

RESEARCH REPORT

The Relation Between Navigation Strategy and Associative Memory: An Individual Differences Approach

Chi T. Ngo, Steven M. Weisberg, Nora S. Newcombe, and Ingrid R. Olson
Temple University

Although the hippocampus is implicated in both spatial navigation and associative memory, very little is known about whether individual differences in the 2 domains covary. People who prefer to navigate using a hippocampal-dependent place strategy may show better performance on associative memory tasks than those who prefer a caudate-dependent response strategy (Bohbot, Gupta, Banner, & Dahmani, 2011), but not all studies suggest such an effect (Woollett & Maguire, 2009, 2012). Here we tested nonexpert young adults and found that preference for a place strategy positively correlated with spatial (object-location) associative memory performance but did not correlate with nonspatial (face-name) associative memory performance. Importantly, these correlations differed from each other, indicating that the relation between navigation strategy and associative memory is specific to the spatial domain. In addition, the 2 associative memory tasks significantly correlated, suggesting that object-location memory taps into processes relevant to both hippocampal-dependent navigation and nonspatial associative memory. Our findings also suggest that individual differences in spatial associative memory may account for some of the variance in navigation strategies.

Keywords: navigation strategies, associative memory, individual differences

Spatial navigation and associative memory are both hippocampal-dependent cognitive operations. For spatial navigation, the hippocampus has long been thought to support the construction of cognitive maps—internal map-like representations of the environment that allow animals to infer direct paths that they have never previously experienced (O’Keefe & Nadel, 1978; Tolman, 1948, for a review, see Burgess, Maguire, & O’Keefe, 2002). For associative memory, the hippocampus has been portrayed as a binding device, linking multiple unrelated items to form a cohesive memory episode (Eichenbaum & Bunsey, 1995; Henke, Buck, Weber, & Wieser, 1997). The topic of how the hippocampus’s role in spatial navigation relates to its role in memory binding has been controversial. However, only a small number of studies have investigated whether differences in cognitive map use are related to episodic memory or associative memory performance (e.g., Bohbot et al., 2011; Maguire, Woollett, & Spiers, 2006; Woollett & Maguire, 2009, 2012).

Previous work has capitalized on the differences in encoding strategies of spatial information between place and response strategies to examine how navigation strategy may relate to memory performance. Place learners use a strategy that relies on survey knowledge, whereas response learners rely on procedural stimulus-response learning. Crucially, place and response strategies are supported by distinct neural networks that may center and depend on the hippocampus and caudate, respectively (e.g., Bohbot et al., 2011; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Packard & McGaugh, 1996; Schinazi, Nardi, Newcombe, Shipley, & Epstein, 2013).

In Bohbot et al.’s (2011) study, participants were instructed to remember the location of four objects within a radial arm maze (4-on-8 Virtual Maze; 4/8 VM), and later categorized as place or response learners based on their encoding strategies. In addition, Bohbot et al. administered spatial (Rey-Osterreith; RO) and nonspatial (Rey Auditory Verbal Learning Test; RAVLT) standardized episodic memory tasks. The RO assesses visuospatial memory; the RAVLT measures item-source memory of two separate 15-item word lists. Participants who used a hippocampal-dependent strategy on the 4/8VM (i.e., encoding object locations in relation to distal landmarks) outperformed those who use a caudate-dependent strategy (i.e., encoding the serial position by tracking the maze’s arms) on both memory tests.

In a different approach to this issue, it has been found that spatial navigation experts (taxi drivers) performed worse than bus drivers on the RO task (Maguire et al., 2006). Woollett and Maguire found that taxi drivers also performed worse than non-experts on some associative memory tasks, including a (spatial)

This article was published Online First October 26, 2015.

Chi T. Ngo, Steven M. Weisberg, Nora S. Newcombe, and Ingrid R. Olson, Department of Psychology, Temple University.

This research project was funded as part of the Spatial Intelligence and Learning Center grant from the National Science Foundation, SBE-1041707. We thank Jon Benton and Chrystyna Colon for their help with data collection. We would also like to thank Steven Marchette for providing the stimuli and for his helpful comments on the initial draft of the manuscript.

Correspondence concerning this article should be addressed to Chi T. Ngo, Department of Psychology, Temple University, 1701 N. 13th Street, Philadelphia, PA 19122. E-mail: chi.ngo@temple.edu

object-location (Woollett & Maguire, 2009, 2012) and (nonspatial) word pair association (Woollett & Maguire, 2009), while performing equivalently on others (e.g., face-name, object pairs). The authors speculated that navigation expertise might actually compromise taxi drivers' ability to retain novel associative information, particularly visuospatial associations.

These findings provide a mixed and inconclusive picture. One limitation of prior investigations is that they focused on group-level comparison (e.g., place vs. response learners, Bohbot et al., 2011; experts vs. nonexperts, Woollett & Maguire, 2009, 2012). However, navigation strategies may exist on a continuum rather than being dichotomous (Bohbot, Lerch, Thorndyraft, Iaria, & Zijdenbos, 2007; Marchette, Bakker, & Shelton, 2011). In fact, when navigation strategy was quantified by the error rates in the landmark-free 4/8 VM test trial, stronger preference for place strategy positively correlated with the right hippocampal gray-matter density, and negatively correlated with caudate gray-matter density (Bohbot et al., 2007). Thus, examining the relation between navigation strategy and associative memory at the group-level may only provide a low-resolution understanding of how these two cognitive processes may covary and the potential cognitive ingredients they may share.

Individual differences in navigation strategies have also been explored using the dual solution paradigm (DSP; Marchette et al., 2011; Furman, Clements-Stephens, Marchette, & Shelton, 2014). The DSP provides a continuous measure of navigation strategy along a dimension from place to response strategies. In the DSP, participants repeatedly learn the same circuitous route through a virtual environment (VE), and then must travel to and from various objects. This task can be solved either by following previously learned routes or taking novel shortcuts. Participants vary in the extent to which they rely on place or response strategies. They can adopt a single strategy or alternate strategies across test trials. Thus, the DSP is an efficient tool to quantify the relative use of the two strategies for each individual. Importantly, relative hippocampal and caudate activity at encoding (Marchette et al., 2011; Furman et al., 2014) and also at retrieval (Furman et al., 2014) predicted the extent to which the place and response strategies were used to solve the task. These findings indicate that individual differences in navigation strategy are present at initial encoding as well as subsequent navigation behaviors.

The current study aims to investigate whether individual differences in navigation strategy relate to associative memory performance among nonexpert young adults. We used the DSP to measure navigation strategy and two associative memory tasks: the object-location (spatial) and face-name (nonspatial) associative memory. Both associative memory tasks have been suggested to depend on the hippocampus and to index memory binding—a process critical for episodic memory (e.g., object-location; Bohbot et al., 1998; Crane & Milner, 2005; Piekema, Kessels, Mars, Petersson, & Fernandez, 2006; Postma, Kessels, & van Asselen, 2008; face-name; Kirwan & Stark, 2004; Sperling et al., 2001, 2003; Zeineh, Engel, Thompson, & Bookheimer, 2003). Correlating navigation strategies with spatial and nonspatial memory measures using continuous measures for each may elucidate whether this relation derives from general memory-binding mechanisms or is specific to spatial memory binding.

Methods

Participants

Fifty-four young adults (28 females, mean age = 23.04 ± 3.20 , age range = 18–34) participated for course credit for \$20 at Temple University. All participants gave informed consent and reported to have normal or corrected-to-normal vision. Four participants were excluded from the analyses due to either motion sickness ($n = 2$) or computer error ($n = 2$). Fifty participants (25 females) were included in the analyses.

Materials and Procedure

The experiment consisted of two sessions; each lasted approximately 50 min and took place on a different day (ranging from 1 to 30 days apart). In Session 1, participants completed the Reading subtest of the Wide Range Achievement Test 4 (WRAT-4; Wilkinson & Robertson, 2006), the Santa Barbara Sense of Direction Scale (SBSOD; Hegarty, Richardson, Montello, Lovelace & Subbiah, 2002), and the DSP in a fixed order. In Session 2, participants completed two associative memory tasks: object-location and face-name, in a counterbalanced order. The order of the sessions was counterbalanced across participants. All measures (except where otherwise noted) were administered on a 19" monitor (1440 × 900 Resolution, 60 Hz refresh rate).

The WRAT-4 Reading subtest was administered on paper and consists of 55 single words, which participants are instructed to aloud with correct pronunciation. The WRAT-4 measures basic reading ability and strongly correlates with general IQ (Strauss, 2006).

The SBSOD consists of 15 questions on a 7-point Likert-scale (Cronbach's $\alpha = .90$) that assesses participants' self-rated navigation ability and their liking for various navigation-related activities. Higher scores indicate stronger self-reported navigation ability. The SBSOD was completed either on the computer or on paper.

The DSP (Marchette et al., 2011) is a VE maze designed to assess navigation strategies (see Figure 1). Participants were randomly assigned to one of the two versions of the VE, designed using the same objects with different spatial layouts. During encoding, participants watched a video tour and were instructed to pay close attention to the spatial layout of 12 objects. The tour repeated nine times, each lasting for 62 s. Interspersed with encoding, separate videos showed a different VE with blue and red spheres appearing along the route. Participants then indicated whether the colors of the first and the last spheres matched by pressing "M" or "Z" on the keyboard for "match" or "do not match," respectively. The purpose of these trials was to keep the encoding phase interactive. Next, participants were instructed on how to maneuver using the controls (i.e., arrow keys and computer mouse) and practiced maneuvering in a novel VE until comfortable. The up, down, left, and right arrow keys on the keyboard corresponded to forward-, backward-, leftward-, and rightward-movements, respectively. Moving the computer mouse resulted in changing direction, such as making a turn. During retrieval, participants attempted to find objects from different starting locations in the environment. Participants were informed of the time restraint, and that the most efficient path might differ from the learned route. For each test trial, the name of the goal object (e.g., fridge) was prompted on the computer screen; participants were then given a 360° view from the starting locations and 45 s to find each object.

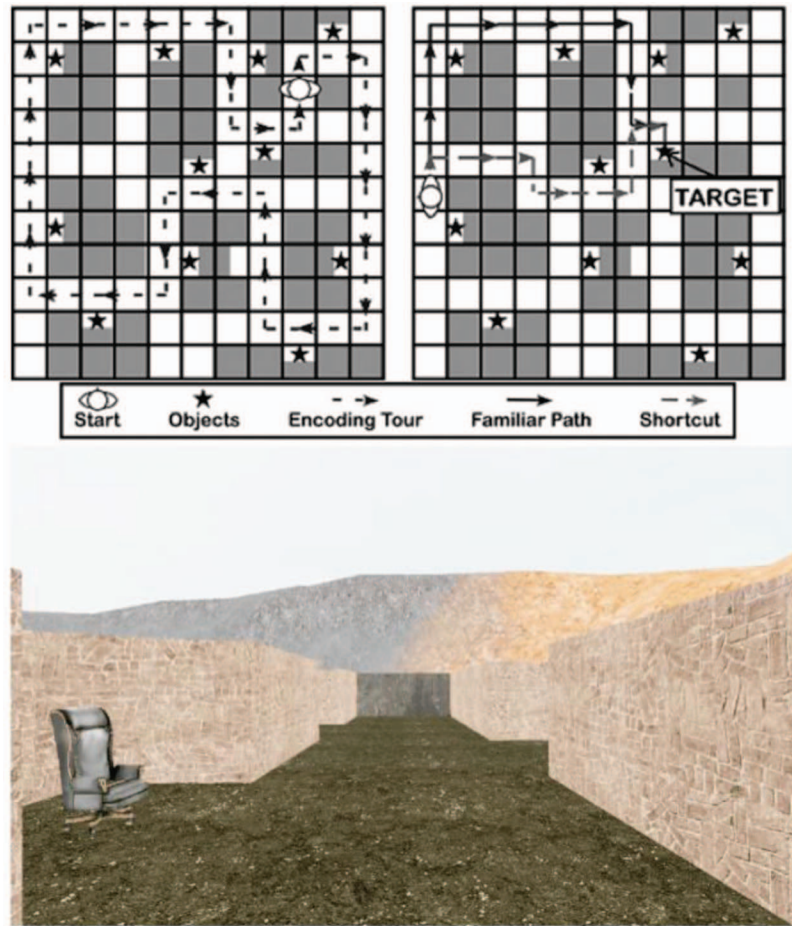


Figure 1. A schematic aerial view of the DSP (Marchette et al., 2011) (top). A screenshot the DSP VE (bottom). See the online article for the color version of this figure.

The test phase included 16 shortcut-available, four familiar-route, and four ambiguous trials, all classified based on the optimal route (i.e., shortest in distance) between the starting location and the goal object. In shortcut-available trials, the optimal routes were novel shortcuts that differed from the encoding route. In familiar-route trials, the familiar route (i.e., the encoding route) was optimal. In ambiguous trials, both the familiar and a novel route were equal in distance. The shortcut-available trials were the only trial type that contributed to measuring navigation strategy. Similar to Marchette et al. (2011)’s study, classification of shortcuts and familiar routes taken to find goals was based on whether the number of steps made along the shortcuts or the familiar route accounts for more of the navigation behavior on a given trial. Trials in which participants took neither the shortcut nor the familiar route, or failed to find the object were excluded. We quantified navigation strategy by calculating the place/response index using the following formula (Marchette et al., 2011):

$$\text{Place/Response Index} = \frac{\# \text{ of shortcuts}}{\# \text{ of shortcuts} + \# \text{ of familiar routes}}$$

The place/response index, ranging 0 to 1, reflected the proportion of shortcuts taken to the total number of shortcuts and familiar routes taken, to successfully find goals. The more frequently

participants took shortcuts as opposed to the familiar route, the higher their place/response index.

Associative Memory Tasks

Object-location task. Seventy-three color photographs of common objects were obtained from Google Image. Stimuli were presented in Microsoft PowerPoint version 14.0 on a MacBook Pro laptop 13” screen.

First, participants completed one practice trial. At study, 16 objects were presented simultaneously in a 10” × 7.5” visual array for 1 minute. All objects were jittered horizontally and vertically with respect to other objects in each row and column. Participants were instructed to name all of the objects aloud and study the position of each object. This was immediately followed by a self-paced test in which an empty screen was presented with 16 objects aligned in a random order at the bottom of the screen (see Figure 2). The task was to precisely relocate each object in the correct position. This study-test procedure was repeated four times with different sets of objects. Accuracy on the object-location task was computed using error (inches)—the absolute distance between where participants placed each object and its original coordinates.

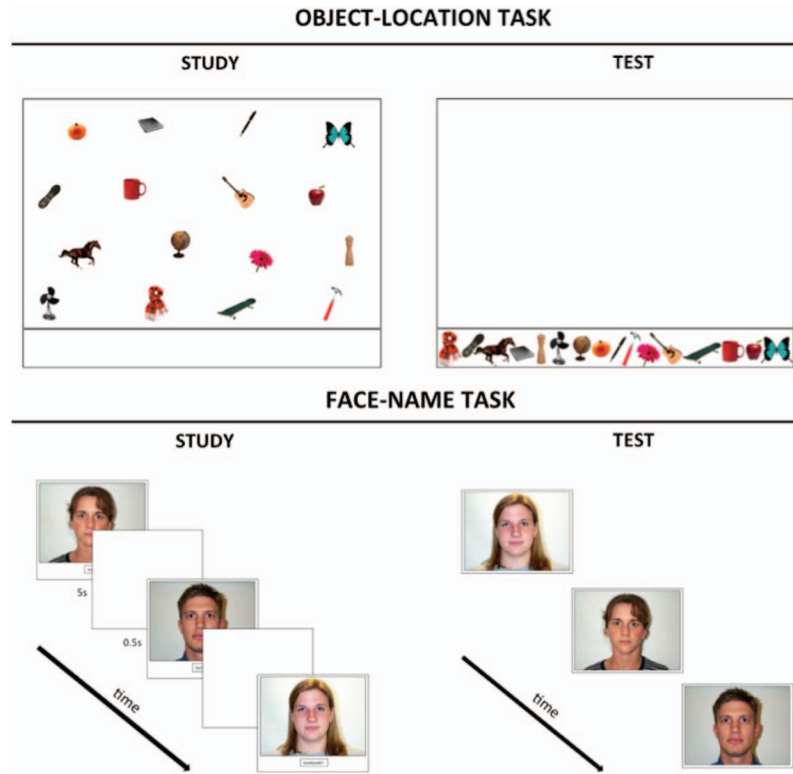


Figure 2. The object-location task procedure (top) and the face-name task procedure (bottom). See the online article for the color version of this figure.

An average error score of all 64 objects was computed for each participant.

Face-name task. Fifty-four color photographs of neutral face stimuli (27 female faces) were sampled from the face database available at <http://agingmind.utdallas.edu/facedb> (Minear & Park, 2004). Fifty-four first names (27 feminine, e.g., “Susan”) were obtained from lists of common first names and were assigned to each face by the experimenter. The task was programmed using E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA).

First, participants began with six face–name practice trials to become familiarized with the task. At study, a series of 12 face–name pairs (see Figure 2) was presented, each for 5 s and each with a 500 ms-blank-screen ISI. The study phase was immediately followed by a self-paced test phase consisting of a series of 10 faces from the study list (the first and last items of the study list were excluded to avoid primacy and recency effects). Participants were instructed to write the name for each face. This study–test procedure was repeated four times with different sets of face–name pairs. The proportion of correctly recalled names of 40 test trials was calculated for each participant. Accuracy was defined by recalling the correct names phonetically; for instance, writing “Jon” for “John” was coded as correct.

Data Analysis

All correlations and partial correlations were conducted using standard Pearson correlation.

Results

Navigation Strategy

The frequency distribution of the place/response index was normally distributed (Shapiro-Wilk = .96, $p = .10$) and showed that participants fully ranged from 0 to 1 (see Figure 3). Similar to previous findings (Furman et al., 2014; Marchette et al., 2011), we found individual differences such that some people were faithful to one strategy (people at the two ends of the index), whereas others flexibly used a combination of both strategies. We found that SBSOD did not correlate with either the place/response index, $r(48) = .19$, $p = .19$, or the total number of goals found during short-cut available trials, $r(48) = -.05$, $p = .75$.

Associative Memory

There was a significant negative correlation between object-location error and face-name performance, $r(48) = -.38$, $p = .006$, indicating that better performance on one associative memory task was related to better performance on the other. This correlation held when controlling for verbal intelligence, as measured by the WRAT-4, $r(47) = -.40$, $p = .004$. SBSOD did not correlate with either the object-location, $r(48) = -.17$, $p = .25$, or face-name, $r(48) = -.01$, $p = .92$, performance.

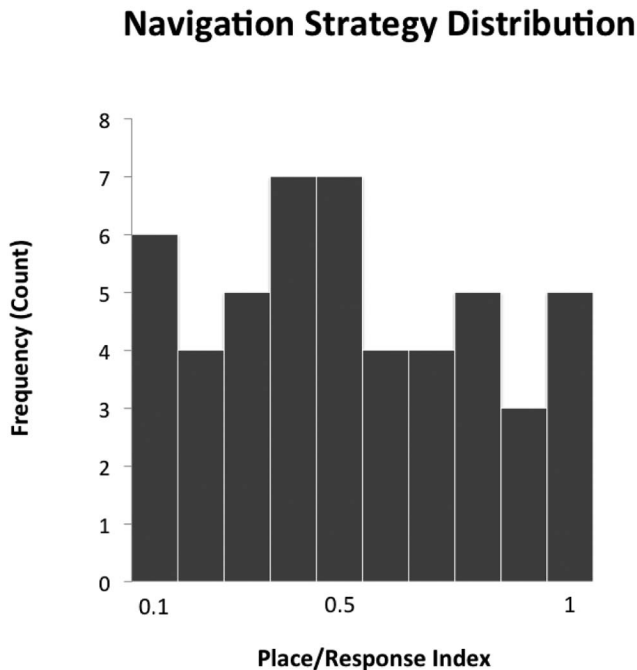


Figure 3. Frequency distribution of place/response index as measured by the dual solution paradigm (Marchette et al., 2011).

Navigation Strategy and Associative Memory

There was a significant negative correlation between place/response index and object-location error, $r(48) = -.47, p = .001$ (see Figure 4). Participants with a higher tendency to take shortcuts, compared with those who prefer to follow the same route, had higher accuracy on the object-location task. To examine whether this correlation is specific to spatial associative memory or partially driven by individual differences in verbal intelligence, general memory-binding performance, or navigation proficiency, we conducted a partial correlation with the following covariates: WRAT-4, face-name performance, and total number of goals found during shortcut-available trials. The correlation held, $r(45) = -.37, p = .011$, suggesting that the relation between navigation strategy and object-location memory performance was specific to spatial associative memory and was not driven by verbal intelligence, general ability to remember associations across different domains, or navigation proficiency.

In contrast, the correlation between place/response index and face-name performance failed to reach significance, $r(48) = .18, p = .21$ (see Figure 4). Controlling for WRAT-4, object-location memory, and total number of goals found during shortcut-available trials, further weakened this correlation, $r(45) = .02, p = .91$.

We also tested whether the correlation between navigation strategy and nonspatial associative memory significantly differed from the correlation between navigation strategy and spatial associative memory. Specifically, we compared two partial correlations: (a) the partial correlation between place/response index and object-location error, controlling for face-name accuracy; and (b) the partial correlation between place/response index and face-name accuracy, controlling for object-location error. The resulting partial correlations are the variance in navigation strategy accounted

for by spatial and nonspatial associative memory when individual differences in general memory binding are held constant. Note that for this analysis, we changed the valence of the correlation between place/response index and face-name performance, as well as the correlation between object-location and face-name performance, because object-location memory was calculated based on error score, whereas face-name performance was calculated based on accuracy. The correlation between place/response index and object-location, $r(48) = -.47, p = .001$, was significantly different from the correlation between place/response index and face-name memory, $r(48) = -.18, p = .21, t(47) = 2.00, p = .05, d = 0.47$.

Discussion

The current study examined how individual differences in navigation strategy relate to associative memory in a nonexpert, young adult population. We found a significant correlation between navigation strategy and spatial (object-location) associative memory, but not between navigation strategy and nonspatial (face-name) associative memory. Crucially, the two partial correlations significantly differed, indicating that although individual differences in navigation strategy and associative memory covary, they appear to be specific to the spatial domain. This divergence occurred despite the fact that performances on the spatial and nonspatial associative memory tasks were positively correlated, suggesting the existence of individual differences in general memory-binding mechanisms.

The current work shows that the ability to accurately bind objects to specific locations predicts the extent to which individuals used a place strategy. Neither general intelligence nor general memory-binding mechanism appeared to drive this correlation, indicating that the relation between navigation strategy and spatial associative memory exists primarily on the basis of spatial processing. Interestingly, the correlation between navigation strategy and face-name memory became virtually nonexistent when controlling for object-location memory. These results provide further support for the idea that spatial navigation in a large-scale environment may not simply be an example of general episodic memory (Burgess et al., 2002).

The differences between the DSP and object-location task may inform theorizing about the nature of their correlation. First, they differ in the format and scale of the spatial information. In the DSP, the spatial layout of the objects is presented sequentially and dynamically. Thus, the spatial relations among objects must be maintained and continuously updated throughout the encoding tour. In the object-location task, the spatial configuration of all 16 objects is simultaneously presented in one static view. Second, the DSP and object-location task differ in their retrieval demands. In the DSP, test trials are time-restricted; and place-based navigation relies on inferred novel shortcuts. In the object-location task, the test phase is self-paced and inferring spatial relation is not required. Given these differences among many others, the correlation between place/response index and object-location memory is unlikely to be due to any procedural similarities between the tasks. Rather, individual differences in spatial memory binding may underlie their correlation.

Both place-based navigation and object-location memory involve accurate memory binding of object identity and spatial location, and they also require memory representations that main-

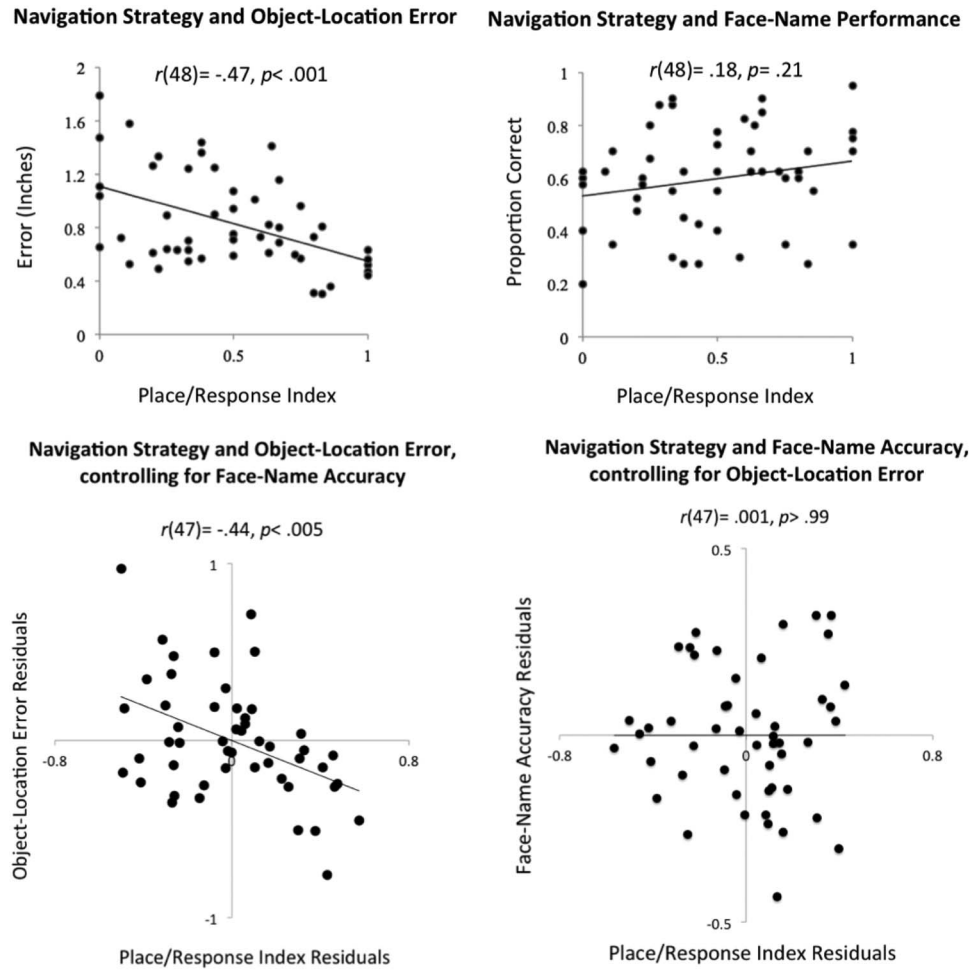


Figure 4. Top panel: A graphical depiction of the significant correlation between place/response index and displacement error on the object-location associative memory task (left), and the nonsignificant correlation between place/response index and recall accuracy on the face-name associative memory task (right). Bottom panel: A graphical depiction of the significant partial correlation between place/response index and displacement error on the object-location associative memory task, controlling for the face-name accuracy (left), and the nonsignificant partial correlation between place/response index and recall accuracy on the face-name associative memory task (right).

tain the spatial relations among these associations. Our findings thus suggest support for the idea that individual differences in navigation strategy (e.g., Hegarty, Montello, Richardson, Ishikawa, & Lovelace, 2006) and object-location memory (e.g., Postma, Jager, Kessels, Kopperschaar, & van Honk, 2004) relate to the ability to encode and maintain metric information of spatial associations. Constructing a cognitive map depends on the encoding, maintaining, and updating of metric information of the entire environment over time because its spatial layout cannot be obtained from a single view (Ittelson, 1973). Similarly, the object-location task requires participants to encode and maintain the coordinate positions of 16 objects in a very short time span, thus heavily taxing visuospatial working memory (Postma et al., 2004; Smith et al., 1995).

The covariation between navigation strategy and spatial associative memory in our study may align with some previous neuroimaging findings showing that place-based navigation and

object-location memory both yield activation in the right hippocampus (e.g., Crane & Milner, 2005; Smith & Milner, 1981; Van Asselen, Kessels, Kappelle, & Postma, 2008), and the right parahippocampus (e.g., Bohbot et al., 1998). Others have found that the posterior hippocampus is preferentially involved in spatial relations, regardless of whether the spatial relations occur in a large-scale environment or in a small-scale object arrays (e.g., Hirshhorn et al., 2012; Hoscheidt, Nadel, Payne, & Ryan, 2010; Ryan et al., 2010). Although we do not have direct evidence to verify these findings, our behavioral data appear to agree that both place-based navigation in large-scale environments and small-scale spatial memory binding may recruit some overlapping brain regions.

Our findings that navigation strategy only related to spatial, but not nonspatial, associative memory contrast with the results of Bohbot and colleagues (2011). One possible explanation for the

inconsistent results may stem from the different navigation tasks used. Bohbot et al. (2011) used the 4/8 VM, which distinguishes participant navigation strategy via differences in encoding strategies. The DSP measures the relative use of navigation behaviors (route-following and shortcut-taking). Although learning spatial relations among landmarks at encoding and inferring novel shortcuts at retrieval are both characteristic of cognitive maps, individual differences emerging from the encoding phase and route-formulation phase may not completely map onto one another. It is possible that differences at encoding relate to both spatial and nonspatial memory binding, whereas differences at retrieval may only relate to the spatial information. Of course, inconsistent findings due to methodological differences would underscore the complexity and multifaceted nature of navigation behavior, so direct investigation of the relations among different assessments is needed. Although encoding strategy plays a significant role, it is important to consider how it may interact with other factors including strategy selection, spatial abilities, working memory, goals, and task demands, during route-formulation at test. Individual differences that exist along these dimensions likely contribute to variability in navigation behaviors (e.g., Shelton et al., 2013).

Another point of contrast with previous work is the examination of navigation strategy categorically (e.g., experts vs. nonexperts; Woollett & Maguire, 2009, 2012; place vs. response learners; Bohbot et al., 2011) as opposed to continuously. Research suggests important individual differences in navigation strategy (e.g., Bohbot et al., 2007; Marchette et al., 2011; Furman et al., 2014; Weisberg, Schinazi, Newcombe, Shipley, & Epstein, 2014) that appear to be continuous in nature. Our findings are theoretically consistent with the approach proposed by Shelton and colleagues (2013). This framework posits that navigation behaviors may be rooted in the basic place- and response-learning mechanisms and that individual differences in strategy selection may emerge from the relative recruitment of these systems. Consistent with our findings that individual differences in place-based navigation and spatial associative memory covary, this framework also predicts that it is the interaction between these two learning systems that reflects how people approach most, if not all spatial tasks (Shelton et al., 2013).

In conclusion, we found that individual differences in navigation strategy in a large-scale environment covary with the ability to perform spatial memory binding in a 2D small-scale format. The current study may reveal an additional factor—spatial memory binding—that contributes to individual differences in navigation strategies. These findings lend evidence in support of the idea that the relative engagement of the place- and response- learning mechanisms may determine how individuals solve spatial tasks.

References

- Bohbot, V. D., Gupta, M., Banner, H., & Dahmani, L. (2011). Caudate nucleus-dependent response strategies in a virtual navigation task are associated with lower basal cortisol and impaired episodic memory. *Neurobiology of Learning and Memory*, *96*, 173–180. <http://dx.doi.org/10.1016/j.nlm.2011.04.007>
- Bohbot, V. D., Kalina, M., Stepankova, K., Spackova, N., Petrides, M., & Nadel, L. (1998). Spatial memory deficits in patients with lesions to the right hippocampus and to the right parahippocampal cortex. *Neuropsychologia*, *36*, 1217–1238. [http://dx.doi.org/10.1016/S0028-3932\(97\)00161-9](http://dx.doi.org/10.1016/S0028-3932(97)00161-9)
- 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*, 10078–10083. <http://dx.doi.org/10.1523/JNEUROSCI.1763-07.2007>
- Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory. *Neuron*, *35*, 625–641. [http://dx.doi.org/10.1016/S0896-6273\(02\)00830-9](http://dx.doi.org/10.1016/S0896-6273(02)00830-9)
- Crane, J., & Milner, B. (2005). What went where? Impaired object-location learning in patients with right hippocampal lesions. *Hippocampus*, *15*, 216–231. <http://dx.doi.org/10.1002/hipo.20043>
- Eichenbaum, H., & Bunsey, M. (1995). On the binding of association in memory: Clues from studies on the role of the hippocampal region in paired-associate learning. *Current Directions in Psychological Science*, *4*, 19–23. <http://dx.doi.org/10.1111/1467-8721.ep10770954>
- 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*, 1375–1391. <http://dx.doi.org/10.3758/s13415-014-0279-6>
- Hegarty, M., Montello, D., 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*, 151–176. <http://dx.doi.org/10.1016/j.intell.2005.09.005>
- Hegarty, M., Richardson, A., Montello, D., Lovelace, K., & Subbiah, I. (2002). Development of a self-report measure of environmental spatial ability. *Intelligence*, *30*, 425–447. [http://dx.doi.org/10.1016/S0160-2896\(02\)00116-2](http://dx.doi.org/10.1016/S0160-2896(02)00116-2)
- Henke, K., Buck, A., Weber, B., & Wieser, H. G. (1997). Human hippocampus establishes associations in memory. *Hippocampus*, *7*, 249–256. [http://dx.doi.org/10.1002/\(SICI\)1098-1063\(1997\)7:3<249::AID-HIPO1>3.0.CO;2-G](http://dx.doi.org/10.1002/(SICI)1098-1063(1997)7:3<249::AID-HIPO1>3.0.CO;2-G)
- Hirshhorn, M., Grady, C., Rosenbaum, R. S., Winocur, G., & Moscovitch, M. (2012). Brain regions involved in the retrieval of spatial and episodic details associated with a familiar environment: An fMRI study. *Neuropsychologia*, *50*, 3094–3106. <http://dx.doi.org/10.1016/j.neuropsychologia.2012.08.008>
- Hoscheidt, S. M., Nadel, L., Payne, J., & Ryan, L. (2010). Hippocampal activation during retrieval of spatial context from episodic and semantic memory. *Behavioural Brain Research*, *212*, 121–132. <http://dx.doi.org/10.1016/j.bbr.2010.04.010>
- 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. *The Journal of Neuroscience*, *23*, 5945–5952.
- Ittelson, W. (1973). Environment perception and contemporary perceptual theory. In W. H. Ittelson (Ed.), *Environment and cognition* (pp. 1–19). New York, NY: Seminar.
- Kirwan, C. B., & Stark, C. E. (2004). Medial temporal lobe activation during encoding and retrieval of novel face-name pairs. *Hippocampus*, *14*, 919–930. <http://dx.doi.org/10.1002/hipo.20014>
- Maguire, E. A., Woollett, K., & Spiers, H. J. (2006). London taxi drivers and bus drivers: A structural MRI and neuropsychological analysis. *Hippocampus*, *16*, 1091–1101. <http://dx.doi.org/10.1002/hipo.20233>
- 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*, 15264–15268. <http://dx.doi.org/10.1523/JNEUROSCI.3634-11.2011>
- Minear, M., & Park, D. C. (2004). A lifespan database of adult facial stimuli. *Behavior Research Methods, Instruments & Computers*, *36*, 630–633. <http://dx.doi.org/10.3758/BF03206543>
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford, UK: Clarendon.
- Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place

- and response learning. *Neuroimaging of Learning and Memory*, 65, 65–72. <http://dx.doi.org/10.1006/nlme.1996.0007>
- Piekema, C., Kessels, R. P., Mars, R. B., Petersson, K. M., & Fernández, G. (2006). The right hippocampus participates in short-term memory maintenance of object-location associations. *NeuroImage*, 33, 374–382. <http://dx.doi.org/10.1016/j.neuroimage.2006.06.035>
- Postma, A., Jager, G., Kessels, R. P., Koppeschaar, H. P., & van Honk, J. (2004). Sex differences for selective forms of spatial memory. *Brain and Cognition*, 54, 24–34. [http://dx.doi.org/10.1016/S0278-2626\(03\)00238-0](http://dx.doi.org/10.1016/S0278-2626(03)00238-0)
- Postma, A., Kessels, R. P., & van Asselen, M. (2008). How the brain remembers and forgets where things are: The neurocognition of object-location memory. *Neuroscience and Biobehavioral Reviews*, 32, 1339–1345. <http://dx.doi.org/10.1016/j.neubiorev.2008.05.001>
- Ryan, L., Lin, C. Y., Ketcham, K., & Nadel, L. (2010). The role of medial temporal lobe in retrieving spatial and nonspatial relations from episodic and semantic memory. *Hippocampus*, 20, 11–18.
- 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, 515–528. <http://dx.doi.org/10.1002/hipo.22111>
- Shelton, A., Marchette, S., & Furman, A. (2013). A mechanistic approach to individual differences in spatial learning, memory, and navigation. In B. Ross (Ed.), *The psychology of learning and motivation* (vol. 59, pp. 223–259). Waltham, MA: Academic Press. <http://dx.doi.org/10.1016/B978-0-12-407187-2.00006-X>
- Smith, E. E., Jonides, J., Koeppel, R. A., Awh, E., Schumacher, E. H., & Minoshima, S. (1995). Spatial versus object working memory: PET investigations. *Journal of Cognitive Neuroscience*, 7, 337–356. <http://dx.doi.org/10.1162/jocn.1995.7.3.337>
- Smith, M. L., & Milner, B. (1981). The role of the right hippocampus in the recall of spatial location. *Neuropsychologia*, 19, 781–793. [http://dx.doi.org/10.1016/0028-3932\(81\)90090-7](http://dx.doi.org/10.1016/0028-3932(81)90090-7)
- Sperling, R. A., Bates, J. F., Cocchiarella, A. J., Schacter, D. L., Rosen, B. R., & Albert, M. S. (2001). Encoding novel face-name associations: A functional MRI study. *Human Brain Mapping*, 14, 129–139. <http://dx.doi.org/10.1002/hbm.1047>
- Sperling, R., Chua, E., Cocchiarella, A., Rand-Giovannetti, E., Poldrack, R., Schacter, D. L., & Albert, M. (2003). Putting names to faces: Successful encoding of associative memories activates the anterior hippocampal formation. *NeuroImage*, 20, 1400–1410. [http://dx.doi.org/10.1016/S1053-8119\(03\)00391-4](http://dx.doi.org/10.1016/S1053-8119(03)00391-4)
- Strauss, E. (2006). *A compendium of neuropsychological tests: Administration, norms, and commentary*. New York, NY: Oxford University Press.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review*, 55, 189–208. <http://dx.doi.org/10.1037/h0061626>
- van Asselen, M., Kessels, R. P., Kappelle, L. J., & Postma, A. (2008). Categorical and coordinate spatial representations within object-location memory. *Cortex*, 44, 249–256. <http://dx.doi.org/10.1016/j.cortex.2006.05.005>
- 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, 669–682. <http://dx.doi.org/10.1037/a0035261>
- Wilkinson, G., & Robertson, G. (2006). *Wide Range Achievement Test-4 (WRAT-4)*. Lutz, FL: Psychological Assessment Resources.
- Woollett, K., & Maguire, E. A. (2009). Navigational expertise may compromise anterograde associative memory. *Neuropsychologia*, 47, 1088–1095. <http://dx.doi.org/10.1016/j.neuropsychologia.2008.12.036>
- Woollett, K., & Maguire, E. A. (2012). Exploring anterograde associative memory in London taxi drivers. *Neuroreport*, 23, 885–888. <http://dx.doi.org/10.1097/WNR.0b013e328359317e>
- Zeineh, M. M., Engel, S. A., Thompson, P. M., & Bookheimer, S. Y. (2003). Dynamics of the hippocampus during encoding and retrieval of face-name pairs. *Science*, 299, 577–580. <http://dx.doi.org/10.1126/science.1077775>

Received March 18, 2015

Revision received July 24, 2015

Accepted July 28, 2015 ■