the steroid hormone cortisol, which impacts hippocampal morphology and fMRI-BOLD responses in humans (Oei et al., 2007) and can impair memory processes (Het et al., 2005). Cortisol may influence the navigation process by impeding the use of hippocampus-based place strategies. Brown, Gagnon, and Wagner (2020) asked participants to learn routes through several environments and then to navigate to the end of the route while under the threat of noxious dermal shock. Participants in this stress condition were more likely to follow previously learned routes to the goal, compared to control participants. In another study, time pressure led to less use of shortcuts compared to previously learned routes (Brunyé, Wood, Houck, & Taylor, 2017). However, not all stressors seem to have the same influence over navigation strategy. Boone (2019) found that neither noxious stress (induced by the cold pressor task) nor social stress (induced by the Trier task) affected participants' strategy in the DSP.

In addition to the transitory effects of stress, women in general report higher spatial anxiety, a trait that is also associated with their preference for route strategies over orientation or place strategies (Lawton, 1994). Moreover, effects of stress on memory retrieval are moderated by sex, and age, with younger men showing more cortisol reactivity and larger effects of stress on memory (Hidalgo et al., 2015; Zoladz et al, 2014). While we are just beginning to examine these effects in the context of navigation in humans, these results suggest that that stress hormones and sex hormones may interact in their effects on retrieval of spatial memories that, in turn, affect differences in navigation strategy. Moreover, effects of anxiety and stress on memory appear to include both state (transitory) and trait (enduring) effects.

2. Understanding wayfinding strategies

2.1. Wayfinding as a complex information processing task

We propose that to fully understand navigation strategies, it is useful to take a comprehensive multilevel approach to the task of wayfinding that does not assume that taking a shortcut is always better, and considers situations in which different strategies might be adaptive. To do so, we consider wayfinding in terms of Marr's (1982) three levels necessary to understand how an intelligent agent carries out a complex information processing task: the computational level, the representation/algorithm level, and the implementation level.

- *Computational level*: In Marr's framework, the computational level specifies the goal of an information processing task, what needs to be computed, and the constraints that need to be satisfied. Importantly, the computational level specifies the navigational task, independently of *how* the task is accomplished or *what type* of information processing system (e.g., human, animal, or robot) is doing the navigating. In the case of wayfinding, we can characterize the goal as planning a path to a specific location in a

familiar environment. The constraints include one's own physical constraints (mobility, energy, etc.) and characteristics of the specific environment in which one is navigating, including environmental scale, affordances for movement, and availability of environmental cues. Examples of affordances are that you can move down a corridor but you cannot move through walls, when driving, you can only move on roads, and when hiking, it is more effortful and potentially dangerous to go off trail.

- ***Representation and algorithm level***: Marr's representational/algorithm level specifies different ways in which an information processing task can be carried out, that is, different strategies. Strategies are distinguished both by how the relevant information is *represented* and the *algorithm* or process that operates on this representation, to accomplish the task. In navigation, place and response strategies depend on different knowledge and algorithms. Place strategies depend on a representation of the configuration of an environment in an allocentric reference frame (a survey representation) and algorithms (processes) that operate on this representation to locate the goal location and compute a navigable path to that location. Response strategies depend on a route representation, that is, a list of actions that are executed in a fixed order at locations in the environment, encoded in an egocentric reference frame, and an algorithm that operates on this representation might be to recall these steps and repeat them in the same order.

- ***Implementation level***: Finally, Marr's implementation level specifies how different representations and algorithms are realized physically by different information processing systems (e.g., humans, animals, or computers). As we have reviewed, different strategies at the representation/algorithm level are implemented by different brain systems in animals and humans, with place-based navigation depending more on a system that involves the hippocampus- and response-based navigation depending more on habit forming striatal regions of the brain (Chorover & Gross, 1963; Hartley et al., 2003), although, as noted, these systems can interact synergistically (e.g., Chersi & Burgess, 2015).

Considering these levels enables us to consider more broadly why we observe a range of strategies in tasks such as the "DSP." First, individual, age, and sex differences in navigation strategies raise questions about the extent to which these strategies reflect differential ability to construct knowledge of the configuration of an environment from experience of a route. Route knowledge is sufficient for use of a response strategy, but taking a novel path to a goal location relies on knowledge of environment configuration. There are large individual differences in the ability to construct a mental survey representation from the experience of learning a specific route through an environment (Ishikawa & Montello, 2006; Weisberg et al., 2014; Weisberg & Newcombe, 2016) and small but systematic sex differences in most measures of navigation ability (Nazareth et al., 2019). Thus, one possibility is that some people use a response strategy because they were unable to construct a survey representation from the learning experience, and therefore, the place strategy is not available to them.

Inability to construct a survey representation from experience in an environment is one plausible explanation for both sex and age differences in navigation strategies. However, a recent study by Boone, Maghen, and Hegarty (2019) suggests that other factors besides

differences in acquiring survey knowledge are also at play. In addition to the standard "go to goal" instructions of the DSP, Boone et al. told participants in some conditions to "take the shortest path to the goal." Both men and women used more shortcuts overall in the "shortest path" condition. This work indicates that use of learned routes does not necessarily imply that a person cannot take a shortcut or does not have survey knowledge. It highlights that navigation strategy is not only determined by the quality of one's spatial knowledge.

Considering the goals and constraints of navigation specified at the computational level, it is clear that there are both physical and computational costs associated with different strategies, with trade-offs, such that shortcutting, in general, involves less physical effort but more cognitive effort. There is also more uncertainty involved in taking a shortcut. In the DSP maze, a participant does not know for sure that the path through the center is clear, as they have never taken that path. Moreover, in the real world, taking a direct but unfamiliar path to a goal location might bring you through a dangerous neighborhood or be cut off due to construction. In these situations, taking a well-learned route, which is less risky, may be the rational choice, if you are not constrained by time pressures and have the physical energy to take the familiar but longer path. This might be particularly true for women, who are at more risk when entering unfamiliar territory. Gagnon et al. (2016, 2018) found that women, who, in general, are more risk averse, were more cautious in their exploration of novel environments, suggesting that a female preference for wayfinding by familiar paths may reflect risk aversion and an adaptive strategy of harm avoidance.

Moreover, considering the implementation level, individual variation in the volume and functioning of the neural structures underlying navigation may affect strategy availability and selection. Gray matter volume of the hippocampus has been linked to navigation ability (Bohbot et al., 2007; Maguire et al., 2000, 2003; Schinazi et al., 2013; Sherrill et al., 2018), although a recent study with a large sample found no evidence for this relationship in healthy young adults (Weisberg, Newcombe, & Chatterjee, 2019). We have also seen that the neural circuits underlying navigation are affected by physiological changes, such as levels of circulating hormones that vary with the menstrual cycle and menopause in humans, with the estrous cycle in animals, and with stress levels. Moreover, changes in the prefrontal cortex as a function of aging might affect the neural circuitry underlying strategy choice (Lester et al., 2017). These physiological changes may limit what strategies are available to the individual, or at least bias which strategies are selected, given other constraints of the task. That is, even if an individual has constructed survey knowledge, based on their past experiences in an environment, this knowledge may not be accessible at a given moment, based on their hormonal state.

Finally, at the representation/algorithm level, we need more precise characterizations (including computational models) of the spatial representations and algorithms that are necessary and sufficient to carry out different strategies. Although taking a shortcut is typically assumed to rely on metric survey knowledge, it is possible that other, weaker forms of configural knowledge could support shortcutting. One type of weaker configural knowledge is a *labeled graph*—a series of connections between network place nodes along path edges—which includes some local metric information but does not include a globally consistent coordinate system. A labeled (or "cognitive") graph allows people to connect between
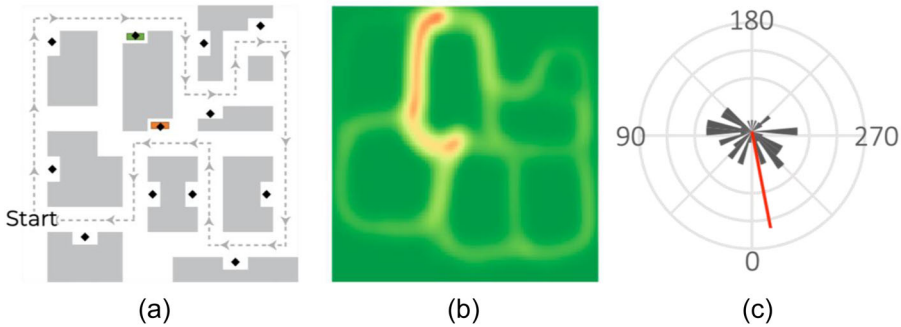
Fig 4. A comparison between shortcutting behaviors and pointing accuracy for a sample trial in He et al. (2020) (Experiment 1: $n = 56$). (a) On the sample trial, participants started at the green landmark (at the top) and were asked to navigate to the orange landmark (in the middle). The gray dash lines illustrate the learned route. (b) The heatmap illustrates that participants tend to take the shortcut. In the offsite direction estimation task, there is a corresponding trial where they started at the same location and were asked to point to the same target. (c) The polar histogram of the pointing error of this trial. The red line indicates the correct direction. The bars show the frequencies of participants' pointing directions.

locations and take detours using paths and streets, but does not require a metric embed-ding within a common reference frame (e.g., Cartesian coordinates) (Byrne, 1979; Chrastil & Warren, 2014; Meilinger, 2008; Montello, 1992). A graph could allow people to learn the topological connections between locations in the DSP maze, but without necessarily learning all the metric distances and angles between locations. Navigators can then use these paths to create shortcuts. We recently found that navigators who can take shortcuts to a target are not always very accurate at pointing to the same target (He, Boone, & Hegarty, 2020), suggesting that they might have had some graph knowledge without survey knowledge (see Fig. 4).

Although we have focused on place and response strategies in this review, other strategies are available in the so-called "DSP" (Boone et al., 2018; 2019; Krichmar & He, 2021). For example, another common strategy to reach the target location is to reverse the learned route. To use this strategy, the navigator must know the turns that they took during the route, and be able to mentally manipulate the spatial information to infer that a previous left turn is now a right turn when reversing. It is also possible to reach the target by wandering, until one eventually crosses paths with the target. However, the wandering cannot involve just going in circles. The navigator must at least know where they have been to reach the target eventually.

2.2. Methodological issues: Are laboratory paradigms representative of wayfinding in the wild?

Human wayfinding strategies have been studied primarily in desktop virtual environments representing maze-like environments. There are many advantages to using desktop virtual environments to study navigation. They provide a controlled environment that you cannot find in the real world, where factors like the weather, traffic, and environmental noise cannot

be controlled. Moreover, desktop virtual studies can be run in a small lab, in fMRI, or even online.

But there are important differences between learning and navigating in virtual and real environments. Desktop virtual environments involve using some interface, such as a mouse and keyboard, or joystick. Facility with these interfaces might be a source of individual, sex, or age differences. The cognitive load associated with just moving through the environment may be greater for those with less interface facility, thus limiting cognitive resources available for environmental learning or computing the most efficient paths. More fundamentally, in desktop virtual environments, self-motion perception is based on vision alone with no feedback from vestibular and other body-based senses. Research suggests that vision alone is sufficient for acquiring graph-based knowledge of an environment, but developing metric, survey knowledge is facilitated by physically walking in an immersive virtual environment, that is, by the addition of body-based cues (Chrastil & Warren, 2013, 2015).

Importantly, in desktop virtual environments, there is little additional physical cost to taking a familiar but longer route to one's destination, so that the trade-off between cognitive and physical effort is not representative of real-world wayfinding. Interestingly, in a recent study on the effect of different types of stress on the performance of the DSP, only physical fatigue (and not noxious or social stress) affected strategy. Specifically, participants who underwent 2 h of stationary biking before performing the wayfinding test trials on the DSP were more likely to take shortcuts than those in an active control condition (Boone et al., 2020), suggesting that the physical demands are important in understanding strategies.

It is possible that the sex and age differences reported earlier (Boone et al., 2018, 2019, Yu et al., 2021) are due to aspects of navigation in desktop virtual environments that are not representative of real-world navigation. Fig. 5 shows representative paths taken by six different participants while using a mouse and keyboard interface to traverse the learned route in a recent study using the DSP environment. The data from three representative young men were smoother than those of three representative young women, suggesting that women were less facile with the interface. Interestingly, in contrast to tasks that involved learning and wayfinding in desktop virtual environments, Yu et al. (2021) found no sex differences in a path integration task when people physically walked in an immersive virtual environment.

It is important therefore to examine whether our results generalize beyond desktop virtual environments. In a recent preliminary study (Hegarty, He, Boone & Chrastil, 2020; Yokota, 2020), we attempted to generalize research on the DSP to navigation in a real, outdoor, environment. In this study, 27 young adults (7 men, 20 women) learned a route through an unfamiliar residential area that was similar in complexity to the route in the desktop virtual environment (see Fig 6). Participants walked the (approximately half-mile) route twice to learn the environment, and then were tested with the DSP task. Importantly, they were not instructed *how* to navigate, so this is similar to the go-to-goal instructions in the DSP. Although participants showed the same type of variation as in the desktop studies, with a range from preference for learned routes to preference for shortcuts, in general people were more likely to take shortcuts in this environment. Interestingly, we have observed no sex differences in solution index so far, although these results are very preliminary (with only 7 men and 20
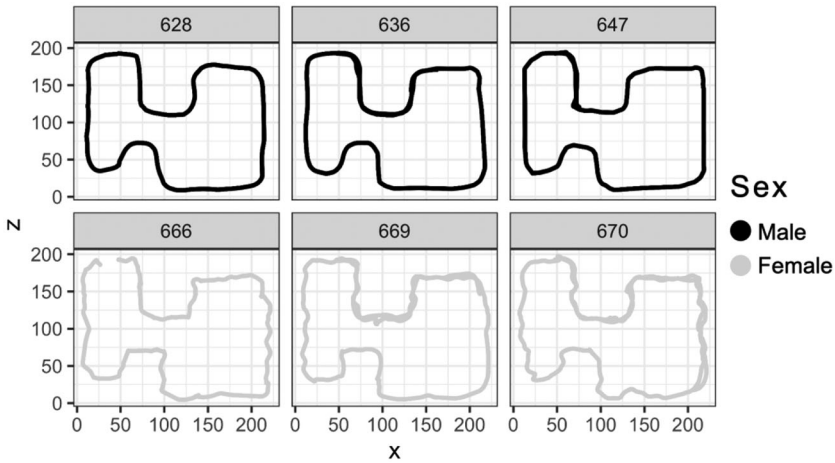
Fig 5. Individual differences in using the mouse and keyboard interface in the DSP environment (He et al., 2020). Plots illustrate six participants' trajectories during the first 90 s of learning the virtual environment by following the learned route. Male participants tend to have more smooth trajectories than females.
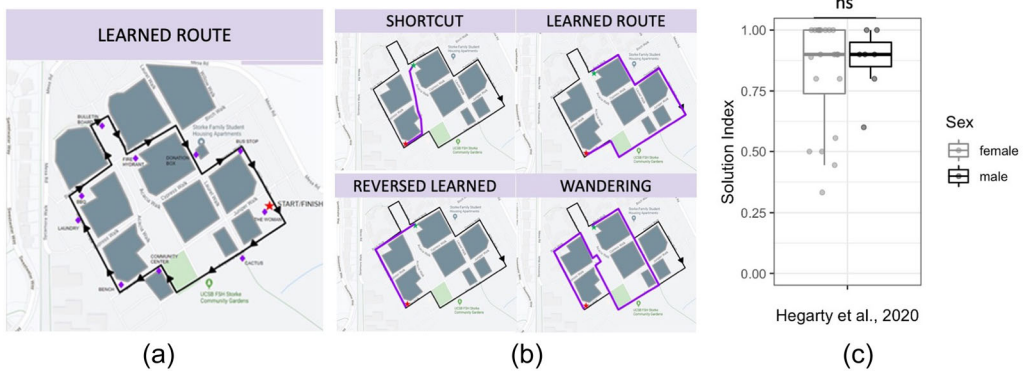

Fig 6. Dual Solution Task in an outdoor environment indicates increased shortcutting and reduced sex differences (Hegarty et al., 2020). (a) The layout of the environment, with black lines showing the learned routes, landmarks indicated by purple dots, the red star sign indicating the start of the learned tour, and the gray areas indicating non-walkable residential areas. (b) Paths representative of different strategies used on a sample trial in which participants started at the green star (on the top) and had to navigate to the red star (at the bottom). (c) The box-plot of the tendency to take shortcuts by sex, quantified here as the Solution Index (number of shortcuts/number of successful trials).

women in the sample) and shortcut use may be subject to a ceiling effect. Although the environment itself was unfamiliar to participants, it is situated in the general area of campus with access to familiar distal landmarks such as the local mountains. Critically, it is larger than the VR environment, and navigating the environment involves physical effort. This preliminary study demonstrates the feasibility of conducting studies of navigation under more naturalistic conditions.

In summary, while recent research has provided important insights into the nature of navigation strategies, there are limits to our current knowledge of navigation strategies. First, most studies to date did not include measures of environmental knowledge, independent of their use in strategies, so it is difficult to discern how much differences in strategy reflect knowledge differences. Second, we are concerned that when wayfinding is measured in desktop virtual environments, individual differences in interface facility may be confounding differences in both environmental learning and use of strategies that depend on that learning.

As a result, we advocate several methodological changes for future research on wayfinding strategies. First, we recommend that people are trained to criterion in the learning phase, so that we can be confident that all participants have some minimum level of knowledge of the environment (e.g., ability to retrace the route). Second, we suggest including measures of interface facility and videogame experience as covariates. Third, we advocate using measures such as pointing as independent measures of environmental knowledge, in addition to strategies, so that we can continue to study the extent to which different strategies reflect differences in knowledge, or access to that knowledge. Finally, it is important to conduct studies in more naturalistic environments (including real and ambulatory virtual environments) and to measure the consistency of wayfinding strategies across different environments, to ensure that strategies in our laboratory experiments are reflective of strategies in real environments.

3. Conclusion

In conclusion, there is strong evidence from both animal and human studies for individual differences in navigation strategies, and evidence that these strategies vary with enduring characteristics of the individual, such as sex and age, and more transitory states such as stress and menstrual cycle stage. However, we are just beginning to understand the factors that influence strategy differences in humans. Navigation strategies vary in their dependence on different types of environmental knowledge (e.g., route vs. survey knowledge) and availability of this knowledge is likely one determinant of strategy use. However, other factors - including risk taking, trade-offs between physical and mental effort, momentary access to different types of knowledge, and ability to switch strategies—can also affect strategy differences. These factors, in turn, depend on characteristics of the navigation task, of the environment, and of the individual (including hormonal states).

We have found that it is useful to consider wayfinding as a complex information processing task using Marr's (1982) framework. This framework characterizes strategy choice at the representation and algorithm level as jointly influenced by the computational level (the goal and constraints of a specific navigation task) and the implementation level (e.g., brain states, which vary as a function of factors such as sex hormones, stress, and aging) that may limit or bias access to neural representations, underlying different strategies). While the account presented here is very unspecified, we hope that it might inspire more precise computational models of the representations and algorithms underling various navigation strategies that complement emerging neural models of these strategies.

Our review also emphasizes the importance of studying wayfinding strategies in naturalistic situations that are representative of navigational demands in the real world, to further document how these strategies vary across the adult age range, and across different physiological states. There are limitations to studying navigation strategies in desktop environments alone, and priorities for future research include considering the role of interface facility in these studies, and relating wayfinding strategies to independent measures of spatial knowledge.

Acknowledgments

References

Bohbot, V. D., Lerch, J., Thorndycraft, B., Iaria, G., & Zijdenbos, A. P. (2007). Gray matter differences correlate with spontaneous strategies in a human virtual navigation task. *The Journal of Neuroscience*, *27*(38), 10078–10083.

Boone, A. P. (2019). *The influence of the human stress response on navigation strategy and efficiency* (Doctoral dissertation). UC Santa Barbara.

Boone, A. P., Bullock, T., MacLean, M. H., Santander, T., Raymer, J., Stuber, A., … Hegarty, M. (2020). Navigation strategy is resilient to physical, psychosocial, and fatigue-based stress. Talk presented at the 61st Annual Meeting of the Psychonomic Society. Virtual Conference, United States.

Boone, A. P., Gong, X., & Hegarty, M. (2018). Sex differences in navigation strategy and efficiency. *Memory & Cognition*, *46*(6), 909-922.

Boone, A. P., Maghen, B., & Hegarty, M. (2019). Instructions matter: Individual and sex differences in navigation strategy and ability. *Memory & Cognition*, *47*(7), 1401–1414. https://doi.org/10.3758/s13421-019-00941-5

Brake, W. G., & Lacasse, J. M. (2018). Sex differences in spatial navigation: The role of gonadal hormones. *Current Opinion in Behavioral Sciences*, *23*, 176–182.

Brown, T. I., Gagnon, S. A., & Wagner, A. D. (2020). Stress disrupts human hippocampal-prefrontal function during prospective spatial navigation and hinders flexible behavior. *Current Biology*, *30*(10), 1821–1833.e8. https://doi.org/10.1016/j.cub.2020.03.006

Brunyé, T. T., Wood, M. D., Houck, L. A., & Taylor, H. A. (2017). The path more travelled: Time pressure increases reliance on familiar route-based strategies during navigation. *The Quarterly Journal of Experimental Psychology*, *70*(8), 1439–1452.

Byrne, R. W. (1979). Memory for urban geography. *Quarterly Journal of Experimental Psychology*, *31*, 147–154

Chersi, F., & Burgess, N. (2015). The cognitive architecture of spatial navigation: Hippocampal and striatal contributions. *Neuron*, *88*(1), 64–77.

Chorover, S. L., & Gross, C. G. (1963). Caudate nucleus lesions: Behavioral effects in the rat. *Science*, *141*(3583), 826–827.

Chrastil, E. R., & Warren, W. H. (2013). Active and passive spatial learning in human navigation: Acquisition of survey knowledge. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *39*(5), 1520–1537.

Chrastil, E. R., & Warren, W. H. (2014). From cognitive maps to cognitive graphs. *PLoS One*, *9*(11), e112544.

Chrastil, E. R., & Warren, W. H. (2015). Active and passive spatial learning in human navigation: Acquisition of graph knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *41*(4), 1162–1178.

Devan, B. D., & White, N. M. (1999). Parallel information processing in the dorsal striatum: Relation to hippocampal function. *Journal of neuroscience*, *19*(7), 2789–2798.

Ferbinteanu, J. (2016). Contributions of hippocampus and striatum to memory-guided behavior depend on past experience. *Journal of Neuroscience*, *36*(24), 6459–6470.

Ferbinteanu, J. (2020). The hippocampus and dorsolateral striatum integrate distinct types of memories through time and space, respectively. *Journal of Neuroscience*, *40*(47), 9055–9065.

Furman, A. J., Clements-Stephens, A. M., Marchette, S. A., & Shelton, A. L. (2014). Persistent and stable biases in spatial learning mechanisms predict navigational style. *Cognitive, Affective, & Behavioral Neuroscience*, *14*(4), 1375–1391.

Gagnon, K. T., Cashdan, E. A., Stefanucci, J. K., & Creem-Regehr, S. H. (2016). Sex differences in exploration behavior and the relationship to harm avoidance. *Human Nature*, *27*(1), 82–97.

Gagnon, K. T., Thomas, B. J., Munion, A., Creem-Regehr, S. H., Cashdan, E. A., & Stefanucci, J. K. (2018). Not all those who wander are lost: Spatial exploration patterns and their relationship to gender and spatial memory. *Cognition*, *180*, 108–117.

Gahnstrom, C. J., & Spiers, H. J. (2020). Striatal and hippocampal contributions to flexible navigation in rats and humans. *Brain and Neuroscience Advances*, *4*, 2398212820979772.

Goldenberg, J. E., Lentzou, S., Ackert-Smith, L., Knowlton, H., & Dash, M. B. (2020). Interindividual differences in memory system local field potential activity predict behavioral strategy on a dual-solution T-maze. *Hippocampus*, *30*(12), 1313–1326.

Hafting, T., Fyhn, M., Molden, S., Moser, M.-B., & Moser, E. I. (2005). Microstructure of a spatial map in the entorhinal cortex. *Nature*, *436*(7052), 801–806.

Harris, M. A., Wiener, J. M., & Wolbers, T. (2012). Aging specifically impairs switching to an allocentric navigational strategy. *Frontiers in Aging Neuroscience*, *4*, 29.

Harris, M. A., & Wolbers, T. (2014). How age-related strategy switching deficits affect wayfinding in complex environments. *Neurobiology of Aging*, *35*(5), 1095–1102.

Hao, J., Janssen, W. G. M., Tang, Y., Roberts, J. A., McKay, H., Lasley, B., … Morrison, J. H. (2003). Estrogen increases the number of spinophilin-immunoreactive spines in the hippocampus of young and aged female rhesus monkeys. *Journal of Comparative Neurology*, *465*(4), 540–550.

Hao, J., Rapp, P. R., Janssen, W. G. M., Lou, W., Lasley, B. L., Hof, P. R., & Morrison, J. H. (2007). Interactive effects of age and estrogen on cognition and pyramidal neurons in monkey prefrontal cortex. *Proceedings of the National Academy of Sciences*, *104*(27), 11465–11470.

Hartley, T., Maguire, E. A., Spiers, H. J., & Burgess, N. (2003). The well-worn route and the path less traveled: Distinct neural bases of route following and wayfinding in humans. *Neuron*, *37*(5), 877–888.

He, C., Boone, A. P., & Hegarty, M. (2020, October). Ability to navigate by novel efficient paths with imprecise spatial knowledge. Data blitz presented at the *3rd Interdisciplinary Navigation Symposium*. Virtual Conference, Italy.

Het, S., Ramlow, G., & Wolf, O. T. (2005). A meta-analytic review of the effects of acute cortisol administration on human memory. *Psychoneuroendocrinology*, *30*(8), 771–784.

Hegarty, M., He, C., Boone, A. P., & Chrastil, E. R. (2020, November). Individual differences in wayfinding strategies in real and virtual environments. Talk presented at the 61st annual meeting of the Psychonomic Society. Virtual Conference, USA.

Hegarty, M., Montello, D. R., Richardson, A. E., Ishikawa, T., & Lovelace, K. (2006). Spatial abilities at different scales: Individual differences in aptitude-test performance and spatial-layout learning. *Intelligence*, *34*(2), 151–176.

Hidalgo, V., Pulopulos, M. M., Puig-Perez, S., Espin, L., Gomez-Amor, J., & Salvador, A. (2015). Acute stress affects free recall and recognition of pictures differently depending on age and sex. *Behavioural Brain Research*, *292*, 393–402.

Hussain, D., Hanafi, S., Konishi, K., Brake, W. G., & Bohbot, V. D. (2016). Modulation of spatial and response strategies by phase of the menstrual cycle in women tested in a virtual navigation task. *Psychoneuroendocrinology*, *70*, 108–117.

Hussain, D., Shams, W., & Brake, W. (2014). Estrogen and memory system bias in females across the lifespan, *Translational Neuroscience*, *5*(1), 35–50. Doi: https://doi.org/10.2478/s13380-014-0209-7

Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: Variability and change with practice. *Journal of Neuroscience*, *23*(13), 5945–5952.

Ishikawa, T., & Montello, D. R. (2006). 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*, 93–129.

Jacobs, E. G., & Goldstein, J. M. (2018). The middle-aged brain: Biological sex and sex hormones shape memory circuitry. *Current Opinion in Behavioral Sciences*, *23*, 84–91,

Jacobs, E. G., Weiss, B. K., Makris, N., Whitfield-Gabrieli, S., Buka, S. L., Klibanski, A., & Goldstein, J. M. (2016). Impact of sex and menopausal status on episodic memory circuitry in early midlife. *Journal of Neuroscience*, *36*(39), 10163–10173.

Koebele, S. V., Palmer, J. M., Hadder, B., Melikian, R., Fox, C., Strouse, I. M., … Bimonte-Nelson, H. A. (2019). Hysterectomy uniquely impacts spatial memory in a rat model: A role for the nonpregnant uterus in cognitive processes. *Endocrinology*, *160*(1), 1–19.

Konishi, K., Mckenzie, K. Etchamendy, N., Roy, S., & Bohbot, V. D. (2017). Hippocampus-dependent spatial learning is associated with higher global cognition among healthy older adults. *Neuropsychologia*, *106*, 310–321.

Korol, D. L., Malin, E. L., Borden, K. A., Busby, R. A., & Couper-Leo, J. (2004). Shifts in preferred learning strategy across the estrous cycle in female rats. *Hormones and Behavior*, *45*(5), 330–338.

Krichmar, J. L., & He, C. (2021). Importance of path planning variability: A simulation study. *Topics in Cognitive Science*. https://doi.org/10.1111/tops.12568

Lawton, C. A. (1994). Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. *Sex Roles*, *30*(11–12), 765–779.

Lawton, C. A. (1996). Strategies for indoor wayfinding: The role of orientation. *Journal of Environmental Psychology*, *16*(2), 137–145.

Lester, A. W., Moffat, S. D., Wiener, J. M., Barnes, C. A., & Wolbers, T. (2017). The aging navigational system. *Neuron*, *95*(5), 1019–1035.

Lever, C., Burton, S., Jeewajee, A., O'Keefe, J., & Burgess, N. (2009). Boundary vector cells in the subiculum of the hippocampal formation. *The Journal of Neuroscience*, *29*, 9771–9777.

Maguire, E. A., Gadian, D. G., Johnsrude, I. S., Good, C. D., Ashburner, J., Frackowiak, R. S. J., & Frith, C. D. (2000). Navigation-related structural change in the hippocampi of taxi drivers. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(8), 4398–4403.

Maguire, E. A., Spiers, H. J., Good, C. D., Hartley, T., Frackowiak, R. S., & Burgess, N. (2003). Navigation expertise and the human hippocampus: A structural brain imaging analysis. *Hippocampus*, *13*(2), 250–259.

Marchette, S. A., Bakker, A., & Shelton, A. L. (2011). Cognitive mappers to creatures of habit: Differential engagement of place and response learning mechanisms predicts human navigational behavior. *The Journal of Neuroscience*, *31*(43), 15264–15268.

Marr, D. (1982). *Vision*. Cambridge, MA: MIT Press.

Meilinger, T. (2008). The network of reference frames theory : A synthesis of graphs and cognitive maps. In C. Freksa, N. S. Newcombe, P. Gardenfors, & S. Wolfl (Eds.), *Spatial Cognition VI* (pp. 344–360). Berlin: Springer.

Montello, D. R. (1992). The geometry of environmental knowledge. In A. U. Frank, I. Campari, & U. Formentini (Eds.), *Theories and methods of spatio-temporal reasoning in geographic space* (pp. 136–152). Springer, Berlin: Heidelberg.

Moser, E. I., Kropff, E., & Moser, M.-B. (2008). Place cells, grid cells and the brain's spatial representation system. *Annual Reviews of Neuroscience*, *31*, 69–89.

Mueller, J. M., Pritschet, L., Santander, T., Taylor, C. M., Grafton, S. T., Jacobs, E. G., & Carlson, J. M. (2021). Dynamic community detection reveals transient reorganization of functional brain networks across a female menstrual cycle. *Network Neuroscience*, *5*, 125–144.

Nazareth, A., Huang, X., Voyer, D., & Newcombe, N. (2019). A meta-analysis of sex differences in human navigation skills. *Psychonomic Bulletin & Review*, *26*(5), 1503–1528.

Oei, N. Y., Elzinga, B. M., Wolf, O. T., de Ruiter, M. B., Damoiseaux, J. S., Kuijer, J. P., … Rombouts, S. A. (2007). Glucocorticoids decrease hippocampal and prefrontal activation during declarative memory retrieval in young men. *Brain Imaging and Behavior*, *1*(1–2), 31–41.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely-moving rat. *Brain Research*, *34*, 171–175.

O'Keefe, J., & Nadel, L. (1978). *The Hippocampus as a cognitive map*. Oxford, UK: Clarendon Press.

Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of Learning and Memory*, *65*(1), 65–72.

Pritschet, L., Santander, T., Taylor, C. M., Layher, E., Yu, S., Miller, M. B., … Jacobs, E. G. (2020). Functional reorganization of brain networks across the human menstrual cycle. *NeuroImage*, *220*, 117091.

Quinlan, M. G., Hussain, D., & Brake, W. G. (2008). Use of cognitive strategies in rats: The role of estradiol and its interaction with dopamine. *Hormones and Behavior*, *53*(1), 185–191.

Rodgers, M. K., Sindone III, J. A., & Moffat, S. D. (2012). Effects of age on navigation strategy. *Neurobiology of Aging*, *33*(1), 202-e15.

Rossetti, M. F., Cambiasso, M. J., Holschbach, M. A., Cabrera, R. (2016). Oestrogens and progestagens: Synthesis and action in the brain. *Journal of Neuroendocrinology*, *28*. https://doi.org/10.1111/jne.12402.

Schinazi, V. R., Nardi, D., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2013). Hippocampal size predicts rapid learning of a cognitive map in humans. *Hippocampus*, *23*(6), 515–528.

Sherrill, K. R., Chrastil, E. R., Aselcioglu, I., Hasselmo, M. E., & Stern, C. E. (2018). Structural differences in hippocampal and entorhinal gray matter volume support individual differences in first-person navigational ability. *Neuroscience*, *380*, 123–131.

Taxier, L. R., Gross, K. S., & Frick, K. M. (2020). Oestradiol as a neuromodulator of learning and memory. *Nature Review Neuroscience*, *21*, 535–550.

Taylor, C. M., Pritschet, L., Olsen, R. K., Layher, E., Santander, T., Grafton, S. T., & Jacobs, E. G. (2020). Progesterone shapes medial temporal lobe volume across the human menstrual cycle. *Neuroimage*, *220*(117125). https://doi.org/10.1016/j.neuroimage.2020.117125

Taylor, C. M., Pritschet, L., Yu, S., & Jacobs, E. G. (2019). Applying a women's health lens to the study of the aging brain. *Frontiers in Human Neuroscience*, *13*, 224.

Taube, J. S., Muller, R. U., & Ranck, J. B. (1990). Head-direction cells recorded from the postsubiculum in freely moving rats. I. Description and quantitative analysis. *Journal of Neuroscience*, *10*(2), 420–435.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, *55*(4), 189–208.

Weisberg, S. M., Schinazi, V. R., Newcombe, N. S., Shipley, T. F., & Epstein, R. A. (2014). Variations in cognitive maps: understanding individual differences in navigation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *40*(3), 669.

Weisberg, S. M., & Newcombe, N. S. (2016). How do (some) people make a cognitive map? Routes, places, and working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *42*(5), 768.

Weisberg, S. M., & Newcombe, N. S. (2018). Cognitive maps: Some people make them, some people struggle. *Current Directions in Psychological Science*, *27*(4), 220–226.

Weisberg, S. M., Newcombe, N. S., & Chatterjee, A. (2019). Everyday taxi drivers: Do better navigators have larger hippocampi? *Cortex*, *115*, 280–293.

Wolbers, T., & Hegarty, M. (2010). What determines our navigational abilities? *Trends in Cognitive Sciences*, *14*(3), 138–146.

Woolley, C. S., & McEwen, B. S. (1992). Estradiol mediates fluctuation in hippocampal synapse density during the estrous cycle in the adult rat. *Journal of Neuroscience*, *12*(7), 2549–2554.

Yagi, S., & Galea, L. A. (2019). Sex differences in hippocampal cognition and neurogenesis. *Neuropsychophar-macology*, *44*(1), 200–213.

Yokota, A. (2020). *Outdoor navigation: An exploratory study*. Honors thesis, University of California, Santa Barbara.

Yu, S., Boone, A. P., He, C., Davis, R., Hegarty, M., Chrastil, E., & Jacobs, E. (2021). Age-related changes in spatial navigation are evident by midlife and differ by sex. *Psychological Science*, *32*(5), 692–704.

Zhong, J. Y., & Moffat, S. D. (2018). Extrahippocampal contributions to age-related changes in spatial navigation ability. *Frontiers in Human Neuroscience*, *12*, article 272.

Zoladz, P. R., Kalchik, A. E., Hoffman, M. M., Aufdenkampe, R. L., Burke, H. M., Woelke, S. A., … Talbot, J. N. (2014). Brief, pre-retrieval stress differentially influences long-term memory depending on sex and corticosteroid response. *Brain and Cognition*, *85*, 277–285.