

RESEARCH REPORT

Superior Cognitive Mapping Through Single Landmark-Related Learning Than Through Boundary-Related Learning

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Cognitive mapping is assumed to be through hippocampus-dependent place learning rather than striatum-dependent response learning. However, we proposed that either type of spatial learning, as long as it involves encoding metric relations between locations and reference points, could lead to a cognitive map. Furthermore, the fewer reference points to specify individual locations, the more accurate a cognitive map of these locations will be. We demonstrated that participants have more accurate representations of vectors between 2 locations and of configurations among 3 locations when locations are individually encoded in terms of a single landmark than when locations are encoded in terms of a boundary. Previous findings have shown that learning locations relative to a boundary involve stronger place learning and higher hippocampal activation whereas learning relative to a single landmark involves stronger response learning and higher striatal activation. Recognizing this, we have provided evidence challenging the cognitive map theory but favoring our proposal.

Keywords: place learning, response learning, landmark, boundary, cognitive map

Navigation between two locations is a crucial task for everyday life and can rely on two different kinds of spatial knowledge. The first involves representing a sequence of responses (i.e., turns) along a path between locations; the other involves representing metric relationships (i.e., straight-line distance and direction) among locations (Siegel & White, 1975). Tolman (1948) originally referred to the second type of knowledge, but not the first, as a cognitive map, analogous to an external map representing metric relationships among places. In the current study, consistent with Tolman (1948) and other researchers (Bennett, 1996; Nadel, 2013; O'Keefe & Nadel, 1978), we considered a cognitive map as a mental representation of metric relations among individual locations. The hallmark functions of a cognitive map are to enable people to infer spatial relations between two locations (Levine, Jankovic, & Palij, 1982; Tolman, 1948), and to judge the spatial configuration among multiple locations (Evans & Pezdek, 1980; Thorndyke & Hayes-Roth, 1982). In the current study, we examined a cognitive map of an environment in terms of these two hallmark functions.

Tolman (1948) attributed the construction of cognitive maps to latent place learning in contrast to response learning through

stimulus–response association. Tolman's cognitive map theory was further developed by O'Keefe and Nadel (1978). They proposed that two systems are involved in spatial learning: the locale system and the taxon system. The locale system, corresponding to place learning, was hypothesized to be a major contribution to cognitive mapping and to rely on the hippocampus. By contrast, the taxon system was assumed to be important in encoding a sequence of responses (e.g., turns along a route), corresponding to stimulus–response association and independent of the hippocampus. In the current article, we refer to theories claiming that the hippocampus and place learning are critical to cognitive mapping as cognitive map theory. Cognitive map theory has been supported by many empirical studies (Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Ekstrom et al., 2003; Hartley, Maguire, Spiers, & Burgess, 2003; Marchette, Bakker, & Shelton, 2011; McDonald & White, 1994; O'Keefe & Dostrovsky, 1971).

However, a growing body of evidence has indicated that metric relations among locations might also be learned and stored independent of the hippocampus (Aguirre & D'Esposito, 1997; Bohbot et al., 1998; Corkin, 2002; Maguire, Nannery, & Spiers, 2006; Miller, Vedder, Law, & Smith, 2014; Moscovitch et al., 2005; Pearce, Roberts, & Good, 1998; Teng & Squire, 1999; Vass & Epstein, 2013; Wolbers & Büchel, 2005). For example, Pearce et al. (1998) reported that rats with hippocampal lesions could find the target location that had a fixed metric relation to a movable landmark across trials. Vass and Epstein (2013; see also Epstein & Vass, 2014) proposed that the retrosplenial complex might be important in encoding locations and directions in a large-scale environment.

Furthermore, some studies have suggested that metric relations can be acquired through response learning and independent of the

This article was published Online First February 4, 2016.

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Supported by the Natural Sciences and Engineering Research Council of Canada and the Qianjiang Scholarship, China.

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hippocampus. Doeller and Burgess (2008) demonstrated that learning locations relative to a single landmark was overshadowed and blocked by learning relative to a continuous boundary. They concluded that spatial learning relative to a landmark involves response learning whereas spatial learning relative to a boundary involves latent place learning. Moreover, the same study demonstrated that participants localized objects with equivalent accuracy when learning with either cue alone, indicating that metric relations can be acquired through response learning. In another neuroimaging study (Doeller, King, & Burgess, 2008), the striatum was shown to be involved in encoding and remembering individual locations relative to a landmark, whereas the hippocampus was involved in boundary-related spatial learning, indicating that people encode individual locations relative to a landmark through response learning that is less hippocampal dependent.

Inspired by these findings, we hypothesized that as long as spatial learning produces the encodings of metric relations from locations to a common reference (e.g., a circular boundary, a landmark), regardless of the extent to which place learning and hippocampus are involved, it would contribute to a cognitive map of the locations. Furthermore, we hypothesized that a cognitive map of locations would be more accurate when the locations are encoded relative to a single reference point than when the locations are encoded relative to multiple reference points. When there is only one reference point, every location is encoded relative to the same reference point (see Figure 1A for illustrations). Suppose, for example, there are two locations—a and b—encoded relative to the single reference point, R. People can compute the vectors between any two locations (e.g., V_{a-b} in Figure 1A) by adding the two vectors from each location and the reference point (e.g., $V_{a-R} + [-V_{b-R}]$). When there are multiple reference points (e.g., R1, R2 in Figure 1B), different locations might be encoded relative to different reference points (e.g., V_{a-R1} , V_{b-R2}). When people compute the vectors between

two target locations (e.g., V_{a-b}), they have to add not only the two vectors between the individual locations and their corresponding reference points, but also the vector between the two reference points (e.g., $V_{a-R1} + [-V_{b-R2}] + V_{R1-R2}$). Extra errors might be involved in encoding and adding the vectors between different reference points (e.g., V_{R1-R2}), leading to a less accurate cognitive map of vectors between locations. We refer to this hypothesis as the vector addition model.

Two experiments were designed to distinguish this vector addition model from cognitive map theory. These experiments were based on the findings that, compared with single landmark–relative learning, boundary-related learning involves more place learning and stronger hippocampal activation (e.g., Doeller & Burgess, 2008; Doeller et al., 2008). According to cognitive map theory, cognitive mapping relies on place learning and the hippocampus. Therefore, boundary-related spatial learning should lead to a better cognitive map of locations. In contrast, according to the vector addition model, people develop a better cognitive map when there is a single reference point than when there are multiple reference points. Because a boundary consists of multiple reference points and a single landmark has one reference point (Mou & Zhou, 2013), spatial learning relative to a single landmark should lead to a better cognitive map.

Experiment 1

Participants learned four objects' locations individually with a boundary cue or a landmark cue. A task requiring inference of the spatial relation between two objects was employed to evaluate the accuracy of the cognitive map of objects' locations in either learning cue condition.

Method

Participants. Forty-eight (24 males and 24 females) students from the University of Alberta participated to fulfill a course requirement.

Materials and design. An immersive virtual environment was displayed using an nVisor SX60 head-mounted display (HMD; NVIS Inc., Reston, VA). Graphics were rendered using the Vizard software (WorldViz, Santa Barbara, CA). Head orientation was tracked with an InterSense IS-900 motion tracking system (InterSense Inc., Billerica, MA). Thus, through head rotation, participants could change their viewpoints. Participants used a joystick to translate, to pick up, and to place back the objects in the virtual environment.

In the virtual environment (see Figure 2), participants learned four locations on infinite grassland by picking up four sequentially presented objects (a candle, a lock, a bottle, and a wood block) and then placing them at the correct locations. Two sets of locations were used (referred to as Configuration 1 and Configuration 2, respectively) and half of the participants learned Configuration 1. The object–location pair was randomized across participants. During the learning phase, either a visually homogeneous, circular wall (the boundary condition, referred to as B; see Figure 2A) or a visually homogeneous traffic cone (the landmark condition, referred to as L; see Figure 2B) was presented as the localization cue. Four different scenes (ocean, forest, mountain, and city) were set at infinity as distal orientation cues (indicated by the surround-

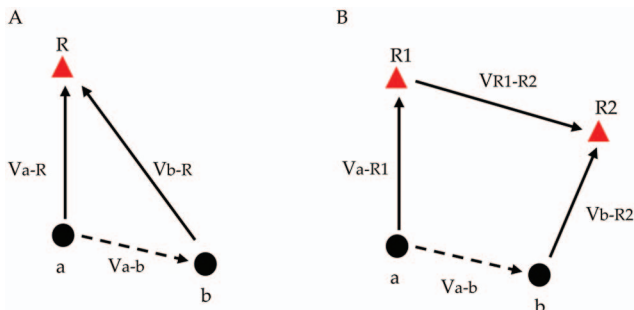


Figure 1. Schematic illustrations of the vector addition model. Panel A infers the spatial relations between locations a and b when both locations are encoded relative to a single reference point, R. Solid lines show the vectors from target locations to the reference point, V_{a-R} and V_{b-R} . Dashed line shows the inferred vector between the two locations, $V_{a-b} = V_{a-R} + (-V_{b-R})$. Panel B infers the spatial relations between locations a and b when a is encoded relative to the reference point R1 and b relative to R2. Solid lines with arrows show, respectively, the encoded vectors from a to R1 (V_{a-R1}), from R1 to R2 (V_{R1-R2}), and from b to R2 (V_{b-R2}). Dashed line shows the inferred vector between the two locations, $V_{a-b} = V_{a-R1} + V_{R1-R2} + (-V_{b-R2})$. See the online article for the color version of this figure.

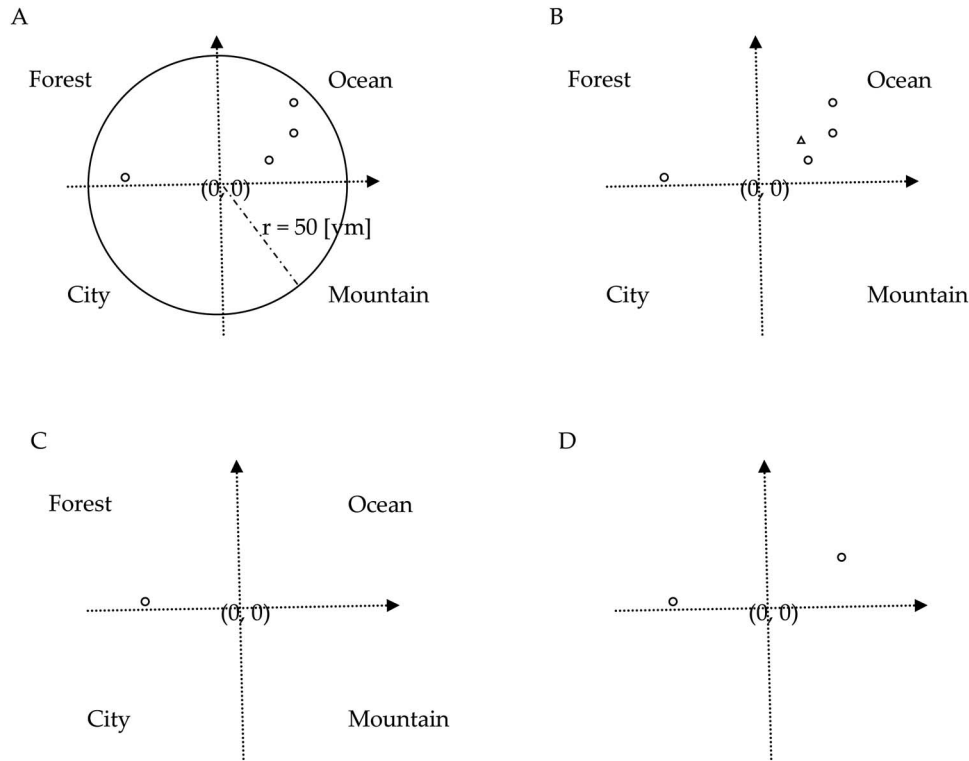


Figure 2. Top-view illustrations of the virtual environments used in Experiments 1 and 2. The learning phase of the boundary condition in both experiments (A). The circle illustrates the wall with a radius of 50 virtual meters (vm), which is also shown as the dashed line in the circle. The two dotted lines with arrows illustrate the coordinate axes where (0, 0) is the origin of the coordinate system (also the center of the wall) used in the virtual reality environment. The axes and the center are marked only for readers. The four dots illustrate the target locations from Configuration 1. The coordinates of the four locations in Configuration 1 are (19.94, 9.30), (29.44, 32.70), (−33.92, 2.37), and (29.35, 19.06), respectively; the coordinates of the four target locations in Configuration 2 (not depicted here) are (35.86, 19.88), (−7.74, −31.05), (−5.14, 6.13), and (−18.02, −12.62), respectively (units in virtual meters). The four labels (ocean, mountain, city, and forest) illustrate the background scenes set at infinity from the center of the environment. The learning phase of the landmark condition in both experiments (B). The triangle illustrates the traffic cone used as the landmark cue, which was placed at (18, 18). The testing phase in Experiment 1 (C). The dot illustrates one of the four objects at its original location used as the testing cue for one particular trial. The original localization cue (the landmark or the boundary) was removed. The testing phase in Experiment 2 (D). The two dots illustrate two of the four objects at their original locations used as the testing cues for one particular trial. Both the original localization cue and the original orientation cues (i.e., the background scenes) were removed.

ing labels in Figure 2). Without distal orientation cues, it is impossible to specify an object's location in terms of the traffic cone or the circular wall. In the testing phase (see Figure 2C), the landmark in L or the wall in B was removed but one of the four objects was presented in each trial as the localization cue, together with the distal orientation cues. Participants needed to replace the other three objects. Because participants never saw the four objects simultaneously, the vectors between the cue objects and the probed objects must have been a product of cognitive mapping. Therefore, participants' testing performances in L or B could reflect the relative accuracy of cognitive mapping in each condition.

Procedure. Participants donned the HMD and sat on a swivel chair at the center of the experiment room. Each participant went through three phases: the pick-up phase, the learning phase, and the testing phase. During the pick-up phase, participants collected the four

objects one by one from their original locations. The learning phase comprised four blocks of four learning trials (one trial per object in each block). For each trial, one of the four objects was probed and participants replaced the probed object using their memory. After the response, the probed object appeared at its original location. Participants were asked to collect it. Participants' starting locations (within 40 virtual meters [vm] from the center of the wall) and facing directions at the beginning of each trial were randomized. During testing, the boundary in B and the landmark in L were removed. For each trial, one of the four objects was shown at its original location as a localization cue together with the distal orientation cues; participants replaced one of the other three objects. The testing phase comprised four blocks of three testing trials. In each block, one of the four objects served as the testing cue in all three trials and each of the other three objects was probed once. No feedback was given in the testing phase.

Results and Discussion

Response errors, measured as the distances between participants' response locations and the corresponding correct locations, were recorded as the dependent variable. Participants' performances during the learning and the testing phases were examined, respectively. We combined the data from the two configurations in the analysis because the data showed the same pattern for these two configurations in this experiment and in Experiment 2. In both experiments, there is no interaction between the configurations and the learning cue conditions on localization accuracy in either the last learning block or the testing blocks.

Performances during the learning phase. The learning effect was examined by mixed-model analyses of variance (ANOVAs) on average response errors over the four learning blocks. Learning block (1–4) was a within-subject variable, whereas learning cue (L or B) was a between-subjects variable.

The analysis revealed a Learning Cue \times Learning Block interaction, $F(3, 138) = 3.84, p = .01, \eta_p^2 = .08$. Illustrated in Figure 3A, a larger learning effect in the L group contributes to the interaction. Repeated-measure ANOVAs showed that participants in both groups improved their localization performances over the learning phase: for the L group, $F(3, 69) = 9.19, p < .001, \eta_p^2 = .29$, and for the B group, $F(3, 69) = 4.10, p = .01, \eta_p^2 = .15$.

Because of the learning effect, only the mean response errors in the last (i.e., fourth) learning block from the two conditions (L and B) were compared to ensure that participants were equally accurate at encoding individual locations relative to the respective cues. Performances were comparable between the two groups ($M_L = 20.05$ vm, $SD_L = 13.22$; $M_B = 19.82$ vm, $SD_B = 7.23$), $F(1, 46) = .006, p = .94, \eta_p^2 < .001$ (see Figure 4A).

Performance during the testing phase. Mean response errors during the testing phase as a function of the learning cue (L or B) were

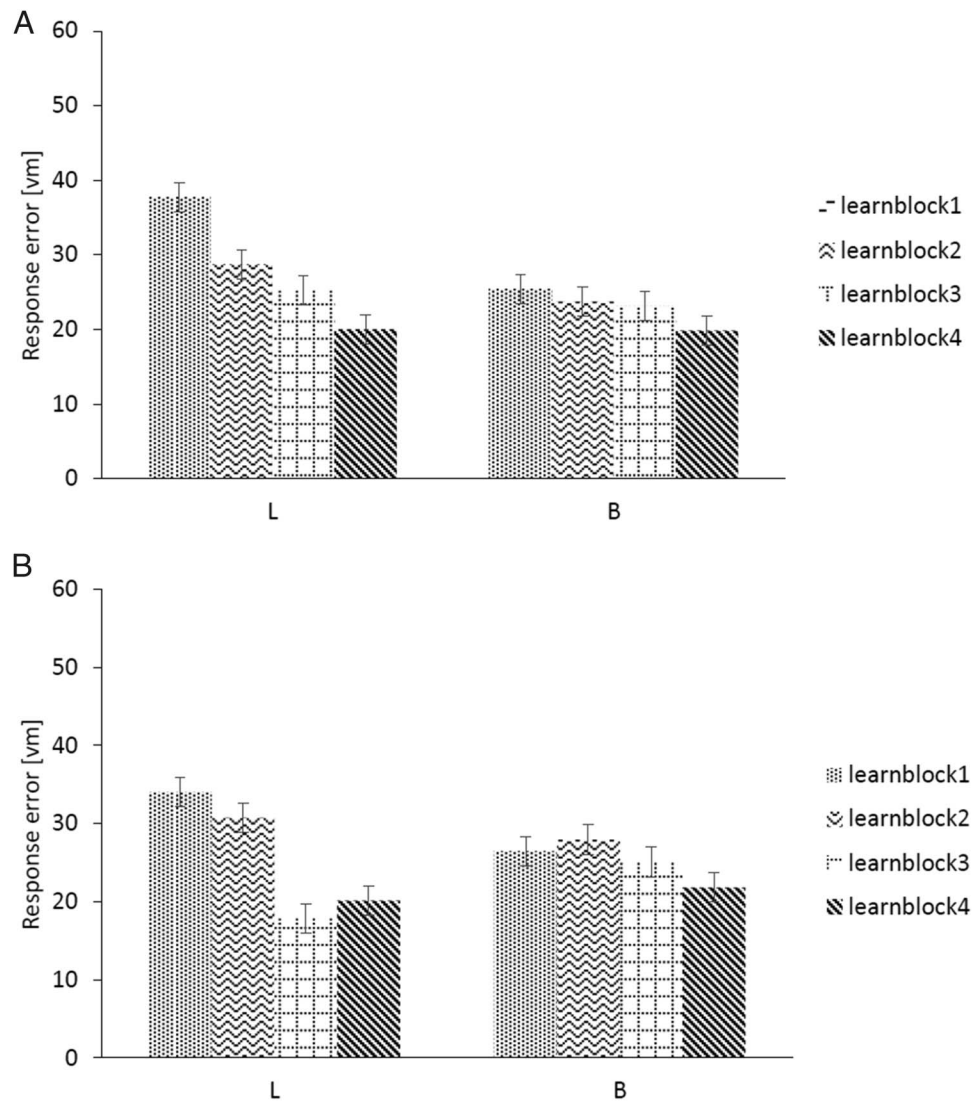


Figure 3. Response errors as a function of both the learning blocks (1–4) and the learning condition (L or B) in Experiment 1 (A) and Experiment 2 (B). Error bars are ± 1 SE.

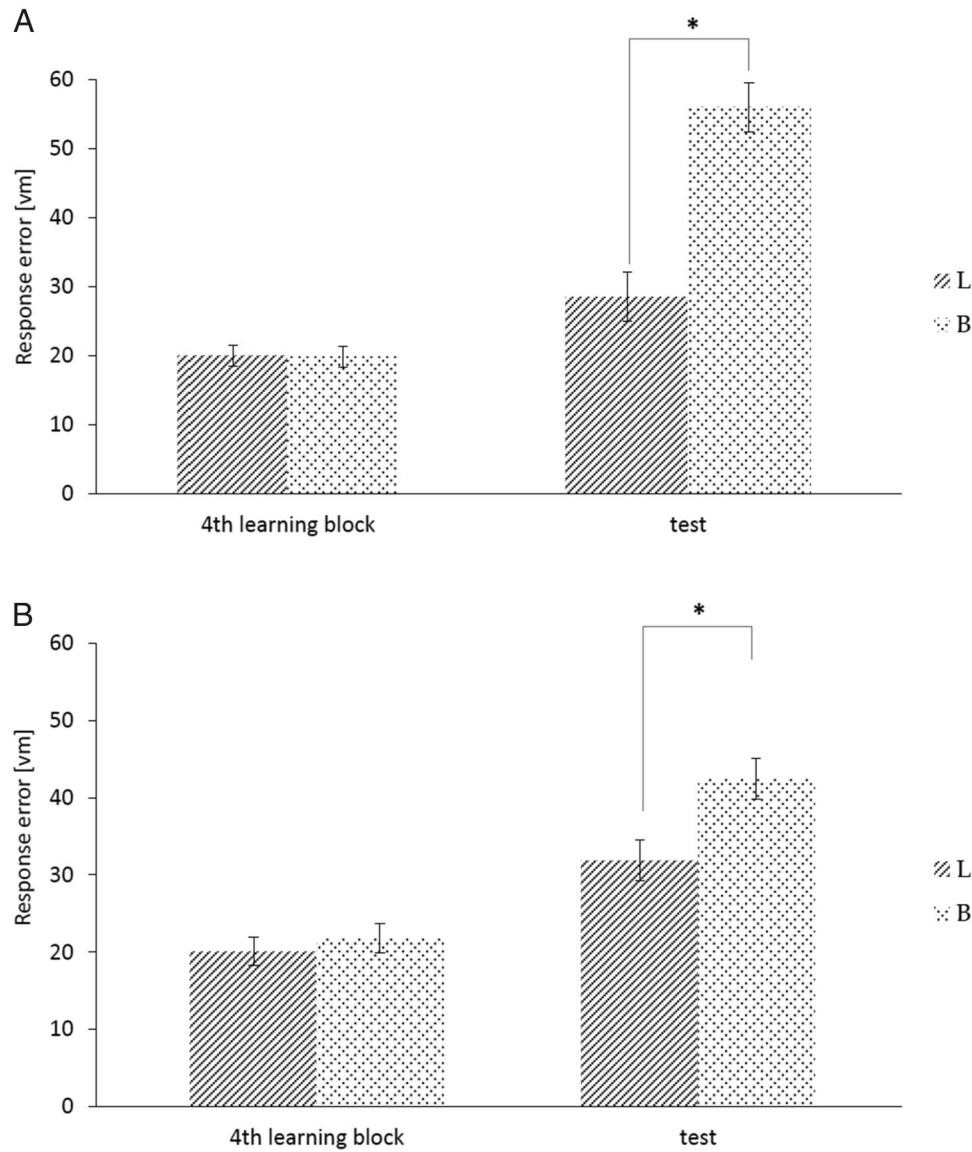


Figure 4. Response errors as a function of the learning condition (L or B) during the last (i.e., fourth) learning block and the testing phase, respectively, in Experiment 1 (A) and Experiment 2 (B). Error bars are ± 1 SE.

plotted in Figure 4A. Participants in L ($M_L = 28.35$ vm, $SD_L = 15.04$) were significantly more accurate than those in B ($M_B = 55.60$ vm, $SD_B = 24.67$), $F(1, 46) = 21.36$, $p < .001$, $\eta_p^2 = .32$. This result implied that the cognitive map in the landmark group allowed a more accurate inference of the vectors between two objects' locations.

The deviation scores of individual response locations (calculated by subtracting the x - y coordinates of the correct target locations from those of the individual response locations) are plotted for both learning cue conditions (see Figure 5A). A smaller distance between one data point and the origin (0, 0) suggests higher accuracy of the corresponding response. The 95% confidence ellipses of the deviation scores and of the mean of the deviation scores are also plotted for both learning cue conditions. The ellipses indicate that participants in either L or B group had no systematic response bias, whereas responses in the

B condition were more dispersed than those in the L condition, confirming that the cognitive map in the landmark group was more accurate.

Experiment 2

In Experiment 2, a task requiring inference of the spatial configuration among three objects was employed to evaluate the accuracy of the cognitive map of objects' locations in either learning cue condition.

Method

Participants. Forty-eight students (24 males and 24 females) from the University of Alberta participated to fulfill a course requirement.

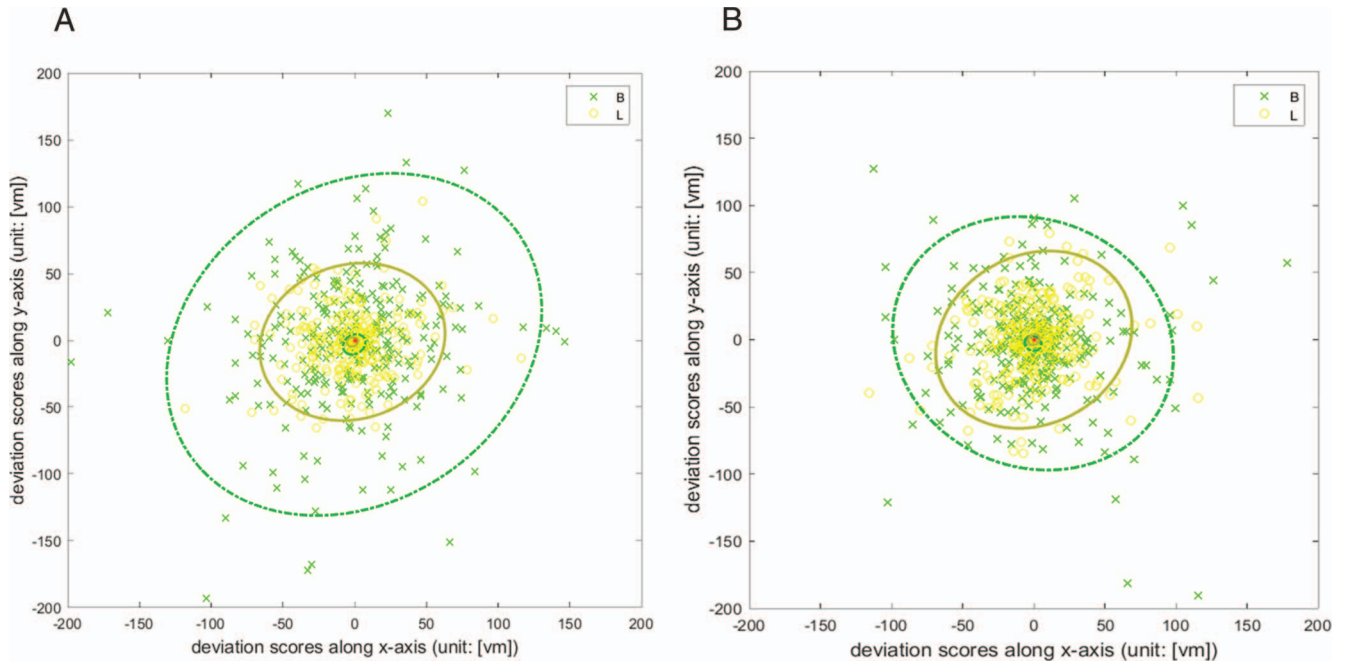


Figure 5. The deviations of all response locations from the correct location collapsed across the four objects and the 95% confidence ellipses of the individual deviations and of the mean of the individual deviations in Experiment 1 (A) and Experiment 2 (B). The red (dark gray) dot at origin (0, 0) illustrates as the correct location. The green (dark gray) crosses represent all response deviations in the boundary condition. The yellow (light gray) circles represent all response deviations in the landmark condition. The green (dark gray) ellipse in dashed line represents 95% confidence ellipses in the boundary condition (the large one is for the deviations and the small one is for the mean of the deviations). The yellow (light gray) ellipse in solid line represents 95% confidence ellipses in the landmark condition (the large one is for the deviations and the small one is for the mean of the deviations). See the online article for the color version of this figure.

Materials, design, and procedure. Experiment 2 was identical to Experiment 1 with the following exceptions. During testing, both the original localization cues (i.e., the wall and the traffic cone) and the distal orientation cues were removed. For each testing trial, two of the four objects were shown at their correct locations as the testing cues; participants replaced one of the other two objects. The combinations of six possible pairs of the cue objects and two possible probed objects for each cue pair yielded 12 testing trials.

Results and Discussion

Performances during the learning phase. Mixed-model ANOVAs were conducted on response errors across the four learning blocks to assess the learning effect. A Learning Cue \times Learning Block interaction was revealed, $F(3, 138) = 5.67$, $p = .001$, $\eta_p^2 = .11$. As shown in Figure 3B, the L group again had a larger learning effect. Repeated-measure ANOVAs on the response errors revealed a learning effect in each condition (L or B): for the L group, $F(3, 69) = 13.01$, $p < .001$, $\eta_p^2 = .36$, and for the B group, $F(3, 69) = 3.13$, $p = .03$, $\eta_p^2 = .12$ (see Figure 3B). Due to the learning effect, the response errors in the last learning block from the two conditions were compared. Localization accuracy did not differ between the two groups ($M_L = 20.11$ vm, $SD_L = 15.73$; $M_B = 21.78$ vm, $SD_B = 9.23$), $F(1, 46) = 0.20$, $p = .66$, $\eta_p^2 = .004$ (see Figure 4B).

Performances during the testing phase. Mean response errors during the testing phase as a function of the learning cue (L or B) were plotted in Figure 4B. Participants in L ($M_L = 31.68$ vm, $SD_L = 11.09$) were more accurate than participants in B ($M_B = 42.24$ vm, $SD_B = 22.21$), $F(1, 46) = 4.35$, $p = .043$, $\eta_p^2 = .09$. This result indicated that the cognitive map in the landmark group allowed a more accurate inference of the configurations among three objects' locations.

The deviation scores and the 95% confidence ellipses of the deviation scores and of the mean of the deviation scores are plotted for both learning cue conditions (see Figure 5B). The ellipses indicate that participants in either L or B group had no systematic response bias whereas responses in the B condition were more dispersed than those in the L condition, confirming that the cognitive map in the landmark group was more accurate.

General Discussion

The current study demonstrated that participants acquired a more accurate cognitive map through spatial learning relative to a single landmark than relative to a boundary. This cognitive map allowed participants to infer the vector between two objects' locations (Experiment 1) and the configuration among three objects' locations (Experiment 2).

These findings raise questions about cognitive map theory because cognitive map theory predicts the opposite pattern of results.

We speculate that cognitive map theory might be primarily applied to the representation of an object's location relative to a boundary. However, the representation of an object's location relative to another object, including a landmark, may not require hippocampus-dependent place learning. Although there is significant evidence showing that hippocampal place cells are sensitive to locations specified in terms of boundaries (O'Keefe & Burgess, 1996; see Barry et al., 2006, for review), there is no direct evidence that hippocampal place cells are sensitive to locations specified relative to a landmark within the boundary (Cressant, Muller, & Poucet, 1997).

Our speculation is consistent with multiple trace theory of spatial memory. Nadel and Moscovitch (1997, see also Moscovitch et al., 2005) proposed that the hippocampus might be important to constructing detailed or episodic spatial memory, which consists of a rich context, whereas extrahippocampal structures might be important to semantic spatial memory. In the current study, a boundary might have provided a rich context for locations within the boundary, whereas the metric relations between a location and a landmark might have lacked episodic or detailed information and, therefore, the representation of such spatial relations might be less hippocampal-dependent.

The vector addition model could well explain the current findings. This model conjectures that people can form a cognitive map as long as they encode metric relations of individual locations to a reference point regardless the learning mechanisms. Furthermore, this model hypothesizes that people develop a better cognitive map when the locations are learned relative to one reference point than to multiple reference points. These conjectures are consistent with the findings of the current experiments. When participants encode four objects' locations relative to the boundary, they might use multiple pieces of the boundary from various directions as reference points for each location, with the larger contribution from the closer boundary pieces (O'Keefe & Burgess, 1996; Hartley, Trinkl, & Burgess, 2004). Participants could select reference points on the homogeneous circular wall using the distal orientation cues. They might segment the wall into pieces and use the orientation cues to differentiate the wall segments (e.g., the wall segment close to forest).

For simplicity, we assume that people only encode each location in terms of the closest boundary piece. Therefore, four different boundary pieces (reference points) are selected and four vectors between each object and the corresponding closest reference point are established. To infer the vector between any two objects, people have to add together the two reference-point-object vectors, as well as the vector between the corresponding reference points (e.g., see Figure 1B). In contrast, when participants encode four objects' locations relative to a single landmark, the landmark serves as a common reference point and the interobject vectors can be obtained by adding the two object-landmark vectors (e.g., see Figure 1A). Because both encoding and adding the vectors between two reference points are prone to errors, participants in the boundary condition should have a less accurate cognitive map.

Compared with cognitive map theory, the vector-addition model offers a better explanation for the current findings. However, it is not the only possible explanation. Another possible explanation is that the homogeneous boundary could not have provided any visually distinctive reference point.¹ To specify a location, reference points as well as a reference direction are required (Klatzky,

1998). According to this explanation, participants in the boundary condition might have inferred a reference point, for example, the center of the boundary. This explanation further assumes that the initial mental representation of a target's location relative to the inferred reference point is comparable to the mental representation of the target's location relative to a visual landmark; however, the spatial representation relative to the inferred reference point is less robust and decays more quickly than that relative to the landmark. Therefore, this explanation is consistent with the finding of the comparably accurate localization in the last learning block in both cue conditions but more accurate localization in the testing blocks in the landmark condition.

This explanation differs from the vector-addition model in terms of the way in which participants used the boundary to localize targets. According to the former, participants inferred a less robust reference point whereas, according to the latter, participants selected multiple reference points (Mou & Zhou, 2013). However, both explanations predict less accurate cognitive mapping in the boundary condition, thereby challenging cognitive map theory. Future studies are needed to distinguish these two explanations to further understand how people use a boundary to localize objects.

The finding that spatial learning relative to a landmark, rather than to a boundary, can lead to a better cognitive map strikingly contrasts with the superiority effect of a boundary cue over a landmark cue in learning individual locations when both cues were presented (Doeller & Burgess, 2008). This contrast indicates that the relative importance of a boundary cue and a landmark cue in spatial learning depends on encoding individual locations when both cues are present or inferring interlocation spatial relations after encoding individual locations with the presence of either cue.

Conclusion

We presented evidence that a more accurate cognitive map for inferring interlocation spatial relations is acquired through learning individual locations relative to a single landmark than through learning individual locations relative to a boundary. We suggest that although spatial learning relative to a single landmark, compared to spatial learning relative to a boundary, might involve less place learning (i.e., more response learning) and depend less on the hippocampus (i.e., more on the striatum), because it involves encoding vectors between locations and the common reference (i.e., wall or traffic cone), it leads to a cognitive map. Furthermore, such representation is more accurate than that acquired through spatial learning relative to a boundary because cognitive mapping is more accurate relative to one reference point than to multiple reference points.

¹ We are grateful to an anonymous reviewer and Dr. John Philbeck for suggesting this alternative explanation.

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Received June 4, 2015

Revision received December 8, 2015

Accepted December 12, 2015 ■