Environment size and the use of feature and geometric cues for reorientation

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1. Introduction

Extant evidence suggests that mobile organisms use both objects in the environment (i.e., features) and the shape of the environment (i.e., geometry) to determine their position in space (for a review, see Cheng & Newcombe, 2005; Spetch & Kelly, 2006). To investigate the use of features and geometry for orientation, researchers often use a reorientation paradigm in which participants are rewarded for approaching a distinctive visual cue located in a corner of an otherwise featureless rectangular enclosure. During subsequent testing, the feature is often moved to another corner or removed entirely, and search performance during these critical test trials is used to determine which specific cue(s) were encoded during training and which specific cue(s) were used for reorientation during testing. Within this reorientation paradigm, disoriented rats (Cheng, 1986), chickens (Vallortigara, Zanforlin, & Pasti, 1990), pigeons (Kelly & Spetch, 2001; Kelly, Spetch, & Heth, 1998), fish (Sovrano, Bisazza, & Vallortigara, 2003), monkeys (Gouteux, Thinus-Blanc, & Vauclair, 2001), and ants (Wystrach & Beugnon, 2009) have all been shown to allocate equivalent choices to the correct and rotationally equivalent corners (i.e., geometrically correct locations) when tested in rectangular environments devoid of distinctive featural information. This “rotational error” phenomenon has also been shown with human children (Hermer & Spelke, 1994; Learmonth, Nadel, & Newcombe, 2002; Learmonth, Newcombe, & Huttenlocher, 2001) and human adults in real environments (Hermer-Vazquez, Spelke, & Katsnelson, 1999), static three-dimensional virtual environments (Kelly & Bischof, 2005, 2008), and dynamic three-dimensional virtual environments (Alexander, Wilson, & Wilson, 2009; Bodily, Eastman, & Sturz, 2011; Sturz, Gurley, & Bodily, 2011; Sturz & Kelly, 2009).

Given the ubiquity of the use of feature and geometric cues for reorientation, much theoretical and empirical work has focused on the mechanism(s) by which these spatial cues are used for orientation; however, debate remains concerning the extent to which learning about feature and geometric cues can be accounted for by the same mechanisms as that of classical and instrumental conditioning (for a review, see Cheng, 2008). For example, research has provided evidence for associative cue-competition effects such as blocking, overshadowing, second-order conditioning, and sensory preconditioning within the spatial domain (e.g., Cheng & Spetch, 2001; Chamizo, Aznar-Casanova, & Artigas, 2003; Jacobs, Laurance, & Thomas, 1997; Molet, Jozefowicz, & Miller, 1998).

We tested associative-based accounts of orientation by investigating the influence of environment size on the use of feature and geometric cues for reorientation. Two groups of participants were trained in dynamic three-dimensional virtual rectangular environments that differed in size to find a distinctly colored bin located at one of the four corners. Subsequently, we probed the reliance on feature and geometric cues for reorientation during test trials by presenting six trial types: Small Geometry Only, Large Geometry Only, Small Cue Conflict, Large Cue Conflict, Small Distal, and Large Distal. During Geometry Only test trials, all bins were black; thus, all distinctive featural information was removed leaving only geometric cues. For Cue Conflict test trials, all colored bins were shifted counter-clockwise one corner; thus, the geometric cues from the trained corner and the trained color were in direct conflict. During Distal test trials, the bin in the geometrically incorrect corner farthest from the trained corner was colored the same as during training; the remaining three bins were black. Thus, only this distant feature cue could be used to determine the location of the goal bin. Results suggested that geometric cues were used across changes in environment size, featural cues exerted greater influence when in conflict with geometric cues, and the far featural cue was used to disambiguate the correct from the rotationally equivalent location. In short, both feature and geometric cues were used for reorientation, and environment size influenced the relative use of feature and geometric cues. Collectively, our results provide evidence against associative-based accounts of orientation.

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The present experiment was to test an associative-based account of orientation by investigating the influence of environment size on the orientation ability of adult human participants within a dynamic three-dimensional (3D) virtual environment. Virtual environment methodology appeared ideal for this purpose because of the ability to easily manipulate environment size while maintaining ecological validity. Perhaps most importantly, virtual environments have been shown to engage similar spatial mechanisms as those used in real environments (see Sturz, Bodily, et al., 2009; Sturz, Brown, et al., 2009; Sturz & Kelly, 2009; Sturz, Kelly, & Brown, 2010).

Employing this virtual environment methodology, we investigated how training in a specifically-sized environment influenced the use of feature and geometric cues for reorientation when environment size remained the same or changed between training and testing. Specifically, we trained two groups of participants, each with different environment sizes (i.e., Small or Large), to search for a distinctly colored bin located in one of the four corners of a dynamic 3D rectangular virtual-environment. The environments were designed in such a way that the length of the long wall in the Small environment was equivalent in length to the short wall in the Large environment (refer to “B” in Fig. 1). During test trials, we presented both environment sizes to both groups of participants for the purposes of assessing the influence of environment size on the exclusive use of geometric cues (i.e., all bins were black), 2) the relative use of feature and geometric cues (i.e., all colored bins were shifted counter-clockwise one corner), and 3) the extent of learning about feature cues (i.e., the bin in the geometrically incorrect corner farthest from the trained corner was colored the same as in training whereas the remaining three bins were black).

2. Theoretical predictions

Under the conditions of the present experiment, associative-based accounts of orientation make definitive predictions regarding a) the allocation of choices relative to chance performance and b) the allocation of choices relative to cue type (i.e., features and geometry) during test trials. During trials in which only geometric cues are available, participants should allocate choices at above chance levels to the geometrically correct locations in an environment equivalent in size to that of training but should allocate choices at below chance levels to the geometrically correct locations in an environment different in size. Specifically, standard associative-based accounts suggest that reorientation is based upon absolute metrics (e.g., wall length) (see Dawson et al., 2010; Miller, 2009; Miller & Shettleworth, 2007; Ponticorvo & Miglino, 2010), Assuming absolute encoding of wall lengths, participants trained in the small environment should allocate choices at an above chance level in the Small environments because the associative strengths of the wall lengths and corner angles in the correct and rotationally equivalent locations would be identical (see Miller & Shettleworth, 2007). However, these participants should allocate choices to the geometrically correct locations at below chance levels (i.e., they should allocate responses to the geometrically incorrect locations) in the large environments because the only cue available that could have acquired associative strength from the Small training environment would be the specific side of a wall “B” units in length (refer to Fig. 1).

Reciprocally, participants trained in the Large environment should allocate choices at an above chance level in the Large environments because the associative strengths of the wall lengths and corner angles in the correct and rotationally equivalent locations would be identical (see Miller & Shettleworth, 2007). However, these participants should allocate choices to the geometrically correct locations at below chance levels (i.e., they should allocate responses to the geometrically incorrect locations) in the Small environments because the only cue available that could have acquired associative strength from the Large training environment would be the specific side of a wall “B” units in length (refer to Fig. 1).

With respect to allocation of choices based upon cue type, associative-based accounts suggest that the saliency of featural
cues is relatively greater in large environments compared to small environments whereas the saliency of geometric cues is relatively greater in small environments compared to large environments (Miller, 2009). During trials in which geometric cues conflict with featural cues, participants should show a greater reliance on feature cues in large environments (regardless of training environment size) and more reliance on geometric cues in small environments (regardless of training environment size) due to these differential saliences of feature and geometric cues within the environments.

Finally, under an associative-based account, feature information situated in corners other than that of the trained corner should not acquire associative strength (i.e., should be considered irrelevant) because they are not situated in the correct location when choices are rewarded (see Miller & Shettleworth, 2007). During trials in which the far featural cue is present (i.e., a cue in the far geometrically incorrect location), participants should allocate choices equally to the two geometrically correct locations. In other words, the far featural cue should not be utilized to disambiguate the correct from the rotationally equivalent location.

3. Method

3.1. Participants

Ninety-six undergraduate students (48 males and 48 females) participated in the study and received extra class credit.

3.2. Apparatus

An interactive, dynamic 3D virtual environment was constructed and rendered using Valve Hammer Editor and run on the Half-Life Team Fortress Classic platform. A personal computer, 19-inch flat-screen liquid crystal display (LCD) monitor, optical mouse, keyboard, and speakers served as the interface with the virtual environment. The monitor (1152×864 pixels) provided a first-person perspective of the virtual environment (see right column, Fig. 1). Participants used the arrow keys of the keyboard, the mouse, and the left mouse button to navigate within the environment. Speakers emitted auditory feedback. Experimental events were controlled and recorded using Half-Life Dedicated Server on an identical personal computer.

3.3. Stimuli

Dimensions are length × width × height and measured in virtual units (vu). Two virtual environments were created (see Fig. 1): Small Rectangle (568 × 284 × 281 vu) and Large Rectangle (1236 × 568 × 281). Each environment contained four raised bins (86 × 86 × 38 vu) arranged one in each corner. Bin colors were red, blue, yellow, green, or black depending on trial type (see below). The environments were illuminated by a light source centered 64 vu below the ceiling. All surfaces were white in color with the exceptions of the floors (gray) and the ceilings (black).

3.4. Procedure

Participants were requested to locate the bin that transported them to the next virtual room. Movement through the environment was via keyboard keys: ↑ (forward), ↓ (backward), ← (left), and → (right). Movement of the mouse changed the view within the environment, and auditory feedback indicated movement (footstep sounds). Participants selected a bin by jumping into it. To jump into a bin, participants simultaneously moved forward (↑) and jumped (left mouse button). Auditory feedback indicated that a jump occurred ("huu" sound). Selection of the rewarded bin resulted in auditory feedback (transport sound from Super Mario Bros™) and a 1 s inter-trial interval (ITI) in which the monitor went black and participants progressed to the next trial. Selection of a non-rewarded bin resulted in different auditory feedback (game over sound from Super Mario Bros™) and required participants to jump out of the current bin in order to continue searching.

3.4.1. Training

Participants were randomly assigned to one of two groups: Group Small or Group Large. Participants assigned to Group Small received all training trials in the small rectangular environment whereas participants assigned to Group Large received all training trials in the large rectangular environment (see Fig. 1). Training consisted of 8 trials. Within each group, participants were also randomly assigned to one of the four corners which was designated as the rewarded corner. Within and across groups, gender and number of participants trained at each corner were balanced. Participants started each trial from the center of the environment (marked “S” in Fig. 1). Participants entered the environment facing random orientations from 0° to 315° in increments of 45°. Each of the four bins was marked in a distinct color: blue, yellow, red and green.
3.4.2. Testing

Testing consisted of 60 trials composed of 12 five-trial blocks. Each trial block was composed of four Training trials and one Test trial. The location of the Test trial within each block was randomized. For each Test trial, one of six trial types was presented: Small Geometry Only, Large Geometry Only, Small Cue Conflict, Large Cue Conflict, Small Distal, and Large Distal (see Fig. 1). “Small” and “Large” reflect the size of the testing environment and were identical to the training environments of Group Small and Group Large, respectively. During Geometry Only test trials, all bins were black; thus, all distinctive featural information was removed leaving only the environmental geometry as an informative cue. During Cue Conflict test trials, all colored bins were shifted counterclockwise one corner; thus, the geometric and featural information as to the location of the goal bin were in conflict. During Distal test trials, the bin in the geometrically incorrect corner farthest from the trained corner remained the same color as during training whereas the other three bins were black. Thus, only this distant feature cue could be used to determine the location of the goal bin.

Within both Blocks 1–6 and Blocks 7–12, the six test trial types were presented once without replacement. As a result, each test trial type was presented two times for a total of 12 test trials. Participants made one choice during Test trials which resulted in no auditory feedback followed by the 1 s ITI and progression to the next trial. Participants entered all environments during Testing from the center of the environments (marked “S” in Fig. 1) facing random orientations from 0° to 315° in increments of 45°.

4. Results

4.1. Training

Fig. 2 shows the mean proportion of participants’ first choices to the rewarded bin plotted by two-trial blocks for the eight trials of Training for males (circles) and females (triangles) in Group Small (filled symbols) and Group Large (unfilled symbols). A three-way mixed analysis of variance (ANOVA) on mean proportion of correct first choices with Group (Small, Large), Gender (Male, Female), and Block (1–4) as factors revealed a main effect of Block, $F(3, 276)=79.95$, $p<.001$, and a significant Gender × Block interaction, $F(3, 276)=2.92$, $p<.05$. The interaction resulted from a difference between the males and females in Block 2, $t(94)=2.07$, $p<.05$, but no significant differences between males and females for the other blocks, $t(94)<1.55$, $p>.13$. Post hoc tests revealed that Blocks 1 and 2 were significantly different from all other blocks ($p<.001$). Blocks 3 and 4 were also significantly different from all other blocks ($p<.05$) but were not different from each other ($p>.05$). One sample $t$-tests revealed that the mean proportion of first choices to the rewarded bin during Block 1 was not significantly different from chance (0.25), $t(95)=1.17$, $p>.05$, but these mean proportion of choices during Blocks 2–4 were all significantly greater than chance, $t(95)>12.48$, $p<.001$.

4.2. Testing

We first conducted an omnibus four-way mixed ANOVA on mean proportion of choices to geometrically correct locations (i.e., trained and rotationally equivalent locations) with Group (Small, Large), Gender (Male, Female), Testing Environment Size (Small, Large), and Test Trial Type (Geometry Only, Cue Conflict, Distal) as factors which revealed a main effect of Test Trial Type, $F(2, 184)=240.88$, $p<.001$, and significant Group × Testing Environment Size, $F(1, 92)=8.46$, $p<.01$, and Group × Testing Environment Size × Test Trial Type, $F(2, 184)=3.71$, $p<.05$, interactions. None of the other main effects or interactions were significant, $F$s $<1.94$, $p$s $>.14$.

As shown in Fig. 3, the source of the Group × Testing Environment Size × Test Trial Type interaction was due to similar choice responding to the geometrically correct locations across changes in Testing Environment Size for all of the Test Trial Types for Group Small, $t(47)<1.84$, $p>.07$, but differences in choice responding to the geometrically correct locations dependent on Testing Trial Type for Group Large. Specifically, choices to geometrically correct locations did not differ across changes in Testing Environments Size for Cue Conflict trials for Group Large, $t(47)=0.57$, $p=.57$, but choices to geometrically correct locations were significantly greater in the Large Testing Environments compared to the Small Testing Environment for both Geometry Only and Distal trials, $t(47)=2.7$, $p<.05$, and $t(47)=2.83$, $p<.01$, respectively.

As also shown in Fig. 3, choices to the geometrically correct locations during Geometry Only trials were significantly above chance (0.5) for both Groups and both Testing Environment Sizes, $t(47)>3.9$, $p<.001$. In addition, choices to geometrically correct locations during Cue Conflicts trials were significantly below chance for both Groups and both Testing Environment Sizes, $t(47)>3.35$, $p<.01$. Moreover, choices to
geometrically correct locations during Distal trials were significantly above chance for both Groups and both Testing Environment Sizes, $t_s(47) > 2.85$, $p < .01$. It should also be noted that mean choices to the geometrically correct location were equivalent to those of the rotationally equivalent location in both Small and Large Geometry Only trials for Group Small, paired-samples $t$-test, $t(47) = -0.13$, $p > .05$, respectively, and Group Large, $t(47) = -1.26$, $p > .05$, respectively. Collectively, these results suggest that participants in both groups encoded the geometric properties of the environment during training with distinctive features present, and they were able to transfer this geometric knowledge to a novel sized environment. However, for Group Large the ability to rely only on geometric information was significantly decreased when reorienting in the smaller environment (although remained above chance).

To illuminate the relative use of feature and geometric cues, we analyzed the mean proportion of choices to the feature correct location during the Cue Conflict trials. Fig. 4 shows the mean proportion of choices to feature correct location collapsed across both presentations of each rectangular environment for both Small and Large Cue Conflict Testing Environments plotted by Group. A three-way mixed ANOVA on mean proportion of choices to the feature correct location with Group (Small, Large), Gender (Male, Female), and Testing Environment Size (Small, Large) as factors revealed no main effects or interactions, $F_{3,52} < 3.52$, $p > .06$.

During the Cue Conflict trials, which placed learned featural and geometric information in conflict, the mean proportion of choices to the location containing the trained feature cue was significantly greater than would be expected by chance (i.e., 0.25) for both Small and Large Testing Environments for Group Small, one-sample $t$-tests,
As a result, it appears that the participants in both groups had encoded the featural properties of the environment during training, and they allocated their choices to the location with the trained feature cue over the location with the trained geometric cues when in conflict. Moreover, this allocation of choices to the trained feature cue was to an equivalent extent regardless of testing environment size.

Finally, to illuminate the extent to which the far featural cue was encoded during training, we analyzed the mean proportion of choices to the correct compared to mean proportion of choices to the rotationally equivalent locations during the Distal test trials. Fig. 5 shows the mean proportion of choices to the trained location (i.e., geometrically correct location) collapsed across both presentations of each rectangular environment for both Small and Large Distal Testing Environments plotted by Group for males (top panel) and females (bottom panel). A three-way mixed ANOVA on mean proportion of choices to the trained corner with Group (Small, Large), Gender (Male, Female) and Testing Environment Size (Small, Large) as factors revealed a significant Group×Testing Environment Size interaction, $F(1, 92) = 5.6, p<.05$. None of the other main effects or interactions were significant, $F_s < 2.75, p_s > .1$. The source of the Group×Testing Environment Size interaction was due to a reduced use of the trained feature cue in the Small environment compared to the Large environment for males in group Large, paired-samples $t$-test, $t(23) = 2.85, p<.01$, whereas the females in Group Large showed equivalent performance in the two different sized environments during the Distal tests, paired-samples $t$-test, $t(23) = 0.9, p > .37$. The source of the Group×Size interaction was due to a greater mean proportion of choices to the trained corner in the Large Distal environment compared to the Small Distal environment for Group Large, paired-samples $t$-test, $t(47) = 2.77, p < .001$, but no difference for Group Small, paired-samples $t$-test, $t(47) = 1.07, p > .05$. As a result, it appears that overall participants trained in the Large environment were able to use the far featural cue to a greater extent in the Large compared to the Small Testing Environment.

In the presence of a distinct cue located at the far geometrically incorrect corner (i.e., the distal trials), the mean proportion of choices was greater to the trained location (where the feature would have been during training) than would be expected by chance (i.e., 0.25).
Such a result was obtained for distal trials in both Small and Large Testing Environments for Group Small, one-sample t-tests, t(47) = 4.45, p < .001, t(47) = 4.23, p < .001, respectively, and for Group Large, t(47) = 3.18, p < .01, t(47) = 6.76, p < .001, respectively. In addition, mean proportion of choices to the trained location was greater than those to the rotationally equivalent location in both Small and Large Distal trials for Group Small, paired-samples t-test, t(47) = 3.99, p < .001, t(47) = 3.51, p < .001, respectively, and Group Large, t(47) = 2.28, p < .05, t(47) = 4.72, p < .001, respectively. These results suggest that overall participants were able to use the presence of a distant feature to disambiguate the correct from the rotationally equivalent location (the exception being the males in group Large when presented with the Small Distal environment).

5. Discussion

Participants in both groups learned to respond to the rewarded bin at equivalent rates and to an equivalent level of accuracy, and testing results appear consistent with extant human and non-human animal research conducted in real (Hermer & Spelke, 1994; Hermer-Vazquez et al., 1999; Learmonth et al., 2001) and virtual (Hartley, Trinkler, & Burgess, 2004; Kelly & Bischof, 2005, 2008; Sturz & Kelly, 2009; Sturz et al., 2011) environments that have documented the encoding of featural and geometric cues for reorientation (for a review, see Cheng & Newcombe, 2005, 2006). In addition, present results are consistent with previous research showing the encoding of relative environmental geometry by humans (Sturz & Kelly, 2009). Moreover, we extend these previous findings by showing the role of environment size on the relative use of feature and geometric cues for reorientation in adult human participants.

With respect to the use of geometric cues for reorientation, participants in both groups showed encoding of geometry. Despite participants being trained with distinctive featural cues that were always predictive of the goal bin, they nonetheless encoded environmental geometry (as evidenced by above chance performance during Geometry Only test trials). While reliance on geometric cues was consistent across changes in environment size for participants in Group Small, performance diminished in the Small testing environment relative to the Large testing environment for participants in Group Large. Such a result appears inconsistent with prior research that has found relatively increased reliance on geometric cues in small environments compared to large environments (Chiandetti et al., 2007; Learmonth et al., 2001; Sovrano et al., 2003; Sovrano et al., 2007; Vallortigara et al., 2005). In addition, such a result appears inconsistent with associative-based accounts of orientation because the saliency of feature cues is predicted to be relatively greater in small environments compared to large environments (Kraus et al., 2005). As a result, associative-based accounts would have predicted that participants should have shown more reliance on geometric cues in small environments (regardless of training environment size).

For the Distal test trials, participants in both groups appeared to have learned about a non-rewarded feature cue (i.e., the bin in the geometrically incorrect corner farthest from the trained corner). Only by using this feature cue could participants have responded to the trained location at above chance levels (i.e., able to distinguish between the correct and rotationally equivalent location). In addition, reliance on feature cues was unaffected by changes in environment size for participants in Group Small but was affected by changes in environment size for participants in Group Large. Specifically, only participants in Group Large allocated choices to the correct location to a greater extent in the Large compared to the Small Distal environment. Although the overall group results appear consistent with prior research that has found relatively increased reliance on feature cues in large environments compared to small environments (Chiandetti et al., 2007; Learmonth et al., 2001; Sovrano et al., 2003; Sovrano et al., 2007; Vallortigara et al., 2005), they appear inconsistent with associative-based accounts of orientation because the saliency of feature cues is predicted to be relatively greater in large environments compared to small environments (Miller, 2009).

As a result, associative-based accounts would have predicted that participants should have shown more reliance on feature cues in large environments (regardless of training environment size). According to these accounts, participants should have shown a greater reliance on the trained feature cue in the Large Cue Conflict environment and a greater reliance on the trained geometric cues in the Small Geometry Only environments. In addition, participants selected geometrically correct locations during the Geometry Only test trials at above chance levels despite changes in environment size from training to testing, and participants selected the trained location during Distal test trials at above chance levels and to a greater amount than choices to the rotationally equivalent corner. These two results seem to be the most problematic for associative-based accounts (i.e., Dawson et al., 2010; Miller, 2009; Miller & Shettleworth, 2007; Ponticorvo & Miglino, 2010). According to these accounts, participants should have shown a greater reliance on the trained feature cue in the Large Cue Conflict environment and a greater reliance on the trained geometric cues in the Small Geometry Only environments. In addition, participants selected geometrically correct locations during the Geometry Only test trials at above chance levels despite changes in environment size from training to testing, and participants selected the trained location during Distal test trials at above chance levels and to a greater amount than choices to the rotationally equivalent corner. Even if granted relative encoding of wall length, associative-based accounts fail explain the use of the far feature cue as well as the conflicting nature of geometry use in large environments and featural cues in small environments (results contradictorily to associative predictions). In short, the ability to use the far featural cue is inconsistent with the notion that the associative strength of the correct and rotationally equivalent locations is equivalent (e.g., Miller & Shettleworth, 2007), that the distal feature cue is irrelevant (e.g., Miller & Shettleworth, 2007), and that reliance on feature or geometric cues is solely influenced by the size of the testing environment (e.g., Miller, 2009). Importantly, our results provide evidence for the influence of training environment size on the relative use of feature and geometric cues for reorientation.

It should be noted that the obtained effects regarding the relative use of feature and geometric cues in the present experiment were relatively subtle, and we acknowledge that the size differences in training environments in the present experiment were relatively modest (i.e., Small was half the size of Large). Whether or not these subtle effects would be amplified or diminished if conducted within environments of drastically different sizes (i.e., environments similar to those encountered during a normal day) remains an open question, but our results...
provide an empirical basis for predictions regarding the relative influence of feature and geometric cues in environments of different size. It remains unclear to what extent potential alternative accounts of spatial learning may be able to account for our obtained results. One potential group of theoretical accounts relates to encoding and storing multiple spatial cues in a hierarchical fashion (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Spetch & Kelly, 2006), and the hierarchy is suggested to be based upon cue characteristics such as previous experience and reliability (see also, Kelly et al., 1998; Newcombe & Ratliff, 2007; Ratliff & Newcombe, 2008). Alternatively, another group of theoretical accounts suggests separate systems for feature and geometry learning (e.g., Doeller & Burgess, 2008; Doeller, King, & Burgess, 2008; Lee & Spelke, 2010; Spelke, Lee, & Izard, 2010), and a feature-based system may conflict with a geometry-based system. Regardless, future research could continue to explore the mechanisms underlying the use of feature and geometric cues within the context of both training and testing environment sizes to delineate the reliance on feature and geometric cues for reorientation and to clarify existing theoretical accounts of spatial learning.

References


