Review

What determines our navigational abilities?

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The ability to find one's way in our complex environments represents one of the most fundamental cognitive functions. Although involving basic perceptual and memory related processes, spatial navigation is particularly complex because it is a multisensory process in which information needs to be integrated and manipulated over time and space. Not surprisingly, humans differ widely in this ability, and recent animal and human work has begun to unveil the underlying mechanisms. Here, we consider three interdependent domains that have been related to navigational abilities: cognitive and perceptual factors, neural information processing and variability in brain microstructure. Together, the findings converge into an emerging model of how different factors interact to produce individual patterns of navigational performance.

Spatial navigation – a complex behavior with large individual differences

The ability to maintain a sense of direction and location while moving about in the environment is a fundamental cognitive function. Mammals rely on spatial cognitive processes for obtaining food, avoiding prey and finding mates. In humans, spatial navigation is indispensable for finding our way in complex environments, planning routes to distant locations and returning to our car after a walk in a new city. As a consequence, when lesions to the brain impair navigational abilities, patients often experience devastating effects on their everyday lives [1].

Spatial navigation can be based on externalized representations such as maps or diagrams and on internal representations derived from sensory experience. This review focuses on internal representations, which includes perceiving spatial information from multiple sensory cues, creating and maintaining spatial representations in short- and long-term memory, and using and manipulating these representations to guide navigational behavior. Given the complexity of cues, representations and processes, it is not surprising that humans differ widely in their navigational abilities. We all know some acquaintances with an excellent sense of direction whereas others easily get lost. This observation has been confirmed under controlled laboratory conditions; however, researchers have only started to address the underlying questions systematically: What are the differences in spatial representations and processes between people with more and less navigational ability? How do people differ in the cues and strategies they use for navigation? And how are these behavioral differences related to potential differences in the organization, functioning and integrity of critical brain structures?

Figure 1 provides an overview of the sensory cues, computational mechanisms and spatial representations involved in most forms of human and animal navigation. Variability in navigational abilities can arise at multiple stages, including the precision with which spatial information is encoded from sensory experiences, the ability to form spatial representations of external environments and the efficacy with which they are used to guide navigational behavior. These levels are highly interdependent (i.e. existing mental representations can affect sensory experience), and many navigational tasks bridge multiple levels (i.e. path integration involves perceiving self-motion cues and forming a spatial representation). Therefore, we have adopted a broad categorization scheme with two sections, the first of which covers findings from behavioral studies and the second addresses underlying factors with regard to neural information processing. Importantly, the existing literature does not allow for these sections to be homologous, as in some cases, individual differences have been examined at one level but not the other (i.e. the behavioral work on individual differences in perspective taking ability has not yet been complemented by corresponding neuroscience experiments). Finally, a treatment of the determinants of navigational abilities might bring up questions about the underlying causes (biological, environmental and interactional). However, most of the research to date has been concerned with identifying the cognitive and neural components that determine navigational ability, as this analysis must precede the systematic study of causal factors.

Glossary

Cognitive map: the term cognitive map was first coined by Tolman [96] to express that rats in his experiments took novel shortcuts to a goal location, thus indicating an understanding of the spatial structure of the environment. The term suggests – and is often used to suggest – that we possess spatial representations similar to a real map, as if the world was represented from a bird's eye perspective. However, when spatial knowledge is acquired from navigation (as opposed to looking at a map), many researchers [97] prefer to think of a cognitive map as a type of 'see through representation' that preserves the ground level perspective but in which distant locations can be accessed through intervening points (i.e. buildings). Here, we conceive of cognitive maps as a flexible internal representation of the structure of the environment that is not associated with a specific orientation, hence spatial relationships (i.e. directions and distances between objects) can be inferred from any perspective.

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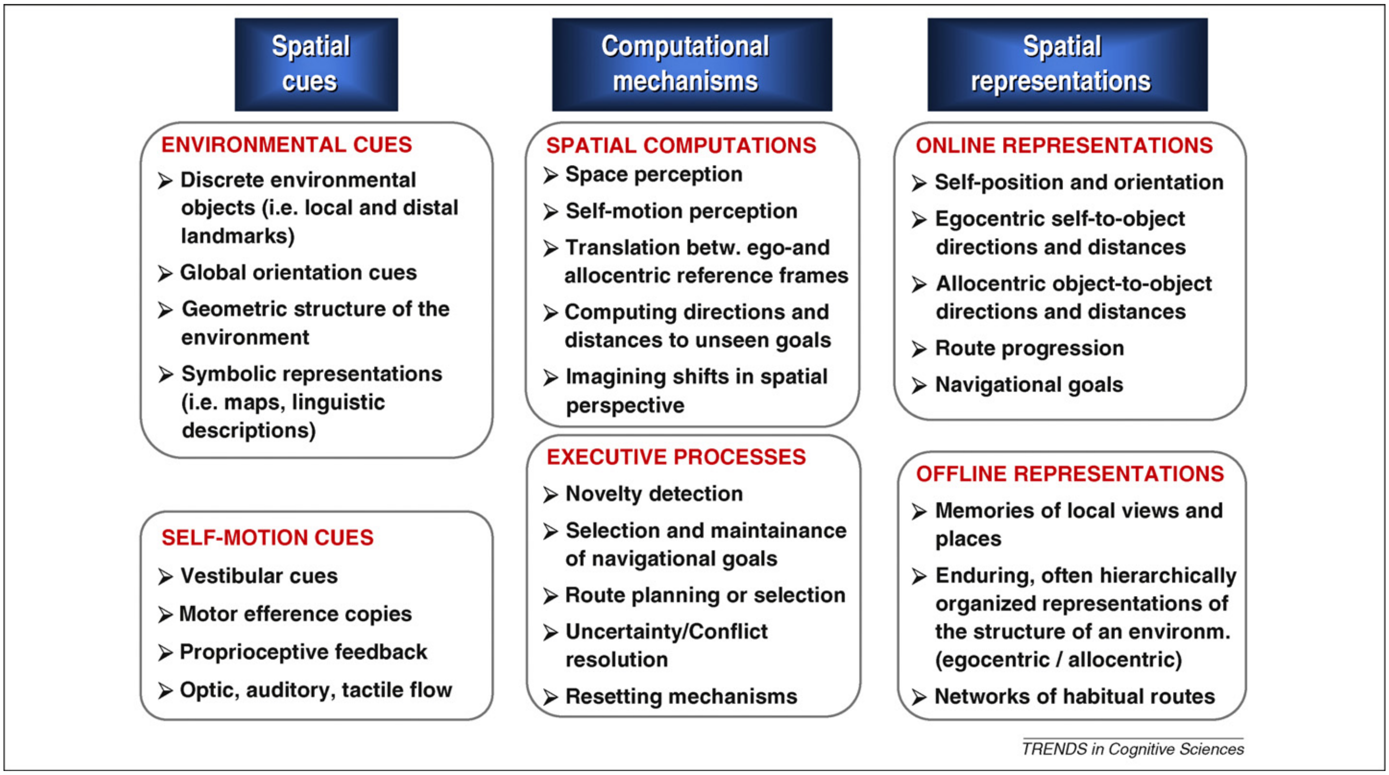

Figure 1. The complexity of spatial navigation. Schematic depiction of the various sensory cues, computational mechanisms and spatial representations that are involved in forming spatial knowledge and in using it to guide navigational behavior. Whereas navigation based on route representations involves sequences of local views that are associated with specific actions (i.e. turn right at the store), navigation based on cognitive maps requires an understanding of the spatial relationships between important features (i.e. landmarks). These relationships can be inferred from a combination of self-localization and the perception of spatial attributes of the environment. Specifically, internal and external self-motion cues can be used to maintain a sense of position and orientation (path integration), and to keep track of the locations of external features (spatial updating). Given that these processes are not error free, familiar visual cues (i.e. salient landmarks) are often used to recalibrate estimates of position and orientation. By contrast, visual information in particular provides us with direct information about spatial attributes of the environment (i.e. geometric layout) and the objects therein (i.e. distances and directions between landmarks). Importantly, given that in most natural environments, not all relevant features can be seen from a single vantage point, keeping track of one's location and orientation is crucial if we are to integrate all relevant features into a comprehensive representation. When using spatial knowledge to plan a route to an unseen goal location, humans either follow a familiar route or compute a novel route based on a cognitive map. In highly familiar environments, both strategies are often simultaneously available, thus requiring efficient decision-making strategies.

Variability in perceptual and cognitive processing

Although people differ in their ability to perceive spatial attributes such as egocentric self-to-object distances and allocentric object-to-object distances [2], the contribution of these differences to the variance in navigation ability remains to be determined. Other potential sources of individual differences include the ability to sense self-motion and to maintain orientation relative to the environment. Although people can update their position and orientation on the basis of sensing self-motion over short distances, a process known as path integration, error accumulates over larger distances, such that people instructed to walk a straight line can literally walk in circles [3]. Individual differences in path integration [4] are predicted by self-reported sense of direction (SOD) [5–7], showing that people are aware of their own skills. SOD predicts ability to update one's position and orientation while walking blindfolded or in visually impoverished environments, and to point to unseen orientations in a familiar environment. Sholl *et al.* [8] reported a particularly high correlation between SOD and the ability to judge the direction in environment-based coordinates from which a photograph of a familiar landmark had been taken. On the basis of this evidence, they proposed that self-reported SOD measures a person's evaluation of their ability to keep track of their facing direction relative to the environment, and that this ability depends on a system equivalent to the rodent head direction system [9].

In addition to self-motion cues, maintaining a sense of position and orientation can also be based on close and distant landmarks and on environmental geometry. In tasks that involve active locomotion, people are equally able to update their position and orientation on the basis of either geometric cues (e.g. room shape) or featural cues (landmarks such as a distinctive wall hanging). However, they differ in the number of cues needed for accurate orientation, particularly when the cues are somewhat ambiguous so that they have to be integrated with body-based senses [10] (Box 1). Furthermore, when humans need to reorient to a space after disorientation, they show substantial differences in the extent to which they rely on environmental geometry versus featural cues [11]. Good navigators need fewer cues to remain oriented and are more flexible in reorienting based on either geometry or landmarks as the task demands.

When humans acquire spatial knowledge from direct experience in an environment or from media such as virtual environments or maps [12–15], individual differences are extremely large and robust. For example, Ishikawa and Montello [15] led participants on the same routes through a novel environment once a week for 10 weeks and measured their ability to estimate straight line directions

Box 1. Sex differences

There have now been several demonstrations of a human male advantage in virtual maze tasks and in spatial learning from navigational experience [11,14,19,53,54], somewhat paralleling sex differences in animal species [55]. Although sex differences are sometimes more pronounced when tested in simulated environments [14,54], they occur with testing in both real and virtual environments [56] and when the analyses control for video game experience that is often greater in males than in females [19].

Superior performance by males is not found in all tasks at the environmental scale. It is typical when people learn spatial layout from direct experience, but not when they learn from maps, and is also more pronounced in measures of survey knowledge than in measures of route knowledge [53,56]. Furthermore, female performance can vary with hormonal fluctuations, such that women can perform as well as males during low-estrogen stages of their cycle [57]. Object location memory often shows an advantage in favor of females, although this can depend on the type of objects, whether self-motion is involved, and the degree of metric precision required [58,59].

Intriguingly, there appear to be qualitative differences in the environmental cues and strategies that women and men use during navigation and orientation. Women typically report navigating on the basis of local landmarks and familiar routes, whereas men report using cardinal directions, environmental geometry and metric distances [60,61], a result which has been supported by neuroimaging findings [62]. Although women do not differ from men in dependence on or ability to use landmarks, they depend less on geometry when reorienting to an environment [11] and are relatively more impaired at finding a target based on directional cues (i.e. environmental slope, [60]). Women also require more environmental cues to remain oriented in an environment [10] and have difficulty following navigation directions based on cardinal directions and metric distances [21]. Thus, strategy preferences can reflect proficiency differences between the sexes in use of geometric cues, as well as relative cue salience.

In terms of causal factors, there is increasing evidence for the influence of sex hormones on navigational performance [25,57,63–65], and several evolutionary theories have been proposed [66]. However, men and women also differ in navigational experience [54,67] and there is some evidence that wayfinding anxiety mediates the differences between the sexes in navigational performance [67].

and distances between locations. Whereas some participants had almost perfect configural knowledge of the environment after one or two learning experiences, others performed at chance even after 10 learning trials. The causes of variance in navigational ability have not been studied systematically in the individual differences literature to date, although navigation ability is clearly influenced by both genetic factors and environmental influences such as parental guidance and exposure to maps [16,17]. There has been more attention given to causal factors in the literature on sex differences (Box 1).

Many studies of individual differences in spatial ability have focused on smaller-scale tasks that involve simple object transformations (i.e. mental rotation), but do these abilities predict individual differences at the scale of environments in which we navigate? Some experiments have shown that individuals classified as high and low in object-based spatial ability also differ in tasks such as route retracing and learning spatial layout [18–21]. However, a recent review of 12 studies found that the median correlation exceeded 0.3 only in two studies, and the majority of correlations were not statistically significant [22]. In contrast, perspective taking ability has been found to be more predictive of the ability to learn spatial layout from navigational experience [12,13,23], presumably because adopting different perspectives is required by many navigational tasks.

Correlational studies are limited in that the correlation between two variables reflects variance specific to each of the tasks, as well as error variance. Using structural equation modeling to control for these sources of variance, Hegarty *et al.* [14] could demonstrate that object-based spatial abilities and the ability to learn the layout of an environment are partially dissociated. As shown in Figure 2, object-based spatial ability was significantly more related to learning from media than to learning from direct experience, whereas sense of direction showed a significant difference in the opposite direction. Moreover, learning from direct experience in an environment was somewhat distinct from learning from media (video and desktop virtual environments; [24]). The authors concluded that object-based and environmental spatial abilities share the ability to encode spatial information from visual input, maintain this information in memory and make inferences from this information. Most importantly, however, learning from direct experience also involves the sensing of self-motion for the purpose of spatial updating and path integration, an ability that cannot be measured with simple object-based tasks in which self-motion cues are neither available nor task-relevant.

Spatial navigation can be based on separate memory representations. One memory system gradually acquires sequences of actions (e.g. repeatedly following a fixed route) and provides rigid route representations, often in an egocentric reference frame and based on local landmarks. The other develops observer-independent, flexible representations (often termed cognitive maps or survey representations) that allow for planning direct paths to unseen goal locations, even over unfamiliar terrain. Individuals can have preferences for route-based vs. survey-based strategies that are often gender-related (Box 1), and animal models suggest that these can also depend on hormonal fluctuations [25]. However, strategy choice can also depend on factors such as the demands of different navigation tasks, the information available to the navigator, and the reliability of available cues [26–29]. Hence, the best navigators appear to be those who switch flexibly between different strategies, depending on what is optimal in a given situation [24].

Variability in structure and function of critical brain circuits

In the previous section, we have discussed behavioral experiments looking for factors that drive individual performance differences in navigational abilities. Studies from animal and human cognitive neuroscience have attempted to link these differences to variability in neural information processing and brain microstructure. For example, whereas the neural mechanisms that cause individual differences in space perception remain to be explored, the precision of self-motion perception could be related to differences in sensory noise. In monkeys, area MST, located in the medial superior temporal cortex, is crucial for computing the direction of self-motion [30], which is partly based on incoming motion cues from

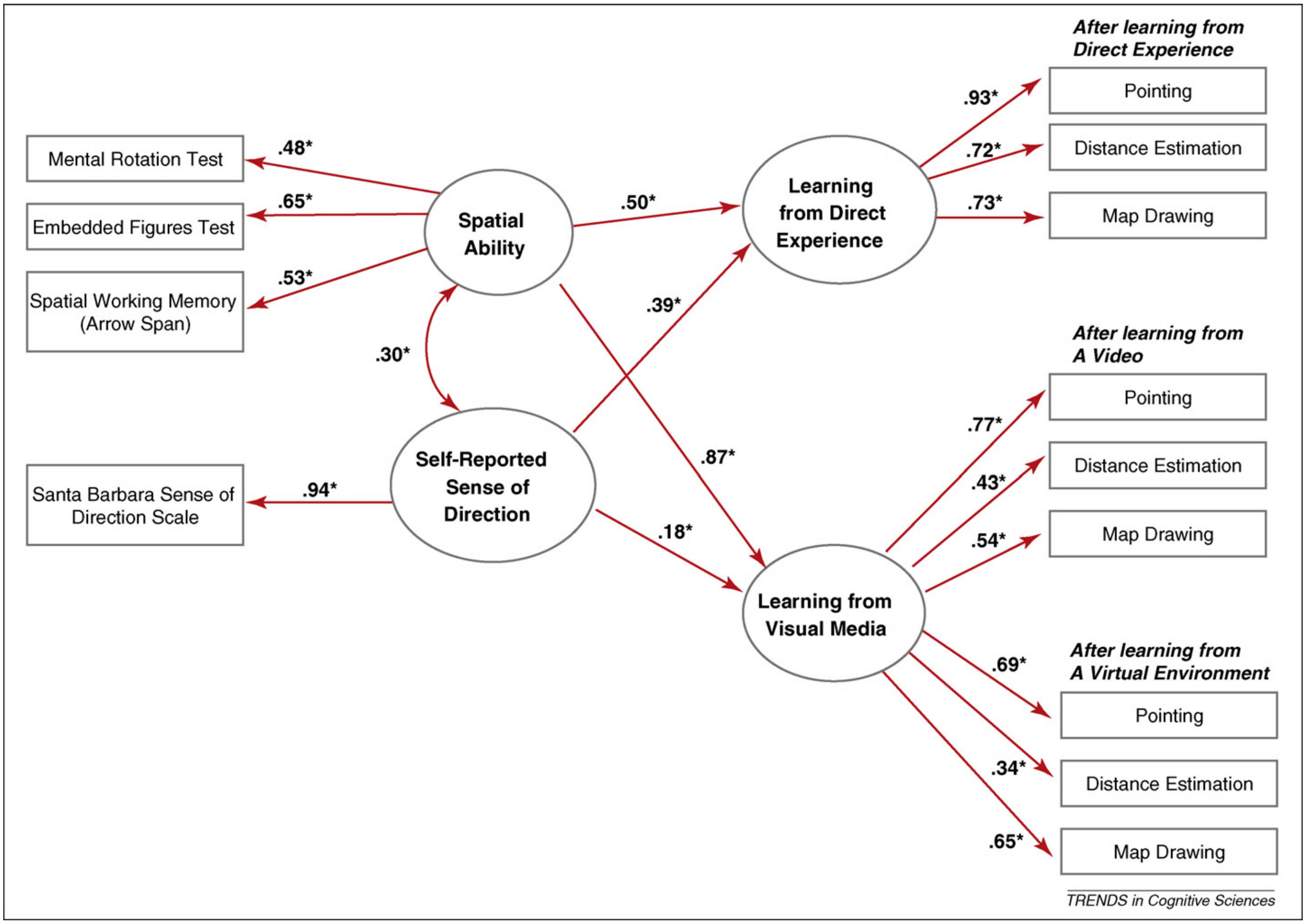

Figure 2. Relations between measures of spatial layout learning, spatial ability and self-reported sense of direction. Results of the structural equation model observed by Hegarty *et al.* [14]. Boxes indicate measured variables and ovals represent latent variables derived from these, which reflect the variance shared by the different measured variables to which they point. Participants learned three different environments from (1) direct experience, (2) watching a video and (3) interacting with a desktop virtual environment. In each case their acquired knowledge was tested with three measures; (1) pointing to unseen locations in the environment, (2) estimating straight-line distances to these locations and (3) drawing a map of the environment. The path coefficients (values labeling each arrow) can be interpreted as standardized regression weights indicating the degree of relation between the predictor and predicted variables after controlling for the effects of the other variables. Note that the path coefficient linking spatial ability and learning from direct experience is 0.5, indicating that these two abilities reflect some common variance but are also somewhat distinct. Measures of spatial ability were relatively more predictive of learning from media than of learning from direct experience, whereas self-reported sense of direction was relatively more predictive of learning from direct experience than from media. These results support a partial dissociation between large- and small-scale spatial abilities and suggest that self-motion perception (important in learning from direct experience but not from media) could be a factor in this dissociation. Figure adapted, with permission, from Ref. [14].

neighboring area MT. In aging monkeys, the signal-to-noise ratio in MT is significantly reduced [31,32] (Box 2), thus conveying less informative motion signals to area MST. Although similar findings remain to be established in younger animals to explain individual performance differences, it is highly likely that the amount of sensory noise in motion processing areas is a decisive factor. Consistent with this assumption, Wolbers *et al.* [33] observed a correlation between systematic pointing errors and functional magnetic resonance imaging (fMRI) responses in a homologous region in the human brain (hMT+) during visual path integration. These findings suggest that local processing in motion sensitive structures affects an individual's uncertainty about the amount of self-rotation and self-translation.

Estimates of self-motion enable us to update our position and to keep track of previously occupied locations. In rodents, entorhinal grid cells are thought to integrate self-motion cues for computing positional estimates, which updates the firing of hippocampal place cells [34]. However, although the entorhinal–hippocampal circuit provides information about the current position of an agent, keeping track of previous locations adds a working memory component that involves medial prefrontal areas, particularly when this information guides navigational decisions [35]. The visual path integration study of Wolbers *et al.* [33] supports this hypothesis by revealing a tight coupling between an individual's uncertainty about the direction to a start location and bilateral responses in the hippocampus and the medial prefrontal cortex (Figure 3). These authors suggested that during navigation, hippocampal place responses are used by the prefrontal cortex to continuously update a homing vector during the outward journey. As a consequence, the degree of recruitment of both areas influenced the precision with which these computations were carried out, thus having a direct impact on an individual's path integration ability.

For most navigational tasks, estimates of self-position and orientation need to be complemented by representations of the outside world. One region involved in forming

Box 2. Individual differences in aging subjects

Individual differences in navigational abilities are particularly prominent at later stages in life. For example, when Monacelli *et al.* [68] tested various groups of subjects on their ability to navigate in a familiar hospital, both healthy and demented elderly subjects scored worse than a young control group on various performance measures. Importantly, even among the healthy aged subjects, some participants had no navigation difficulties whereas others made substantial navigational errors. In the extant literature on age-related changes in spatial memory, such individual deficits have predominantly been linked to sensory, mnemonic and executive processes.

(i) Motion processing. The accuracy of visual motion processing varies across aging humans, and individual motion thresholds are predictive of navigational abilities [69]. Given that aging monkeys show reduced signal-to-noise ratios in the motion sensitive area MT [31,32], difficulties with extracting the speed and direction of self-motion from optic flow could impair path integration [70] and spatial updating, processes that are important for self and object localization [34,71] and that can enable us to link views of scenes or places with accurate spatial positions.

(ii) Hippocampal processing. Although the firing patterns of hippocampal place cells in rats with age-related memory impairments do not differ from the ones of unimpaired or young animals, these cells often fail to encode changes in the environment and to create new representations for novel environments [72]. These findings could reflect an imbalance between pattern completion and pattern separation in the hippocampus [73], which could in turn be related to the level of hippocampal neurogenesis [74]. In addition, place cells can exhibit differential firing behavior upon repeated exposure to the same environment [75], suggesting deficits with forming stable links between environmental cues and spatial representations. Finally, genes that control synaptic transmission and morphology in the hippocampus are associated with age-related spatial learning impairments [76]. Taken together, these findings suggest that the efficiency of information processing and storage within the hippocampus is an important determinant of age-related changes of spatial abilities.

(iii) Executive functions. Moffat and Resnick [77] demonstrated that aging humans often show inefficient search strategies in a virtual Morris water maze. Specifically, some elderly individuals took longer to find the platform and traveled longer distances in the very first trial when spatial representations were yet to be formed. These subjects were reluctant to disengage from locations that had been adequately explored, suggesting problems with strategic control mechanisms. A follow-up study revealed that individual performance was correlated with gray and white matter volumes in various extrahippocampal structures, including the prefrontal cortex [52]. As a consequence, a reduced integrity of brain structures involved in executive control could further impinge upon the individual navigational abilities of aging humans.

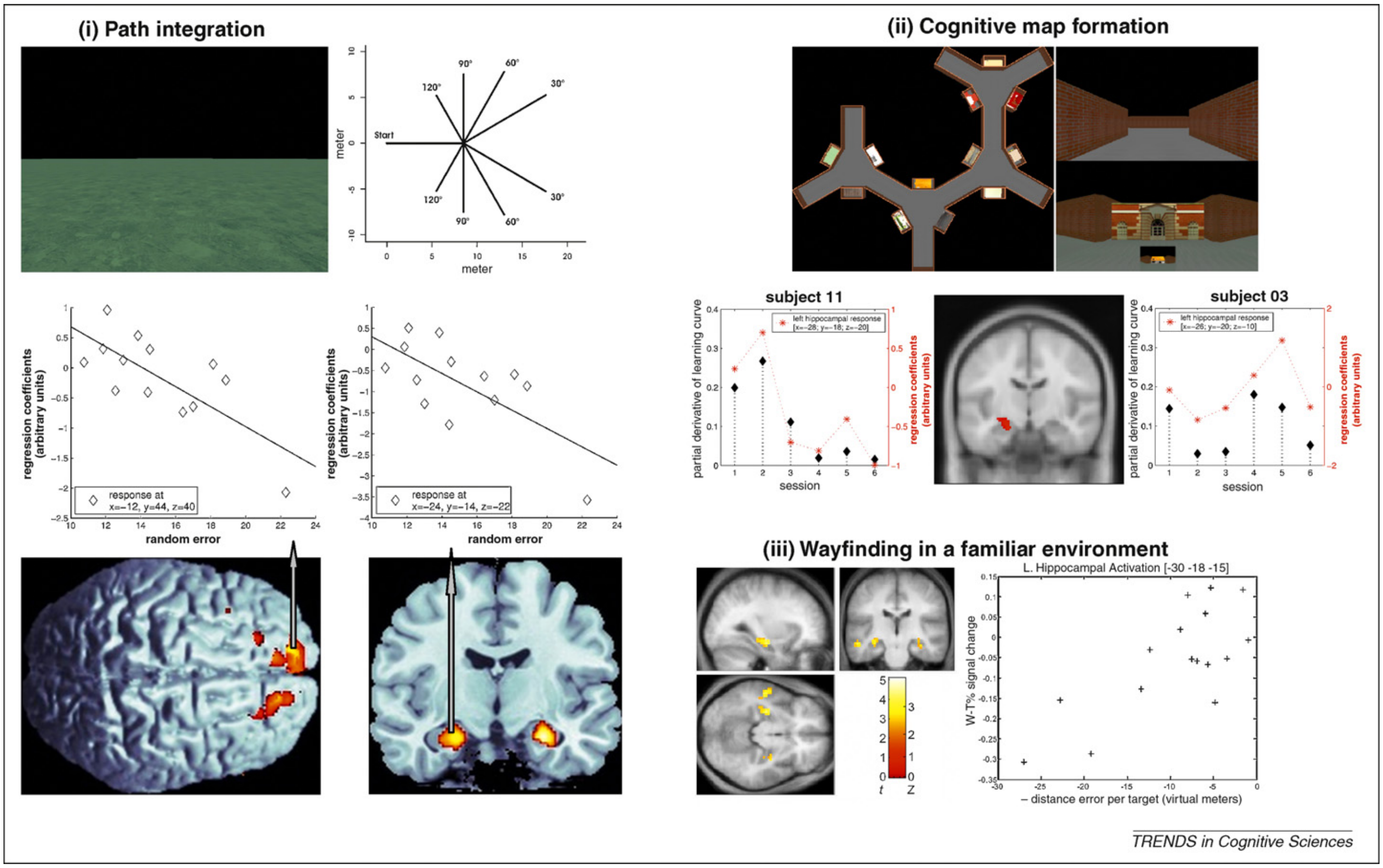

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Figure 3. Variability in neural information processing. **(i)** Neural correlates of individual variability in path integration performance. During fMRI scanning, subjects were virtually moved along two legs of a triangle before pointing towards the origin of travel. Hippocampal and medial prefrontal activation during encoding of the outbound path was greater in those participants who showed higher response consistency. This suggests that a consistent engagement of both structures is crucial for updating self-positions and maintaining previously occupied locations in working memory. **(ii)** Upper panels: in the study of Wolbers *et al.* [38], participants were repeatedly moved throughout a complex virtual environment, thereby encountering 12 distinct landmarks. Subjects were instructed to infer the spatial layout of the environment and the correct landmark locations, knowledge that was tested with a subsequent retrieval task. Lower panels: anterior hippocampal recruitment during cognitive map formation predicts the speed of learning. Hippocampal activation (shown in red) in subject 11 was strongest in the initial learning stage and decayed rapidly after performance had reached level in session 3. In contrast, the slower learning process in subject 03 was paralleled by stronger hippocampal activation in the second half of the experiment. As a consequence, anterior hippocampal activation appears to be most prominent whenever substantial performance improvements are observable. **(iii)** Hippocampal activation during wayfinding in a familiar virtual town correlated with performance across subjects, demonstrating a greater engagement in better navigators than in poorer navigators. Similar results were observed in the head of right caudate during route following (not shown), suggesting a dissociation between the retrieval of a cognitive map and the retrieval of habitual routes. Figure adapted, with permission, from Refs. [33,38,44].

these representations is the parahippocampal cortex, because it supports the learning of places from individual views. In good navigators, parahippocampal responses show greater differences between novel and familiar places and between novel and familiar views compared with bad navigators [36]. These findings indicate that individuals vary as to how useful parahippocampal representations are for distinguishing between different places and different views.

In order for place representations to be useful for navigation, we need to integrate them into a representation that preserves some degree of spatial relationships (i.e. topological, metric, action based, etc.). Whereas action-based route representations have been linked to the dorsal striatum, observer-independent cognitive maps critically depend on retrosplenial cortex and the hippocampus [27,37,38]. As a consequence, interpretations of neural data require a precise control or identification of the type of representation used in a given task. Wolbers *et al.* [38,39] developed one such task (Figure 3) and their results showed that anterior hippocampal recruitment determines the speed with which an individual forms a cognitive map. These and other results that have linked memory consolidation in the hippocampus to navigational skills [40] are supported by animal findings, suggesting that the learning-related hippocampal circuits of fast learners are better suited to solve spatial tasks than those of slow learners. Specifically, the latter require structural reorganization to form spatial memories as opposed to the more economic mechanism of altering synaptic efficacy used by the former [41].

Hippocampal activation is not only observed during cognitive map formation but also during retrieval, with some studies suggesting an anterior–posterior functional division in the hippocampus [27,42], reminiscent of the dorsoventral differentiation in rodents [43]. At retrieval, more accurate navigators show greater hippocampal activation when navigating to an unseen goal in a familiar environment [44]. Importantly, the same individuals show greater caudate responses when following a well-learned route, whereas poor navigators show the reverse pattern. Hence, the relative engagement of the hippocampus and the caudate seems to determine the individual proficiency of forming and retrieving cognitive maps and route-based representations. In addition, given that a chosen strategy might not be optimal for the task at hand, the ability to flexibly switch between hippocampal and striatal representations is a further characteristic of successful navigators [45].

Although preliminary reports of associations between brain microstructure and navigational abilities [46,47] need to be qualified by studies that control for unspecific variables that could also account for the anatomical variability, extended navigational experience induces plastic changes in the brain. Maguire *et al.* [48,49] demonstrated that the posterior hippocampal volume of London taxi but not bus drivers – the latter experiencing similar levels of stress, driving and self-motion – correlates with driving experience. Hence, the extensive use of a flexible spatial representation in the taxi drivers – as opposed to the fixed routes that the bus drivers follow – enlarges the volume of the posterior hippocampus to allow for this representation to be elaborated, a finding that has also been reported in other species (i.e. pigeons, [50]).

Finally, creating and retrieving spatial representations also relies upon executive functions such as planning and spatial working memory, and lesions to the prefrontal cortex, a key player for the control of executive functions, can severely impair navigational abilities [51]. Importantly, even in healthy humans, preliminary evidence suggests that regional brain volumes in prefrontal areas are associated with learning performance in a virtual version of the Morris water maze [52]. This indicates that the efficiency which with prefrontal areas carry out executive functions can further determine overall navigational proficiency.

Concluding remarks

Spatial navigation involves multiple sensory cues, interacting processes and representations, and performance differences can arise at various stages. On the sensory side, people differ with regard to the accuracy with which

Box 3. The impact of genetic factors

The structural and functional integrity of neuronal circuits is jointly determined by environmental and physiological factors, the latter including genetic predispositions. Genetic association studies in animals have demonstrated various genetic influences on hippocampal processes involved in spatial navigation [78]. Specific examples include the brain derived neurotrophic factor (BDNF) that is known for its role in activity-dependent plasticity and hippocampal long-term potentiation. Both processes are thought to underlie the formation of new learning and memories, and suppression of BDNF synthesis impairs spatial learning in rodents [79]. Although direct effects of BDNF on human navigational learning remain to be established, BDNF modulation of hippocampal engagement is a key process in the initial acquisition of information about novel indoor and outdoor scenes [80]. In addition, polymorphisms of the BDNF gene have also been associated with hippocampal volume [81], which could contribute to preferences for specific strategies in a navigational task [46].

A second route for genetic predispositions to affect hippocampal processing and hence navigational abilities involves pattern separation. To distinguish between environments or regions within an environment, hippocampal subfields create orthogonal representations [82]. This ability to pattern separate is directly related to neurogenesis in the dentate gyrus, which is in turn controlled by several genes [83]. Given that ablation of pattern separation in mice induces deficits in spatial learning in a radial arm maze [84], it appears probable that individual genetic predispositions that control hippocampal neurogenesis can have direct effects on navigational abilities via differences in pattern separation.

Finally, as spatial navigation also involves executive control processes that involve subdivisions of the prefrontal cortex [33,85], genes that regulate prefrontal functioning should have the potential to influence navigational abilities. For example, given the dopaminergic metabolism in the prefrontal cortex, the gene producing catechol-*O*-methyltransferase (COMT) is thought to have a major impact on functions such as the manipulation of information [86] and the resolution of uncertainty [87], both of which are involved in spatial navigation. Moreover, COMT polymorphisms also affect prefrontal–hippocampal coupling [88], which is crucial for navigational planning [35].

Taken together, although the existing animal findings strongly suggest genetic influences on navigational abilities, a direct demonstration remains to be established in humans. Given the complexity of spatial navigation, genetic variability is likely to affect navigational functions at multiple processing stages.

Box 4. Outstanding questions and future directions

- Age-related differences in navigational abilities have only been studied in cross-sectional experiments. This makes it difficult to determine the underlying causes: Was this variability already present at a younger age or is it specifically linked to different developmental trajectories? If the latter, what mechanisms account for those trajectories, both on the neural and the behavioral level? And is there a potential to alleviate or even stop age-related decline in spatial abilities?
- Extensive navigational experience leads to structural changes in the hippocampus, but does this pave the way for acquiring new spatial representations more easily and more accurately? The finding that anterior hippocampal volume was negatively correlated with driving experience in the taxi drivers studied by Maguire *et al.* [48,49] is not in line with this conjecture, but it remains to be tested directly.
- Psychiatric conditions such as pathological anxiety, depression or post-traumatic stress disorder can have navigational consequences, which have been related to functional changes in the hippocampus and to reduced hippocampal volume [89–92]. Moreover, anxiety has also been proposed as a mediating factor in sex differences in navigational ability [67]. These issues require further investigation to identify the specific navigational processes that are impaired and to characterize how potential treatments affect navigational behavior.
- Spatial navigation experiments have employed a large variety of paradigms that differ with regard to how spatial information is acquired (i.e. locomotion, learning from maps or virtual animations, etc.) and retrieved (i.e. estimating distances and directions, navigating to a goal, map drawing, etc.). In addition, the scale of the environment differs widely: whereas in tasks such as the Morris water maze (and virtual renditions thereof) most of the relevant spatial information can be apprehended from a single vantage point, learning complex environments is much more demanding as observers need to infer spatial relationships between distant locations. To identify sources of individual variability common to different studies, we need to develop a comprehensive taxonomy of spatial navigation tasks and the participating processes [93].
- Is it possible to improve navigational functions? People with a poor sense of direction experience daily problems with navigation, sometimes even in familiar environments [94]. With the widespread use of GPS-based navigation aids, these problems become even more severe when the technology fails [95] or is unavailable (i.e. indoors). Given that many expert navigators can use spatial cues that are ignored by the majority of us, it is important to investigate if and how efficient navigational strategies can be learned to overcome individual difficulties.

they perceive spatial properties of the environment. In addition, variability in self-motion perception, probably related to signal-to-noise ratios in cortical areas involved in (self-)motion processing, could influence the accuracy with which people keep track of their orientation and position relative to the environment. This ability to path integrate further depends on efficient hippocampal recruitment. The second level of individual differences pertains to the cues and strategies we use when acquiring spatial information: whereas some people prefer featural cues to maintain orientation and to infer spatial relationships, others focus on geometric properties such as the layout of an environment. Furthermore, humans differ with regard to their preferred strategies for acquiring spatial information, with route-based strategies depending on the dorsal striatum and cognitive mapping involving the hippocampus. Because these systems allow for different types of navigational behavior, the ability to choose the adequate strategy for a given situation appears to be a key characteristic of successful navigators. In combination with planning operations and working memory processes, such executive functions critically depend on efficient processing in prefrontal circuits.

Individual differences in navigational abilities are particularly prominent at later stages in life and can determine how independently elderly people can go about their lives. Thus, even though much progress has been made, it is important to arrive at a more comprehensive characterization of the factors that influence our navigational abilities. This will need to include a more detailed understanding of the impact of biological predispositions (Box 3) and could ultimately help us understand how to achieve optimal developmental trajectories for successful aging (see Box 4 for a list of outstanding questions and priorities for further research).

References

1 Aguirre, G.K. and D'Esposito, M. (1999) Topographical disorientation: a synthesis and taxonomy. *Brain* 122, 1613–1628

2 Norman, J.F. *et al.* (2005) The perception of distances and spatial relationships in natural outdoor environments. *Perception* 34, 1315–1324

3 Souman, J.L. *et al.* (2009) Walking straight into circles. *Curr. Biol.* 19, 1538–1542

4 Loomis, J.M. *et al.* (1993) Nonvisual navigation by blind and sighted: assessment of path integration ability. *J. Exp. Psychol. Gen.* 122, 73–91

5 Hegarty, M. *et al.* (2002) Development of a self-report measure of environmental spatial ability. *Intelligence* 30, 425–447

6 Kozlowski, L.T. and Bryant, K.J. (1977) Sense-of-direction, spatial orientation, and cognitive maps. *J. Exp. Psychol. Hum. Percept. Perform.* 3, 590–598

7 Sholl, M.J. (1988) The relationship between sense of direction and mental geographic updating. *Intelligence* 12, 299–314

8 Sholl, M.J. *et al.* (2006) Allocentric-heading recall and its relation to self-reported sense-of-direction. *J. Exp. Psychol. Learn. Mem. Cogn.* 32, 516–533

9 Taube, J.S. (2007) The head direction signal: origins and sensory-motor integration. *Annu. Rev. Neurosci.* 30, 181–207

10 Kelly, J.W. *et al.* (2009) Individual differences in using geometric and featural cues to maintain spatial orientation: cue quantity and cue ambiguity are more important than cue type. *Psychon. Bull. Rev.* 16, 176–181

11 Sandstrom, N.J. *et al.* (1998) Males and females use different distal cues in a virtual environment navigation task. *Brain Res. Cogn. Brain Res.* 6, 351–360

12 Allen, G.A. *et al.* (1996) Predicting environmental learning from spatial abilities: an indirect route. *Intelligence* 22, 327–355

13 Fields, A.W. and Shelton, A.L. (2006) Individual skill differences and large-scale environmental learning. *J. Exp. Psychol. Learn. Mem. Cogn.* 32, 506–515

14 Hegarty, M. *et al.* (2006) Spatial abilities at different scales: individual differences in aptitude-test performance and spatial-layout learning. *Intelligence* 34, 151–176

15 Ishikawa, T. and 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. *Cogn. Psychol.* 52, 93–129

16 Szechter, L.E. and Liben, L.S. (2004) Parental guidance in preschoolers' understanding of spatial-graphic representations. *Child Dev.* 75, 869–885

17 Uttal, D.H. (2000) Seeing the big picture: map use and the development of spatial cognition. *Dev. Sci.* 3, 247–286

18 Blajenkova, O. *et al.* (2005) Individual differences in the representations of novel environments. *J. Environ. Psychol.* 25, 97–109

19 Moffat, S.D. *et al.* (1998) Navigation in a "virtual" maze: sex differences and correlation with psychometric measures of spatial ability in humans. *Evol. Hum. Behav.* 19, 73–87
20 Pazzaglia, F. and DeBeni, R. (2006) Are people with high and low mental rotation abilities differently susceptible to the alignment effect? *Perception* 35, 369–383
21 Saucier, D.M. *et al.* (2002) Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behav. Neurosci.* 116, 403–410
22 Hegarty, M. and Waller, D. (2005) Individual differences in spatial abilities. In *The Cambridge Handbook of Visuospatial Thinking* (Shah, P. and Miyake, A., eds), Cambridge University Press, pp. 121–169
23 Kozhevnikov, M. *et al.* (2006) Perspective-taking vs. mental rotation transformation and how they predict spatial navigation performance. *Appl. Cogn. Psychol.* 20, 397–417
24 Liben, L.S. *et al.* Identifying locations and directions on field and representational mapping tasks: predictors of success. *Spat. Cogn. Comput.* (2010)
25 Korol, D.L. *et al.* (2004) Shifts in preferred learning strategy across the estrous cycle in female rats. *Horm. Behav.* 45, 330–338
26 Etchamendy, N. and Bohbot, V.D. (2007) Spontaneous navigational strategies and performance in the virtual town. *Hippocampus* 17, 595–599
27 Doeller, C.F. *et al.* (2008) Parallel striatal and hippocampal systems for landmarks and boundaries in spatial memory. *Proc. Natl. Acad. Sci. U. S. A.* 105, 5915–5920
28 Foo, P. *et al.* (2005) Do humans integrate routes into a cognitive map? Map- versus landmark-based navigation of novel shortcuts. *J. Exp. Psychol. Learn. Mem. Cogn.* 31, 195–215
29 Hölscher, C. (2009) Adaptivity of wayfinding strategies in a multi-building ensemble: the effects of spatial structure, task requirements and metric information. *J. Environ. Psychol.* 29, 208–219
30 Britten, K.H. (2008) Mechanisms of self-motion perception. *Annu. Rev. Neurosci.* 31, 389–410
31 Liang, Z. *et al.* Aging affects the direction selectivity of MT cells in rhesus monkeys. *Neurobiol. Aging.*(2010)
32 Yang, Y. *et al.* (2009) Aging affects the neural representation of speed in Macaque area MT. *Cereb. Cortex* 19, 1957–1967
33 Wolbers, T. *et al.* (2007) Differential recruitment of the hippocampus, medial prefrontal cortex, and the human motion complex during path integration in humans. *J. Neurosci.* 27, 9408–9416
34 Jeffery, K.J. (2007) Self-localization and the entorhinal-hippocampal system. *Curr. Opin. Neurobiol.* 17, 684–691
35 Jones, M.W. and Wilson, M.A. (2005) Theta rhythms coordinate hippocampal-prefrontal interactions in a spatial memory task. *PLoS Biol.* 3, e402
36 Epstein, R.A. *et al.* (2005) Learning places from views: variation in scene processing as a function of experience and navigational ability. *J. Cogn. Neurosci.* 17, 73–83
37 Burgess, N. (2008) Spatial cognition and the brain. *Ann. N. Y. Acad. Sci.* 1124, 77–97
38 Wolbers, T. and Büchel, C. (2005) Dissociable retrosplenial and hippocampal contributions to successful formation of survey representations. *J. Neurosci.* 25, 3333–3340
39 Wolbers, T. *et al.* (2004) Neural foundations of emerging route knowledge in complex spatial environments. *Brain Res. Cogn. Brain Res.* 21, 401–411
40 Janzen, G. *et al.* (2008) Memory consolidation of landmarks in good navigators. *Hippocampus* 18, 40–47
41 Sandi, C. *et al.* (2004) Neurobiological and endocrine correlates of individual differences in spatial learning ability. *Learn. Mem.* 11, 244–252
42 Iaria, G. *et al.* (2007) Retrosplenial and hippocampal brain regions in human navigation: complementary functional contributions to the formation and use of cognitive maps. *Eur. J. Neurosci.* 25, 890–899
43 Moser, M.B. and Moser, E.I. (1998) Functional differentiation in the hippocampus. *Hippocampus* 8, 608–619
44 Hartley, T. *et al.* (2003) The well-worn route and the path less traveled. Distinct neural bases of route following and wayfinding in humans. *Neuron* 37, 877–888
45 Iaria, G. *et al.* (2003) Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *J. Neurosci.* 23, 5945–5952
46 Bohbot, V.D. *et al.* (2007) Gray matter differences correlate with spontaneous strategies in a human virtual navigation task. *J. Neurosci.* 27, 10078–10083
47 Iaria, G. *et al.* (2008) Navigational skills correlate with hippocampal fractional anisotropy in humans. *Hippocampus* 18, 335–339
48 Maguire, E.A. *et al.* (2000) Navigation-related structural change in the hippocampi of taxi drivers. *Proc. Natl. Acad. Sci. U. S. A.* 97, 4398–4403
49 Maguire, E.A. *et al.* (2006) London taxi drivers and bus drivers: a structural MRI and neuropsychological analysis. *Hippocampus* 16, 1091–1101
50 Cnotka, J. *et al.* (2008) Navigational experience affects hippocampus size in homing pigeons. *Brain Behav. Evol.* 72, 233–238
51 Ciaramelli, E. (2008) The role of ventromedial prefrontal cortex in navigation: a case of impaired wayfinding and rehabilitation. *Neuropsychologia* 46, 2099–2105
52 Moffat, S.D. *et al.* (2007) Extrahippocampal contributions to age differences in human spatial navigation. *Cereb. Cortex* 17, 1274–1282
53 Montello, D.R. *et al.* (1999) Sex-related differences and similarities in geographic and environmental spatial abilities. *Ann. Assoc. Am. Geogr.* 89, 515–534
54 Waller, D. (2000) Individual differences in spatial learning from computer-simulated environments. *J. Exp. Psychol. Appl.* 6, 307–321
55 Jonasson, Z. (2005) Meta-analysis of sex differences in rodent models of learning and memory: a review of behavioral and biological data. *Neurosci. Biobehav. Rev.* 28, 811–825
56 Coluccia, E. and Louse, G. (2004) Gender differences in spatial orientation: a review. *J. Environ. Psychol.* 24, 329–340
57 Chabanne, V. *et al.* (2004) Sex differences and women's hormonal cycle effect on spatial performance in a virtual environment navigation task. *Curr. Psychol. Cogn.* 22, 351–375
58 Voyer, D. *et al.* (2007) Gender differences in object location memory: a meta-analysis. *Psychon. Bull. Rev.* 14, 23–38
59 Burgess, N. *et al.* (2004) Orientational manoeuvres in the dark: dissociating allocentric and egocentric influences on spatial memory. *Cognition* 94, 149–166
60 Chai, X.J. and Jacobs, L.F. (2009) Sex differences in directional cue use in a virtual landscape. *Behav. Neurosci.* 123, 276–283
61 Lawton, C.A. (1994) Gender differences in wayfinding strategies: relationship to spatial ability and spatial anxiety. *Sex Roles* 30, 765–779
62 Grön, G. *et al.* (2000) Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nat. Neurosci.* 3, 404–408
63 Bell, S. and Saucier, D.M. (2004) Relationship among environmental pointing accuracy, mental rotation, sex, and hormones. *Environ. Behav.* 36, 251–265
64 Burkitt, J. *et al.* (2007) Evidence for the influence of testosterone in the performance of spatial navigation in a virtual water maze in women but not in men. *Horm. Behav.* 51, 649–654
65 Driscoll, I. *et al.* (2005) Virtual navigation in humans: the impact of age, sex, and hormones on place learning. *Horm. Behav.* 47, 326–335
66 Jones, C.M. *et al.* (2003) The evolution of sex differences in spatial ability. *Behav. Neurosci.* 117, 403–411
67 Lawton, C.A. and Kallai, J. (2002) Gender differences in wayfinding strategies and anxiety about wayfinding: a cross cultural comparison. *Sex Roles* 47, 389–401
68 Monacelli, A.M. *et al.* (2003) Spatial disorientation in Alzheimer's disease: the remembrance of things passed. *Neurology* 61, 1491–1497
69 Duffy, C.J. (2009) Visual motion processing in aging and Alzheimer's disease: neuronal mechanisms and behavior from monkeys to man. *Ann. N. Y. Acad. Sci.* 1170, 736–744
70 Mahmood, O. *et al.* (2009) Age differences in visual path integration. *Behav. Brain Res.* 205, 88–95
71 Wolbers, T. *et al.* (2008) Spatial updating: how the brain keeps track of changing object locations during observer motion. *Nat. Neurosci.* 11, 1223–1230
72 Wilson, I.A. *et al.* (2003) Place cell rigidity correlates with impaired spatial learning in aged rats. *Neurobiol. Aging* 24, 297–305
73 Wilson, I.A. *et al.* (2006) Neurocognitive aging: prior memories hinder new hippocampal encoding. *Trends Neurosci.* 29, 662–670
74 Drapeau, E. *et al.* (2003) Spatial memory performances of aged rats in the water maze predict levels of hippocampal neurogenesis. *Proc. Natl. Acad. Sci. U. S. A.* 100, 14385–14390

75 Barnes, C.A. *et al.* (1997) Multistability of cognitive maps in the hippocampus of old rats. *Nature* 388, 272–275

76 Burger, C. *et al.* (2007) Changes in transcription within the CA1 field of the hippocampus are associated with age-related spatial learning impairments. *Neurobiol. Learn. Mem.* 87, 21–41

77 Moffat, S.D. and Resnick, S.M. (2002) Effects of age on virtual environment place navigation and allocentric cognitive mapping. *Behav. Neurosci.* 116, 851–859

78 Ruiz-Opazo, N. and Tonkiss, J. (2006) Genome-wide scan for quantitative trait loci influencing spatial navigation and social recognition memory in Dahl rats. *Physiol. Genomics* 26, 145–151

79 Mizuno, M. *et al.* (2000) Involvement of brain-derived neurotrophic factor in spatial memory formation and maintenance in a radial arm maze test in rats. *J. Neurosci.* 20, 7116–7121

80 Hariri, A.R. *et al.* (2003) Brain-derived neurotrophic factor val66met polymorphism affects human memory-related hippocampal activity and predicts memory performance. *J. Neurosci.* 23, 6690–6694

81 Bueller, J.A. *et al.* (2006) BDNF Val66Met allele is associated with reduced hippocampal volume in healthy subjects. *Biol. Psychiatry* 59, 812–815

82 Colgin, L.L. *et al.* (2008) Understanding memory through hippocampal remapping. *Trends Neurosci.* 31, 469–477

83 Kempermann, G. *et al.* (2006) Natural variation and genetic covariance in adult hippocampal neurogenesis. *Proc. Natl. Acad. Sci. U. S. A.* 103, 780–785

84 Clelland, C.D. *et al.* (2009) A functional role for adult hippocampal neurogenesis in spatial pattern separation. *Science* 325, 210–213

85 Spiers, H.J. and Maguire, E.A. (2007) A navigational guidance system in the human brain. *Hippocampus* 17, 618–626

86 Goldman, D. *et al.* (2009) The role of COMT Val158Met in cognition. *Biol. Psychiatry* 65, e1–e2 author reply e3–e4

87 Frank, M.J. *et al.* (2009) Prefrontal and striatal dopaminergic genes predict individual differences in exploration and exploitation. *Nat. Neurosci.* 12, 1062–1068

88 Bertolino, A. *et al.* (2006) Prefrontal-hippocampal coupling during memory processing is modulated by COMT val158met genotype. *Biol. Psychiatry* 60, 1250–1258

89 Bremner, J.D. *et al.* (2008) Structural and functional plasticity of the human brain in posttraumatic stress disorder. *Prog. Brain Res.* 167, 171–186

90 Herrero, A.I. *et al.* (2006) Individual differences in anxiety trait are related to spatial learning abilities and hippocampal expression of mineralocorticoid receptors. *Neurobiol. Learn. Mem.* 86, 150–159

91 Kalisch, R. *et al.* (2006) Anxiety and hippocampus volume in the rat. *Neuropsychopharmacology* 31, 925–932

92 Sheline, Y.I. *et al.* (2002) The hippocampus and depression. *Eur. Psychiatry* 17 (Suppl. 3), 300–305

93 Wiener, J.M. *et al.* (2009) Towards a taxonomy of wayfinding tasks: a knowledge-based approach. *Spat. Cogn. Comput.* 9, 152–165

94 Iaria, G. *et al.* (2009) Developmental topographical disorientation: case one. *Neuropsychologia* 47, 30–40

95 Aporta, C. and Higgs, E. (2005) Satellite culture: global positioning systems, Inuit wayfinding, and the need for a new account of technology. *Curr. Anthropol.* 46, 729–753

96 Tolman, C.E. (1948) Cognitive maps in rats and man. *Psychol. Rev.* 55, 189–208

97 Thorndyke, P.W. and Hayes-Roth, B. (1982) Differences in spatial knowledge acquired from maps and navigation. *Cogn. Psychol.* 14, 560–589