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Orienting in virtual environments: How are surface features and environmental geometry weighted in an orientation task?

Debbie M. Kelly [a,*], Walter F. Bischof [b]

[a] Department of Psychology, University of Saskatchewan, 9 Campus Drive, Saskatoon, SK, Canada S7N 5A5
[b] Department of Computing Science, University of Alberta, Edmonton, Alta., Canada

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ABSTRACT

We investigated how human adults orient in enclosed virtual environments, when discrete landmark information is not available and participants have to rely on geometric and featural information on the environmental surfaces. In contrast to earlier studies, where, for women, the featural information from discrete landmarks overshadowed the encoding of the geometric information, Experiment 1 showed that when featural information is conjoined with the environmental surfaces, men and women encoded both types of information. Experiment 2 showed that, although both types of information are encoded, performance in locating a goal position is better if it is close to a geometrically or featurally distinct location. Furthermore, although features are relied upon more strongly than geometry, initial experience with an environment influences the relative weighting of featural and geometric cues. Taken together, these results show that human adults use a flexible strategy for encoding spatial information.

1. Introduction

The initial, and necessary, step required for successful navigation is obtaining a sense of orientation. Many different mechanisms and environmental cues have been reported to be used by animals to accurately establish a sense of direction (for reviews see Gallistel, 1990; Healy, 1998; Shettleworth, 1998). When an animal needs to determine which direction to travel, what information does it use to orient? To examine this question, many researchers have focused on how animals can use cues such as objects within the environment to obtain a sense of direction. In many such studies, an object is located either directly at the goal site or within the area surrounding the goal. In the first case, a beacon homing strategy (also referred to as beaconing) may be used. The animal can simply direct itself towards the object to locate the goal – the object becomes a beacon. In the second case, the animal needs to calculate a distance and direction vector between the goal and the object, a strategy known as landmark piloting – the object becomes a landmark.

Animals are, however, not limited to only using objects within an environment to orient. Cheng (1986) showed that disoriented rats were able to use the geometric shape of the environment itself to determine which direction to begin heading when in search of a goal location. In a reference memory task, disoriented rats were trained to search for food that was constantly located in one corner of a fully enclosed rectangular environment (see Fig. 1A). Each corner of the environment contained an identical food container and a panel with unique features (these panels differed according to color, texture, shape, and olfactory information). The rat needed to learn to identify, presumably by using the distinctive featural cues, the corner that had the container with a food reward. Although, with a significant amount of training, the rats could learn to solve this task, they made many errors. The errors were quite systematic in that the rats would not only select the container in the corner that was associated with

* Corresponding author. Tel.: +1 306 966 2941; fax: +1 306 966 6630.
E-mail address: Debbie.Kelly@usask.ca (D.M. Kelly).

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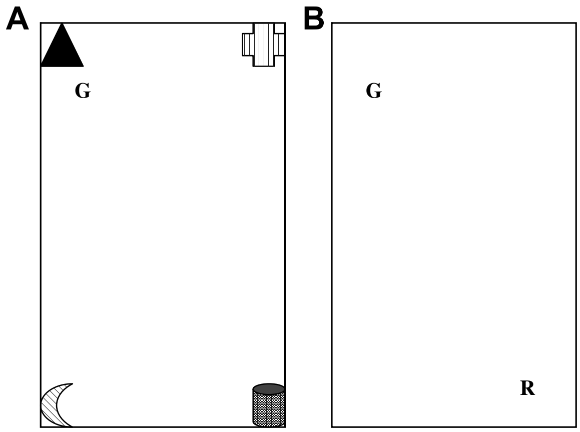

Fig. 1. (A) Schematic representation of rectangular environment used in Cheng (1986). The symbols represent the unique panels located in each corner. The "G" indicates an example goal location. (B) The same schematic rectangular environment with all unique featural cues removed. The "G" indicates the same goal location as in (A) and the "R" indicates the geometrically equivalent location (the location of systematic rotational errors).

reinforcement, but also in the corner diagonally opposite to the correct one. In this rectangular environment, the two corners, although very different according to featural information, were identical according to the environmental geometry (see Fig. 1B). Thus, the rats were showing strong control by the geometric properties of the environment to solve the task.

Many researchers have adopted Cheng's paradigm to investigate whether other species are able to encode an environment's geometric properties. The majority of these studies have shown that a number of species are able to use both featural cues and geometric cues to orient (e.g., fish: Sovrano, Bisazza, & Vallortigara, 2002, 2003; pigeons: Kelly, Spetch, & Heth, 1998; chicks: Vallortigara, Zanforlin, & Pasti, 1990; rhesus monkeys: Gouteux, Thinus-Blanc, & Vauclair, 2001; and adult humans: Hermer & Spelke, 1994, 1996; Hermer-Vazquez, Spelke, & Katsnelson, 1999; Ratliff & Newcombe, 2005; also see Cheng & Newcombe, 2005 for an excellent review of this literature). These studies have provided an opportunity to examine how animals use featural and geometric cues and how these two types of information are used in conjunction. For example, Vallortigara et al. (1990) and Kelly et al. (1998) adopted Cheng's paradigm to examine how chicks and pigeons, respectively, use featural and geometric cues to orient. The researchers found that both bird species readily learned to use the features and they also encoded the geometric properties of the environment. However, the two species did not encode the featural information to the same extent. Transformation tests which removed the featural cues in the two geometrically correct corners showed that chicks were not able to use the distant features alone (the two cues in the geometrically incorrect corners) to isolate the correct corner. Pigeons, however, could use the distant featural cues to guide them to the correct corner. Although this difference may be attributed to species differences (or ontological differences) it is also possible that the chicks and the pigeons were using different encoding strategies when representing the location of the goal relative to the featural information. For instance, it is possible that the chicks used a beacon homing strategy, i.e., they were encoding only the feature that directly marked the rewarded corner, whereas the pigeons may have adopted a landmark piloting strategy and thus were able to use surrounding features as landmarks to locate the goal.

Many studies of non-human animal navigation have shown that, when navigating through an environment, animals process the relationship between a goal location and a beacon differently than the relationship between a goal location and a landmark. In particular, Poucet, Save, and colleagues have shown that landmark piloting can be severely disrupted in rats by lesioning the hippocampal region, whereas such a lesion does not disrupt beacon homing (Save & Poucet, 2000; Poucet, Lenck-Santini, & Save, 2003). However, few studies have examined how the relationship between featural cues and an environment's geometry influence whether a beacon homing strategy or a landmark piloting strategy is used to encode a goal location. In particular, the majority of studies to date have made featural and geometric information redundant regarding the goal location – the goal is typically in a corner of a rectangular environment in which an object is situated or the corner is positioned between two different colored walls. This spatial relationship may encourage a beacon homing strategy rather than a landmark piloting strategy, influencing the nature of the spatial representation. Thus, in this study, we were interested in examining whether the arrangement of featural and geometric cues, relative to a goal location, would influence the relative encoding, and subsequent weighting, of featural and geometric information.

1.1. Spatial representations

The strategy an animal uses to encode the featural and geometric information within an environment, a beacon homing strategy or a landmark piloting strategy, may influence the nature of the spatial representation stored in memory. Many studies of human navigation have carefully explored the representation formed as people navigate through their environment. In particular, these studies have focused on whether the representation of a spatial environment is stored in an orientation-free or orientation-specific manner. An orientation-free representation allows a navigator to relocate to a desired position independent of his/her position within the environment – the spatial representation is *free* from the learned orientation. An orientation-specific representation limits the navigator such that s/he needs to view the environment from the same orientation as learned during training in order to accurately relocate to a desired position – the spatial representation is *specific* to the learned orientation.

Previous research has suggested that the mode of learning an environment may influence the type of spatial representation that is generated (Shelton & McNamara, 2004; Sholl, 1987; Sholl & Nolin, 1997; Sun, Chan, & Campos, 2004). For instance, participants who had learned a spatial environment using a map were very accurate at determining the direction of a particular object when they were viewing the real environment from the same vantage point as the learned map. However, accuracy decreased when the vantage point was misaligned with the learned map orientation (e.g., Sholl, 1987). This is in contrast to studies where participants were required to learn the location of a goal within an environment through active navigation (Sun et al., 2004). In this case, participants showed similar accuracy independent of whether the vantage point at testing was novel or experienced. More recently, researchers have shown that other considerations, in addition to viewpoint, may influence whether the spatial representation formed is orientation-free or orientation-specific. For example, McNamara and colleagues have shown through several studies that the selection of intrinsic frames of reference significantly influence how individuals remember the spatial relationship between objects within an environment (e.g., Diwadkar & McNamara, 1997; Mou, Zhao, & McNamara, 2007; Mou, Fan, McNamara, & Owen, 2008; Kelly & McNamara, 2008). Although the issue of whether the representation stored during navigational tasks is orientation-specific or orientation-free has received considerable study in recent years, few studies have considered how the spatial relationship between a goal location and cues presented on the surface of the environment itself influences the type of representation formed. For instance, does the encoding of a goal location using a beacon strategy lead to an orientation-specific representation, whereas the encoding of a goal location using a landmark piloting strategy leads to an orientation-free representation? Our study was designed to address this question using a simple virtual reality environment.

1.2. Cue weighting

Whether a navigator encodes a goal location using a beacon homing strategy or landmark piloting strategy may influence the relative reliance on featural and geometric information around the goal site. Several studies have shown that although animals may encode many different types of information in spatial search tasks, these cues tend to be weighted or ranked hierarchically (e.g., Brodbeck, 1994). Recently, Stankiewicz and Kalia (2007) examined the encoding of featural cues (referred to as *object landmarks* by the authors) and geometric cues (referred to as *structural landmarks* by the authors) in a virtual navigation task. Participants were initially asked to explore a virtual environment and instructed that they would be asked to recall information "about the hallways and pictures in the environment" (p. 382). The researchers found that the geometric cues were recalled more accurately than the featural cues, even when features were more informative than the geometry. This study shows that although both geometry and featural information were encoded in a navigation task they were not remembered to the same degree. Studies, such as Stankiewicz and Kalia (2007), have examined whether geometric and featural information are accurately recalled, or if initial experience with an environment influences the relative weighting of featural and geometric cues (Kelly et al., 1998). It is, however, not known whether the arrangement of featural and geometric cues relative to a goal location affects how participants weight this information. In the Stankiewicz and Kalia study, for example, the featural or geometric cue itself was the goal location, making the navigation task easily solved using a beacon homing strategy, at least once the individual was within visual range of the cue. Thus, it is not known whether the accuracy of recalling the features and the geometry, or the relative weighting of these two types of cues, would have been different if the participants had to not only navigate to these cues, but use the cues subsequently to find a goal that was located separate from the cue itself (i.e., a landmark piloting task). Our study was designed to examine how the relationship between featural and geometric cues influences the encoding and relative weighting of these two cue types.

1.3. Summary

The present study used a virtual environment to investigate two central issues concerning the influence of cue arrangement on the encoding of featural and geometric information in an orientation task by adult humans.

First, we examined whether the representation generated in training (either orientation-specific or orientation-free) would be different when participants could encode the featural cues using either a beacon homing strategy or a landmark piloting strategy (Experiment 1). To do so, we first needed to demonstrate that the participants had encoded both the featural cues (this was shown through training accuracy) and the environmental geometry (this was shown through a transformation test where all distinctive featural cues were removed leaving only the geometric properties of the environment) before we could examine the nature of representation formed.

Second, we examined whether the arrangement of featural cues relative to the goal location would influence the hierarchical ranking of the featural and geometric cues: (1) when only the featural information was manipulated from that of training, (2) when only the geometric information was manipulated from that of training, and (3) when the two types of cues provided conflicting information regarding the location of the goal.

2. Experiment 1

Experiment 1 was designed to examine two main issues. First, we were interested in examining whether the arrangement of featural cues (e.g., the color of the walls) relative to the geometric cues (e.g., the shape of the environment) would influence how accurate participants were at finding a hidden goal location. Based on featural information alone, we hypothesized that by presenting the goal at a boundary between two different featural cues (e.g., at the boundary between a red and a yellow wall segment), participants could use this featural boundary as a beacon. In contrast, by presenting the goal at a fixed position along a featural segment (e.g., along a red wall segment), participants would have to use the featural information in a landmark fashion, i.e., by encoding the direction and distance from the goal location to the featural boundary. However, if participants encoded both the featural and geometric properties of the environment, the conjoining of these cues would allow for precise localization of the goal, independent of the feature–goal relationship.

Second, once we established that on average the participants were encoding both, featural and geometric information, we investigated whether the information encoded during training would generalize to novel views of the environment when the distinctive featural cues were either present or absent. Would the absence of the distinctive featural cues influence the ability to locate the goal from a novel view, i.e., does viewpoint independency require featural cues? We investigated whether participants would be able to transfer their knowledge of the goal location from a limited number of training views, all with distinctive featural cues present, to novel views of the environment either with or without the featural cues available. We hypothesized that the participants would indeed show an orientation-free representation and that this strategy would not require the presence of distinctive featural cues, i.e., that participants would be able to transfer accurate goal-directed search.

2.1. Method

2.1.1. Participants

The participants were 35 students from the University of Nebraska-Lincoln, 19 women (with age ranging from 18 to 23 and an average age of 20.1) and 16 men (with age ranging from 18 to 31 and an average age of 19.8).

2.1.2. General procedures

Participants sat on a chair in front of a laptop computer monitor (Sony Vaio Notebook). All responses were made with a mouse, both for making choices and for proceeding to the next trial. The participants were trained and tested individually.

Once seated in front of the computer monitor, participants were told that they would see a series of images presented one at a time. In these images they would see four black squares. Their task was to determine which black square was "correct" and, using the mouse, click on that square. This would cause the image to disappear and be replaced by a feedback screen indicating whether their choice had been correct, incorrect or that no feedback was available. Once they had read the message on the feedback screen, clicking the mouse button would remove the screen and present the next image. They were told that after several trials the black squares in the images would get smaller and smaller, and would eventually disappear completely. At this point, they had to determine where they thought a black square should be and, using the mouse, click on that spot. Once the participants indicated that they had understood the instructions, the researcher started the experiment.

These instructions were formulated so as not to include any reference to spatial information, that is, words like landmarks, geometry, distance, direction, walls, and so forth were not used to ensure that the instructions would not bias the participants' encoding of the geometric and featural information. Furthermore, for comparative purposes (Kelly & Spetch, 2004; Kelly & Bischof, 2005) participants were not shown where the goal was located, but rather needed to deduce which black square was correct using the feedback provided after each trial.

2.1.3. Virtual environments

2.1.3.1. Training environments. Images of virtual environments were created using POV-Ray (2002) to depict a rectangular environment with a granite floor and cork-textured walls that were painted with different colors (see Fig. 2 for examples). On the floor, there were four identical black response patches (referred to as "black squares" in the instructions to participants), which were visible during training only. Depending on the training phase, the patches were either large, small (half the size of the large patches) or invisible (no patch). Each wall or each corner of the environment was painted a unique color (i.e., blue, green, yellow and red, in clockwise order). Images of two types of rectangular environments were generated, the Rectangular-Boundary environment, where the color boundaries and the corners of the rectangular room were contiguous, that is, each wall had a single color (Fig. 2a), and the Rectangular-Segment environment, where each corner of the room had a single color, that is, the color boundaries were located in the middle of the walls (Fig. 2b).

Eight images of each environment (i.e., Rectangular-Boundary and Rectangular-Segment environments) were created. These images depicted the environments as viewed from each of the four corners, and from the middle of each of the four walls. Each image depicted the environments from an elevated viewpoint. The images were generated with a resolution of 896 by 672 pixels, and they subtended a visual angle of 35.0° by 27.6° at the viewing distance of 40 cm.

In training, six of the images were selected from each environment. The remaining two images (namely a view from one of the corners and the view from the middle of the long wall adjacent to that corner) were used for the Novel Viewpoint tests to investigate whether the participants had encoded an orientation-specific or orientation-free representation of the environment.

2.1.3.2. Testing environments. Testing was conducted with the response patches invisible. Participants were instructed to click on the location where they thought the response patch should be positioned. Two testing conditions were administered. The first testing condition was the *Novel Viewpoint tests*, which consisted of the two test types: (a) the Novel Viewpoint With Features test, which showed images depicting the training environment from the two novel orientations not shown in training (see previous paragraph and Fig. 2c), and (b) the Novel Viewpoint Without Features test, which consisted of the same two images, but without any distinctive features present (see previous paragraph and Fig. 2d). The second testing condition was the *Geometry test*, which consisted of the six training images with all of the distinctive featural information

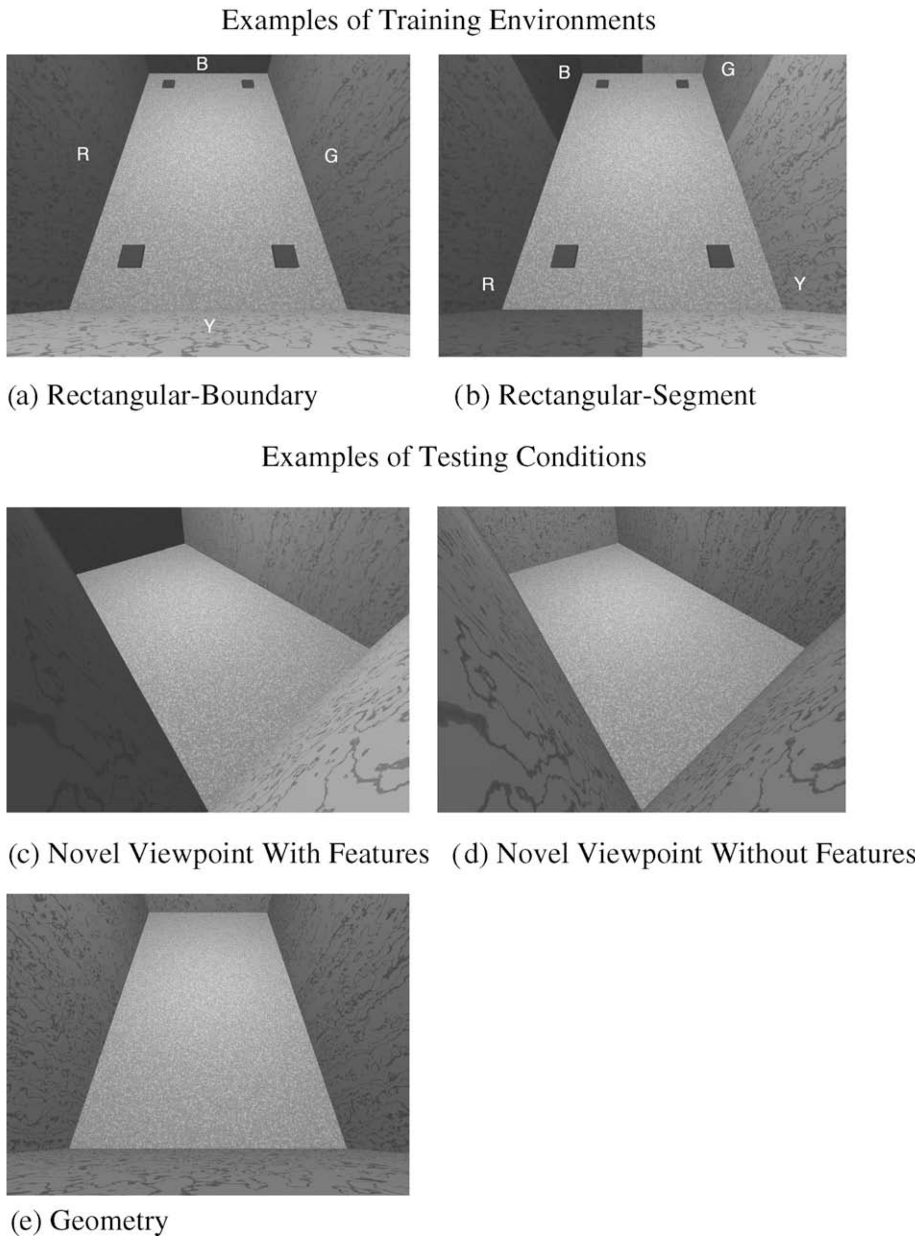

Fig. 2. Examples of the images used in training: (a) Rectangular-Boundary and (b) Rectangular-Segment. Examples of images used in testing: (c) Novel Viewpoint With Features test, (d) Novel Viewpoints Without Features test, and (e) Geometry test. The response patches shown in these images were only visible during training. The white letters indicate the color of the wall segments (R, red; B, blue; G, green and Y, yellow) and were not present in the actual stimuli.

removed, i.e., the four walls were all a uniform brick color (see Fig. 2e).

2.1.4. Training procedures

Participants were randomly assigned to one of two groups based on type of training they were to receive: group Beacon and group Landmark (see Table 1 for a description of the design). Participants in group Beacon were trained with the six images depicting the Rectangular-Boundary environments, whereas participants in group

Table 1
Summary of experimental training and testing conditions for Experiment 1

	Group Beacon	Group Landmark
Training	Rectangular-Boundary	Rectangular-Segment
Testing	Novel Viewpoint test With Features Novel Viewpoint test Without Features Geometry test	Novel Viewpoint test With Features Novel Viewpoint test Without Features Geometry test

Landmark were trained with the six images depicting the Rectangular-Segment environments. The response patch (and thus the associated featural and geometric cues) designated as correct was counterbalanced across participants. All training environments were presented with feedback. Training proceeded in three stages. In the first stage, the six images of the environments with the large response patches were presented in random order. If the participant chose correctly on 80% of the trials, s/he moved to the second training stage; otherwise the first training stage continued, and accuracy was again calculated after each additional six trials. The second training stage was identical to the first, except that the images of the environments were presented with the small response patches. Again, once the participant met the accuracy criterion s/he moved on to the third training stage; otherwise stage two training continued, and accuracy was again calculated after each additional six trials. In the third training stage, the images of the environments were shown with the invisible response patches. A response was accepted, if it was given within a radius of 150 pixels (5.9° visual angle) from a nominal patch position. If the participant chose his/her goal location correctly on 80% of the trials, s/he moved on to the testing stage; otherwise the third training stage continued, and accuracy was again calculated after each additional six trials.

2.1.5. Testing procedures

During the testing phase of the experiment three types of trials were presented: baseline trials, control trials and test trials. In the baseline trials, the training environments were presented and participants received feedback as to whether their choice was correct or incorrect. These trials were provided to continue to give participants feedback during testing (see Kelly & Spetch, 2004). During the control trials, the training environments were again presented, but participants were not given feedback as to whether their choice was correct or incorrect. These trials were used as a means of comparing non-feedback performance with the training images to performance on the testing images (which were always presented without feedback). The test trials were used to examine responding when the participants were presented with the transformed environment. The order of presentation for the test conditions was blocked; all participants were first presented with the Novel Viewpoints test (Novel Viewpoint With Features followed by Novel Viewpoint Without Features) and subsequently with the Geometry test. In total the participants received 12 baseline, 12 control, and 20 test trials (four Novel Viewpoint tests and 16 Geometry tests). The presentation order of the trials, within each testing condition, was randomized. See Table 2.

2.1.6. Data analysis

Participants' choices were analyzed as follows. Given the virtual camera parameters (i.e., position, direction and angle) and screen parameters (i.e., width and height), every response choice (the location of the participant's mouse click) was mapped onto the floor of a virtual 3D room model (Foley, van Dam, Feiner, & Hughes, 1996). Classification of responses proceeded as follows. In addition to the four positions corresponding to the response patches, four intermediate positions were defined midway between adjacent response patches. These intermediate positions corresponded to the location of the color boundaries on the walls of the Rectangular-Segment environments. Using a minimum distance criterion, responses were then classified as corresponding to one of these eight (response patch and color boundary) positions.

Table 2
Summary of experimental training and testing conditions for Experiment 2

	Group Rectangular-Beacon	Group Rectangular-Landmark
Control	Rectangular-Boundary	Rectangular-Segment
Both cues manipulated	Circular-Segment	Circular-Boundary
Shape manipulated	Circular-Boundary	Circular-Segment
Cue Conflict	Rectangular-Segment	Rectangular-Boundary

2.2. Results

A participant was classified as having failed training if s/he never achieved at least 80% accuracy in a block of eight training trials or if s/he did not achieve at least 60% accuracy averaged over all training trials. In group Beacon, one participant failed to learn the task (a woman; 462 trials). One outlier in group Beacon (a woman) was removed according to the Mahalanobis distance test because her responses were significantly different from all other participants ($T^2 = 29.4$, $p < .001$). Data of participants who failed training were not used; the following analyses are based on a total of 33 participants.

2.2.1. Featural cue arrangement

To examine whether the relationship between the featural cues and the goal location influenced the rate at which participants were able to learn the task, we compared the number of training blocks required to learn the task for the men and women in groups Beacon and Landmark. Both, the men and the women, showed no difference in the average number of training blocks required to learn the task (Men: 5.75 and 4.38 for group Beacon and Landmark, respectively, $t(14) = 0.83$, $p > .1$; Women: 5.27 and 5.67 for group Beacon and Landmark, respectively, $t(15) = 0.37$, $p > .1$).

To examine whether there were any significant differences in accuracy once the participants had learned the task, we conducted a between-subjects ANOVA examining performance accuracy during training (percent accuracy to the correct response patch), with factors group (Beacon and Landmark) and sex (Men and Women). No significant main effects or interactions were found: group [$F(1,29) = 0.02$, $p > .1$], sex [$F(1,29) = 0.96$, $p > .1$] and group × sex [$F(1,29) = 0.49$, $p > .1$]. This result indicates that participants were equally accurate at locating the goal, independent of whether the goal was positioned at the boundary of two color segments, and thus a beacon homing strategy could have been adopted, or located at a fixed position along one color segment, thus a landmark piloting strategy could have been adopted.

2.2.2. Encoding of geometry

During training, the participants could have learned the position of the goal by using the featural information alone or in combination with the geometric information provided by the shape of the environment. To examine this, we analyzed the location of responses during the Geometry test trials, in which all featural cues were removed, leaving only the environmental geometry. If the participants had encoded both types of cues we would expect that they would divide their choices equally between the two geometrically correct goal locations. If they had only encoded the featural cues, which were now unavailable, we would expect that they would randomly choose among the four possible locations. We also examined whether the position of the goal in relation to the featural information (i.e., at a boundary between two colors or at position along a color segment) influenced the encoding of featural and geometric information. For the following analyses, responses to the correct goal location and the location diagonally opposite to the correct one were summed because, according to geometric information only, these two positions are indistinguishable (see Training Section for further discussion). An ANOVA with group (Beacon and Landmark) and sex (Men and Women) as factors revealed no significant main effects or interactions: group [$F(1,29) = 0.00$, $p > .1$], sex [$F(1,29) = 0.15$, $p > .1$], group × sex [$F(1,29) = 1.53$, $p > .1$].

One-sample t-tests showed that participants in both groups were able to use geometric information to choose the two geometrically correct locations significantly above chance level [chance = 50%; $M = 69.2\%$, $t(18) = 4.67$, $p < .001$ and $M = 68.4\%$, $t(13) = 3.14$, $p < .01$, for groups Beacon and Landmark, respectively]. Furthermore both, men and women encoded geometric information when trained with distinctive features present during training [chance = 50%; $M = 68.1\%$, $t(15) = 3.55$, $p < .01$ and $M = 69.6\%$, $t(16) = 4.24$, $p < .001$, for men and women, respectively]. The left panel of Fig. 3A shows average choice when distinctive features were present (Control condition), and the right panel shows average choice when only the geometric information was available (Geometry test). When the participants were presented with the environment void of distinctive featural cues, they divided their choices equally between the two geometrically correct locations [$t(32) = 1.09$, $p > .1$, $M = 36.5\%$ and 32.3% for the correct location and the geometrically equivalent location, respectively]. Thus, when the featural information was presented on the environment's surfaces both men and women encoded geometry. This result is particularly interesting because in our previous study (Kelly & Bischof, 2005), where the featural information was presented as discrete objects, the featural information overshadowed the encoding of geometry for women. Taken together, these results show that how women encode spatial information is dependent upon how cues are presented within an environment, and this factor must be considered in future studies of spatial cue use, not only for studies of orientation, but also in studies of navigation in general.

2.2.3. Viewpoint dependency

To examine whether participants were able to transfer their spatial encoding to novel viewpoints of the same environment, we analyzed response accuracy during test trials, separately for the two types of novel testing conditions: Novel Viewpoint With Features and Novel Viewpoint Without Features. For the Novel Viewpoint With Features tests, a mixed-factor ANOVA with group (Beacon and Landmark) and sex (Men and Women) as between-subjects factors, and viewpoint (six familiar training viewpoints and two Novel Viewpoints With Features) as a within-subject factor on accuracy scores showed no effect of group [$F(1,29) = 0.03$, $p > .1$], no effect of sex [$F(1,29) = 0.92$, $p > .1$], no effect of viewpoint [$F(7,203) = 0.38$, $p > .1$], and none of the interactions were significant. Overall average accuracy for the familiar training viewpoints was 99.3%, and accuracy for the novel viewpoints was 99.9% (see Fig. 3B left panel).

For the Novel Viewpoint Without Features tests, responses to the two geometrically correct locations were summed (refer to the discussion in the Testing Section for details). A mixed-factor ANOVA with group (Beacon and Landmark) and sex (Men and Women) as between-subjects factors, and viewpoint (six familiar training viewpoints and two Novel Viewpoints Without Features) as a within-subject factor on accuracy scores showed no effect of group [$F(1,29) = 0.05$, $p > .1$], no effect of sex [$F(1,29) = 0.21$, $p > .1$], no effect of viewpoint [$F(7,203) = 1.66$, $p > .1$], and none of the interactions were significant. Overall average accuracy for the familiar training viewpoints was 68.9%, and accuracy for the novel viewpoints was 63.7% (see Fig. 3B right panel). One-sample t-tests show that accuracy for the familiar and novel viewpoints was significantly greater than chance [$t(32) = 5.59$, $p < .001$ and $t(32) = 2.87$, $p < .01$ for the familiar and novel viewpoints, respectively; chance = 50%]. Furthermore, the participants were dividing their choices equally between the two geometrically correct goal locations [$t(32) = 0.90$, $p > .1$]. Together, the results from the two types of Novel Viewpoints tests (with and without features) clearly indicate that learning was generalized from the familiar viewpoints to the novel viewpoints, both when distinctive featural information was available and when only geometric information was available during testing.

2.3. Discussion

This experiment was designed to examine two main questions: (1) Does the relationship between the goal location and the particular arrangement of featural cues influence the encoding of featural and geometric information. (2) Are participants able to generalize the information encoded from familiar training images to novel images of the environment with or without distinctive featural cues present?

Our results show that adults can easily learn to use featural properties on the surfaces of a virtual environment in order to locate a goal area. The accuracy with which participants learned the task did not depend on the arrangement of the featural cues relative to the goal location. Participants

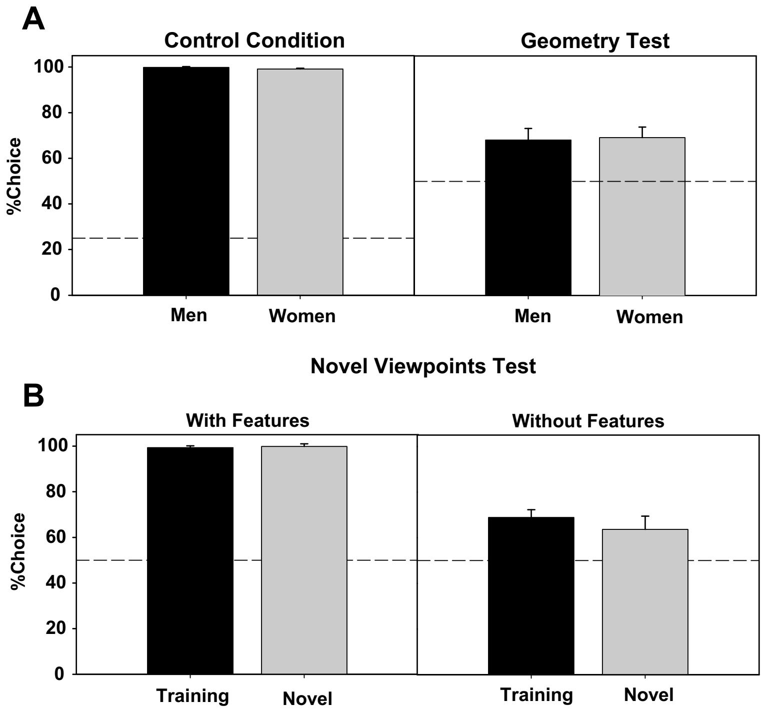

Fig. 3. (A) *Left panel:* Average percentage of choices to the correct corner by men and women for the Control condition. Error bars represent the standard errors of the mean. The dashed line indicates chance level (25%). *Right panel:* Average percentage of choices to the two geometrically correct corners by men and women for the Geometry test. Error bars represent the standard errors of the mean. The dashed line indicates chance level if the participants had encoded geometry (50%). (B) *Left panel:* Average percentage of choices to the correct corner for the familiar viewpoints and the Novel Viewpoint With Features tests. Error bars represent the standard errors of the mean. The dashed line indicates chance level of 50%. *Right panel:* Average percentage of choices to the two geometrically correct corners for the familiar viewpoints and the Novel Viewpoint Without Features tests. Error bars represent the standard errors of the mean. The dashed line indicates chance level of 50%.

who could use the boundary between two different colored segments as a beacon to direct their search (group Beacon) did not perform more accurately than participants who could not use this featural boundary (group Landmark) nor did they learn the task more quickly. This suggests that the participants may have used the environmental geometry in addition to the featural cues to learn the location of the goal. Indeed, results from the Geometry test, where all distinctive featural information was removed, indicated that the two groups were encoding the geometric properties of the environment even though, especially for group Beacon, this was not necessary to accurately locate the goal position. Thus, having a featural boundary available as a beacon cue did not enhance performance, nor did it influence encoding of the geometric cues – the ability to use featural cues did not *overshadow* the geometry.

This latter result is particularly interesting, because our earlier study (Kelly & Bischof, 2005) found that when trained with *discrete* and distinctive featural information overall women did not show an encoding of the geometric information – encoding only the featural cues. The critical difference between the two studies is the relationship between the featural and geometric information. In this study, participants were trained in virtual environments where the features were integrated with the continuous surfaces of the environment, whereas in the previous study the features were discrete objects placed in the corners of the virtual environment. We find this an intriguing finding that suggests that for women integrating featural and geometric information results in the geometric information becoming more salient. Few studies have directly compared the relative encoding of featural and geometric information by adult men and women in an orientation task, but studies examining navigation show quite robust sex differences (Astur, Ortiz, & Sutherland, 1998; Dabbs, Chang, Strong, & Milun, 1998; MacFadden, Elias, & Saucier, 2003; Sandstrom, Kaufman, & Huettel, 1998; Saucier, Bowman, & Elias, 2003), indicating that men primarily use geometric-based information whereas women show a stronger reliance on featural-based information. We would like to emphasize that we are not suggesting that women are unable to encode the geometric properties in these environments. Indeed, previous studies have shown that, when women are required to learn the geometric properties of an environment to solve a place finding task, their accuracy is comparable to men (e.g., Kelly & Bischof, 2005). What we are suggesting is that, for women, featural information might be a primary or a preferred cue type. The majority of studies to date that have examined navigational strategies have used discrete objects as featural cues. It would be interesting to investigate whether women show a shift in their reliance on featural and geometric information in navigational tasks, from a primary encoding of featural cues to an integration of features and geometry, when these cues are conjoined; the results from our current experiments suggest that this is likely.

Our findings, from this study and our previous study, show that men and women differentially encode environmental information when encoding discrete featural cues but not surface-based featural cues during an *orientation* task. These results are important in that they show that sex differences are present during orientation which is the initial step of navigation. Thus, future studies of navigation must consider how the initial encoding of spatial information during orientation influences later cue selection when individuals are navigating through an environment – this important relationship has not yet been considered. Furthermore, our studies show that we can abolish the typical sex difference by equating for spatial cue saliency. Thus, the implications of these results are not only important for our understanding of how men and women utilize spatial cues for orientation, but suggest the need to consider how orientation influences later navigational strategies by the two sexes.

Not only did the participants in this study show spontaneous encoding of the geometric properties of the environment, but they were also able to transfer this knowledge when searching for the goal from novel viewpoints either with or without featural cues. Our results are different from those found by Kelly and Spetch (2004), who trained adult participants on a similar task, but one that presented 2-dimensional (2D) schematic images rather than our 3-dimensional (3D) environments. In their study, Kelly and Spetch trained two groups of participants to locate the position of a hidden goal area; one group had featural and geometric information available, whereas the second had only geometric information available. Kelly and Spetch found two results that supported an orientation- and sense-specific encoding strategy. First, the participants in the geometry-only training environment found the task very difficult to learn, whereas the group trained with features learned easily. Second, although the group trained with features was able to rely on geometry when all distinctive featural cues were removed, this was limited to viewpoints that were seen during training; the participants were unable to generalize to novel viewpoints.

Several differences may have influenced the discrepant geometric encoding strategies in these two studies. For instance, participants in the Kelly and Spetch study were presented with 2D overhead views of a rectangular environment in images void of any relevant depth (distance) cues. In our study, participants were presented with side views from a slightly elevated viewpoint in environments containing multiple depth cues, including perspective and texture cues. The more natural viewpoints and the richer image information in our study may have been more conducive to the generation of an orientation-free representation than the schematic images presented in the Kelly and Spetch study. Indeed, previous research suggests that the type of experience with an environment may result in very different spatial representations (Sun et al., 2004). In particular, research has supported that learning a spatial layout from a survey or map perspective may favor an orientation-specific encoding, where as navigating through the environment may favor an orientation-free representation.

Our current results provide evidence for an orientation-free spatial representation, consistent with the conclusions of our earlier study (Kelly & Bischof, 2005). In our previous study, as in Kelly and Spetch (2004), two groups of participants were trained to locate a hidden goal in images of a rectangular environment. One group was shown the environment void of distinctive featural cues, whereas the other group had uniquely colored and shaped objects located in each corner. Similar to the present study, participants viewed the rectangular environment from an elevated viewpoint and many depth cues were available. We concluded in that study that the participants did not use separate viewpoint dependent codes for encoding the geometric information, when trained with either geometry alone or in conjunction with featural cues. However, this conclusion was based on indirect evidence related to the ease with both groups were able to learn the task, compared to the group differences reported by Kelly and Spetch. In contrast, the present study provides direct evidence for the conclusion that participants encoded the geometric (and featural) properties into an orientation-free representation.

3. Experiment 2

In Experiment 1, we examined how the spatial arrangement of featural cues relative to a goal location influenced place learning by adults orienting within a virtual environment. We found that participants showed similar localization accuracy when the goal was located along the length of a featural cue (landmark cue), as when the goal was located at the boundary between two different featural cues (the boundary acting as a beacon). The similarity in number of trials to learn the task, the performance accuracy once the task was learned, and the responses during the transformation tests (i.e., Geometry test and the Novel Viewpoint tests) support the conclusion that the participants in both groups were encoding the featural cues on the walls of the environment and the geometric properties from the shape of the environment itself to locate the goal.

The participants in Experiment 1 needed to encode the featural information in order to successfully pass the training requirements. Transformation tests showed that they also encoded the geometric properties. However, we did not specifically examine the extent to which the geometric information may have been used to guide or focus the participants' goal-directed search behavior. For instance, were the participants in group Landmark learning to search in the corner (a geometric property) that contained the correct featural information, or learning to search at an absolute distance along a segment of color? All training and testing environments were rectangular-shaped and thus informative geometric information was always available to guide search behavior – there was never a situation where the participants were required extract metric information from features alone in order to locate the goal. Thus, in Experiment 2 we examined the search accuracy in environments void of informative geometry through the use of isotropic circular environments.

Furthermore, in the testing conditions of Experiment 1, either (a) the featural and geometric information were available and in agreement as to the location of the goal (i.e., Novel Viewpoint With Features test), or (b) only the geometric information was available (i.e., Novel Viewpoint Without Features test and the Geometry test). Therefore, although we were able to show that the two groups were using both featural and geometric information to locate the goal we were unable to examine whether the two groups relied to different degrees on the featural and geometric cues. Although previous studies have examined whether pretraining with one cue type influences relative weighting of featural and geometric cues in subsequent testing situations (e.g., Kelly et al., 1998) few studies have examined how the *spatial* relationship between these cues, during training, influences relative cue use in orientation tasks.

Therefore, Experiment 2 was designed to examine two main questions. First, would the participants continue to show accurate goal-directed search behavior when the informative environmental geometry was removed, requiring them to use only featural information? We hypothesized that both groups would show very accurate performance when tested with only the featural information available to guide their choices. Second, would the two groups weight featural and geometric cues differently? We hypothesized that the spatial relationship between featural and geometric cues would have a significant influence on the relative cue use during testing conditions in which featural and geometric information provided conflicting information regarding the goal location. We expected that, in the Cue Conflict tests, the participants trained to find the goal at a featural boundary (group Beacon) would rely more strongly on featural cues than the participants trained to find the goal along a featural segment (group Landmark).

3.1. Method

3.1.1. Participants

The participants were 32 students from the University of Nebraska-Lincoln, 16 women (with age ranging from 18 to 22 and an average age of 21.4) and 16 men (with age ranging from 18 to 31 and an average age of 21.6).

3.1.2. General procedures

The general procedures were identical to the those used in Experiment 1.

3.1.3. Virtual environments

The environments were similar to those used in Experiment 1, so only the differences are described here. Two sets of environments were created: rectangular virtual environments (anisotropic) and circular virtual environments (isotropic). The rectangular environments were identical to the training environments used in Experiment 1 (i.e., Rectangular-Boundary and Rectangular-Segment, see Fig. 4a and e for group Beacon and group Landmark, respectively). The two types of circular environments were generated to be used in testing, type Circular-Boundary (see Fig. 4c and f), which had shorter blue and yellow segments and longer red and green segments (in proportion to that of the Rectangular-Boundary environments), and type Circular-Segment (see Fig. 4b and g), which had shorter red and green segments and longer blue and yellow segments (in proportion to that of the Rectangular-Segment environments). The ratio of short to long walls was 7:12, matching the ratio of short to long walls in the rectangular environments, and the order of colors segments was also the same, namely red, blue, green, and yellow, in clockwise order. The diameter of the circular environment was chosen such that the walls coincided with the corners of the rectangular environment. As the circular environments were only used in testing the response patches were invisible in these environments.

3.1.4. Training procedures

Training procedures were identical to Experiment 1, with the exception that the participants were trained on all eight viewpoints (rather than six as in Experiment 1).

3.1.5. Testing procedures

As in Experiment 1, during the testing phase of the experiment three types of trials were presented: baseline trials, control trials and test trials. The rationale for using these three types of trials was identical to that described in Experiment 1. In the baseline trials, all eight training environments (based on group affiliation) were shown, and participants received feedback as to whether their choice was correct or incorrect. In the control trials, the same eight training environments were shown but participants were not given feedback. In the test trials, the three novel environments were shown (i.e., group Beacon was tested with the Rectangular-Segment, Circular-Boundary and Circular-Segment environments, whereas group Landmark was tested with the Rectangular-Boundary, Circular-Boundary and Circular-Segment environments. Each of the three environments was shown from eight different viewpoints) and no feedback was given. The order of presentation was randomized, and each of the three testing environments was presented a total of three times.

The testing conditions allowed for the examination of the relative weighting of the featural and geometric cues by manipulating each cue in isolation or by manipulating both cues simultaneously. This resulted in three types of cue manipulation tests: (a) both featural and geometry manipulation tests, (b) geometry manipulation tests (which we will refer to as "shape manipulation test" so as not to be confused with the Geometry test in Experiment 1) and (c) featural manipulation tests (referred to as the Cue Conflict test as explained later).

Transformation tests, which manipulated both the featural and geometric information, presented images of the virtual environment in which the shape of the environment was changed from rectangular to circular, and the length and absolute location of the color segments was modified. Specifically, the length of the color segments was changed to specifications of the other group – i.e., the length of the color segments used in training for group Beacon was presented to group Landmark (but in a circular room) and group Landmark was shown the length of the color segments used in training for group Beacon (but in

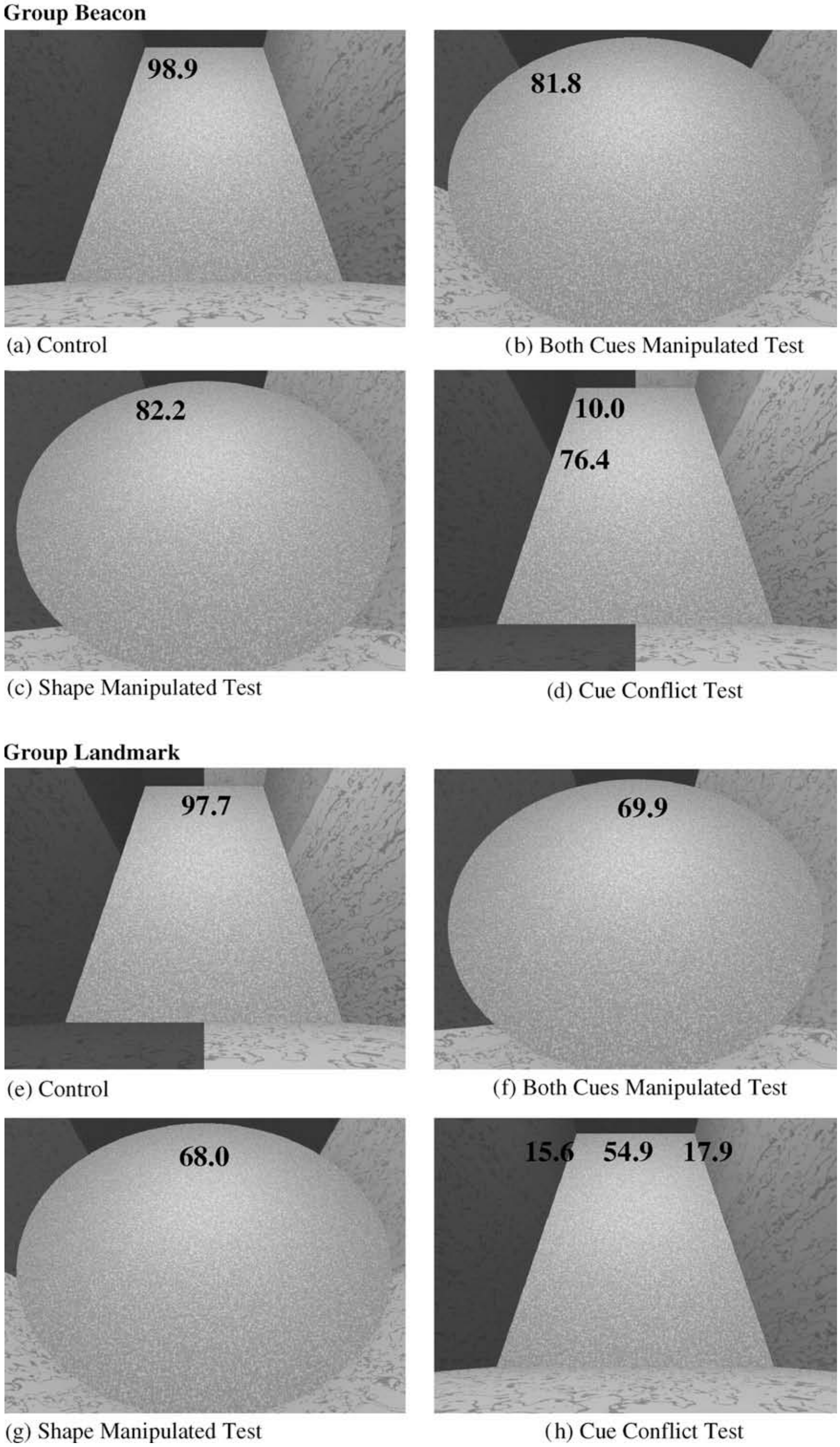

Fig. 4. *Top panel:* Examples of the images for group Beacon in (a) control, (b) both cues manipulated, (c) shape manipulated, and (d) Cue Conflict test. *Bottom panel:* Examples of the images for group Landmark in (a) control, (b) both cues manipulated test, (c) shape manipulated test, and (d) Cue Conflict test. All of these examples are illustrated from the same viewpoint. The values are average percent choice to each location for the group. Although the correct location was counterbalanced across participants, for illustrative purposes all values have been transposed such that uppermost-left corner for group Beacon is the correct goal location and uppermost feature boundary for group Landmark is the correct goal location. Only values greater than 10% are shown.

a circular room). This manipulation test allowed us to examine search behavior when the geometric and featural properties were manipulated from that of the training arrangement.

Shape manipulation tests changed only the geometric shape of the environment. Thus, the shape of the environment was changed from rectangular to circular but the arrangement and lengths of the featural segments remained as in training.

Finally, featural manipulation tests changed only the featural information. The testing environment was rectangular as in training, but the length of the color segments were changed to specifications of the other group (i.e., the length of the color segments used in training for group Beacon was presented to group Landmark, and group Landmark was shown the length of the color segments used in training for group Beacon). This test is particularly interesting because it sets up a conflict situation – therefore, we will refer to this test herein as the Cue Conflict test. Based on the geometric information the participants should search in one of the geometrically correct corners (as encoded during training). However, the featural information now indicates that the goal position should be along one of the walls, not in a corner. Thus, if the participants weighted the geometric cues more heavily than the features we would expect them to divide their choices between the two geometrically correct corners as learned during training, but if they weighted the featural information more heavily than the geometry they should search at the point along the wall where the featural cues matched that of training (i.e., at the correct featural boundary for group beacon and at the correct distance along the featural segment for group Landmark).

3.1.6. Data analysis

The data analyses were the same as in Experiment 1.

3.2. Results

As in Experiment 1, a participant was classified as having failed training if s/he never achieved at least 80% accuracy in a block of eight training trials, or if s/he did not achieve at least 60% accuracy averaged over all training trials. None of the participants failed to learn the task nor were any of the participants considered outliers in this experiment.

3.2.1. Influence of featural cue arrangement

As in Experiment 1, to examine whether cue arrangement influenced the rate at which participants were able to learn the task, we compared the number of training blocks required to learn the task for the Men and Women in groups Beacon and Landmark. Both, men and women, showed no difference in the average number of training blocks required to learn the task [Men: 12.0 and 5.75 for group Beacon and Landmark, respectively, $t(14) = 1.27$, $p > .1$; Women: 7.38 and 7.63 for group Beacon and Landmark, respectively, $t(14) = 0.07$, $p > .1$].

To examine whether there were any significant differences in accuracy once the participants had learned the task, we conducted a between-subjects ANOVA examining performance accuracy during training, with factors group (Beacon and Landmark) and sex (Men and Women). No significant main effects or interactions were found: group [$F(1,28) = 3.10$, $p > .05$], sex [$F(1,28) = 0.42$, $p > .1$] and group × sex [$F(1,32) = 3.79$, $p > .05$]. As in Experiment 1, this result indicates that participants were equally accurate at locating the goal, independent of whether the goal was positioned at the boundary of two color segments or located at a fixed position along one color segment.

3.2.2. Cue weighting

We examined how the two groups weighted featural and geometric cues by conducting three manipulation tests (to be compared to the Control condition). A between-subjects ANOVA was conducted on overall accuracy scores with factors group (Beacon and Landmark) and cue manipulation test (control, both cues manipulated, shape manipulated, cue conflict). The analysis revealed a marginally significant main effect of group [$F(1,28) = 4.17$, $p = .05$] a main effect of cue manipulation test [$F(3,84) = 26.83$, $p < .001$] and a marginally significant interaction of group by cue manipulation test [$F(3,128) = 0.17$, $p = .07$].

To better understand how the groups were being influenced by the cue manipulations, we conducted two separate ANOVAs, one for each group, analyzing the main effect of the cue manipulation tests. Newman–Keuls Multiple Comparison tests were conducted following significant F ratios to examine differential responding during the cue manipulation tests.

For group Beacon, a one-way ANOVA showed a significant main effect of cue manipulation test [$F(3,64) = 9.08$, $p < .001$]. Although, the majority of choices were directed to the location where the featural cues matched that of training, the percentage of featurally-directed choices was significantly greater during the control trials than during all the cue manipulation tests, which were not significantly different from each other (M = 98.9%, 82.2%, 81.8% and 76.4%, for control, both cues manipulated, shape manipulated and cue conflict, respectively; see Fig. 4a, b, c and d, as well as Fig. 5). Thus, manipulating the geometric information (i.e., the shape of the environment), or both featural and geometric information, or placing the featural and geometric cues in conflict caused a drop in featurally-guided choices compared to the training environment. In

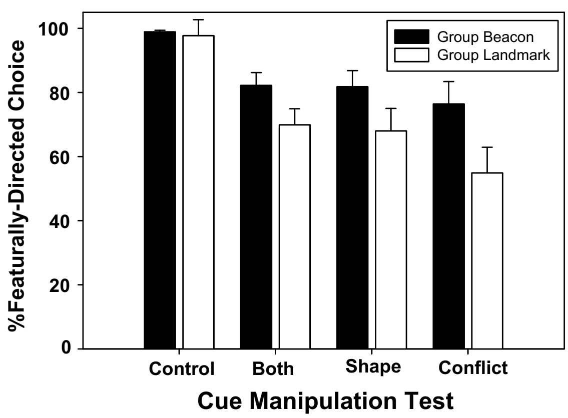

Fig. 5. Average percentage of featurally-directed choices during the cue manipulation tests (control, both cues manipulated, shape manipulated and Cue Conflict test) for group Beacon and group Landmark. Error bars represent the standard errors of the mean.

all cases, however, the participants followed the correct featural cue arrangement even when it was in a geometrically incorrect location or in a room with a novel shape.

For group Landmark, a one-way ANOVA showed a significant main effect of cue manipulation test [$F(3,64) = 19.10$, $p < .001$]. Accuracy was significantly greater during the control trials than during any of the cue manipulation tests, and it was lowest during the tests that placed the geometric and featural cues in conflict ($M = 97.7\%$, 69.9%, 68.0% and 54.9%, for control, both cues manipulated, shape manipulated, and cue conflict, respectively; Fig. 4e, f, g and h, as well as Fig. 5). Thus, manipulating the geometric information or the featural and geometric information together caused a drop in featurally-guided choices compared to the training environment. Placing the geometric and featural cues in conflict caused the most significant disruption of featurally-guided choices.

3.2.3. Cue Conflict tests

The Cue Conflict tests allowed for an examination of how the participants in the two groups weighted geometric and featural cues when these cues give conflicting information regarding the goal location. Specifically, group Beacon was trained in the Rectangular-Boundary environment, where the goal was always located at one corner of the environment (geometric information) which contained a feature boundary (featural information). In testing, this group was presented with the Rectangular-Segment environment where the geometric information still indicated the goal was located in one of the corners, but the featural information now indicated that the goal was located along one of the walls (see Fig. 4d for group Beacon for an example). The opposite was true for group Landmark, which was initially trained in the Rectangular-Segment environment, where the goal was located at one corner of the environment (geometric information) but the corner always provided only one color cue (featural information). In testing, this group was presented with the Rectangular-Boundary environment where the geometric information still indicated the goal was located in one of the corners, but the featural information now indicated that the goal was located along one of the walls (see Fig. 4h for group Landmark for an example). Therefore, we examined featurally-guided choices and geometrically-guided choices to understand whether the two groups showed differences in how the featural and geometric cues were weighted when the two cue types provided conflicting information.

Paired *t*-tests showed that the two groups differed in the percentage of choices directed at the featurally correct corner [$t(15) = 2.18$, $p < .05$, 76.4% and 54.9% for group Beacon and Landmark, respectively]. Both groups showed a similar secondary peak of responses to the geometrically correct corner that was closest to the featurally correct corner [$t(15) = 1.06$, $p > .05$, 10.6% and 17.9% for group Beacon and Landmark, respectively]. However, group Landmark also searched at the geometrically incorrect corner which contained partially-correct featural information (15.6%). Interestingly, for group Landmark, choices to these two corners were not significantly different from each other [$t(15) = 0.37$, $p > .05$]. This suggests that, for group Landmark, the majority of choices were directed to the correct location according to featural information (even through this location was geometrically incorrect), but the geometric information surrounding the correct feature controlled choices more so than for group Beacon.

3.3. Discussion

The relative spatial arrangement of featural and geometric information provided in the two different training environments did not influence the accuracy or number of training blocks required to learn the task, in either Experiment 1 or 2. However, the transformation tests conducted in Experiment 2 show that initial training influenced how the two groups of participants weighted featural and geometric cues.

The search behavior of the participants during the Cue Conflict tests is surprising in light of previous studies that have used Cue Conflict tests (or affine transformations) to examine the weighting of featural and geometric cue use. Kelly and Bischof (2005) reported that both, men and women, showed a strong reliance on featural cues when reorienting in a virtual environment. Furthermore, the majority of non-human animal studies that have conducted Cue Conflict tests have likewise shown a strong weighting of featural cues (e.g., Vallortigara et al., 1990 or Kelly et al., 1998 who examined the influence of training on the weighting of featural and geometric information). In these previous studies, geometrically-guided choices were in the form of systematic rotational errors as defined by Cheng (1986), choices to the two corners equivalent in regards to metric plus sense properties (e.g., both geometrically correct corners have a long wall to the right and a short wall to the left). The results of our study differ in that the geometrically correct but featurally incorrect corner was rarely chosen at all. Although the participants had encoded the geometric properties of the environment, when presented with a conflict test most searching was directed to the location containing the correct featural information, even when it was geometrically incorrect. For group Landmark, this was followed by a secondary peak of searching at the two corners (local geometry) with partially-correct featural information. However, for group Beacon the majority of searches was directed to the featural boundary. It is likely that the participants in this group learned the goal location using a combination of featural information and sense (i.e., the distinction between left and right), without actually encoding the metric information supplied by the length of the walls (Sovrano & Vallortigara, 2006). Therefore, during the conflict test the participants searched primarily at the location that had the correct arrangement of featural cues (e.g., red wall to the left and blue wall to the right). Group Landmark would not have been able to use this type of strategy because the encoding of metric information was required to learn the location of the goal during training. Thus, although the two groups of participants responded in very similar ways during training and with geometric manipulations, subtle differences were seen when featural and geometric information were placed in conflict requiring the participants to weight the spatial cues; this indicates that the representations formed by the two groups differed and were influenced by the initial cue–goal relationship learned at training.

4. General discussion

The present study was designed to investigate two central issues concerning the encoding of featural and geometric cues by adult humans orienting in a virtual environment. In order to examine these issues we first established whether participants in both the Landmark group and the Beacon group would encode the featural and geometric information when learning to relocate the hidden goal area. In doing so, we further examined whether the arrangement of featural cues relative to a goal location would influence how accurately and how quickly the participants would learn an orientation task. To investigate the issue of viewpoint specificity of the representation formed when learning the location of the goal we examined whether the arrangement of featural cues in relation to the goal would influence whether the representation generated at training was orientation-specific or orientation-free, and subsequently whether this representation would include both featural and geometric information (Experiment 1). To investigate the issue of cue weighting, we explored how the relationship between featural information and a goal location would influence the relative weighting of featural and geometric cues when these cues were manipulated or provided conflicting information regarding the goal location (Experiment 2).

4.1. Arrangement of featural cues relative to the goal

Overall, reliance on featural information was stronger than reliance on geometric information. This result is similar to our previous findings obtained in rooms with discrete featural cues (Kelly & Bischof, 2005). Experiment 1 showed that both groups learned to locate the goal area with similar speed and accuracy, indicating that the relationship between the featural information and the goal did not influence place learning in our task. Furthermore, the geometric transformation test presented to the participants in Experiment 1 showed that both groups encoded the geometric properties of the environment when trained to find the goal in a room with distinctive featural cues. Thus, the ability to use either featural or geometric cues was similar for both groups.

In our investigation of whether both groups of participants would encode the geometric properties of the environment when trained with distinctive features, we found an interesting result: both, men and women, showed an encoding of the geometric properties during training. This finding is significant because in our previous study women did not encode geometry when trained with distinctive features available (Kelly & Bischof, 2005). In this previous study the featural cues were discrete objects placed in the corners of the environment, whereas in the present study the featural cues were integrated with the geometric cues. Thus, the integration of featural and geometric information is the critical factor accounting for the different encoding strategies used by women. Many studies that have examined the use of environmental cues by men and women suggest that women rely more strongly on objects or landmarks for navigating, whereas men rely more on cardinal directions (e.g., Astur et al., 1998; Dabbs et al., 1998; MacFadden et al., 2003; Sandstrom et al., 1998; and Saucier et al., 2003). Thus, having the featural information integrated with the geometric information likely caused the geometry to become more salient for the women. In contrast, when featural information was provided by discrete objects, which were independent of the geometric cues, the featural cues overshadowed the environmental geometry. It is important to consider that by changing cue saliency we were able to abolish the typical sex difference in spatial cue use. Furthermore, future studies examining sex differences in spatial cue use during navigational tasks must take into consideration whether or not men and women are *orienting* using different cues, and whether subsequent sex differences for navigation are stemming from this initial step within the navigational process.

4.2. Spatial representations

Many studies have examined whether adult humans develop an orientation-specific or an orientation-free representation when they learn a particular spatial layout. Investigations of spatial navigation typically support the conclusion that people generate orientation-specific spatial representations when learning a spatial layout through the use of a map (survey learning), and that they are more accurate and faster at locating a position when they are in the same spatial orientation as in training. This finding is commonly referred to as the *alignment effect* (e.g., Rossano & Warren, 1989; Warren, Rossano, & Wear, 1990). However, when people are asked to learn a route by navigating through an environment, the spatial layout may be encoded in an orientation-free representation. Two theories that attempt to explain these differences in the encoding of spatial information focus on different aspects of the spatial experience. The *multiple vantage points theory* (Sun et al., 2004) argues that, when a spatial environment is learned from only one perspective, an orientation-specific representation is built, and that multiple views of the scene are necessary to develop a orientation-free representation. The *primary learning theory* (Sun et al., 2004) focuses on the proprioceptive experience of the navigator. Proponents of this theory argue that, for an orientation-free representation to be constructed, the navigator must be engaged in active navigation, i.e., the person must actively locomote through the environment. If the navigator is passive (i.e., the navigator is stationary but the environment is rotated or translated), the person will represent the environment in an orientation-specific manner.

With these two theories in mind, it is curious that our participants developed orientation-free representations in a passive, survey-like task: accuracy was not reduced when participants needed to find the goal location from a viewpoint that differed from the original training views. Two aspects of our experiments may have encouraged an orientation-specific representation. First, our images were presented in a survey-like fashion; the entire environment could be seen from each viewpoint, much like typical map-learning or survey-learning tasks (for further discussion see Siegel, 1981). Second, the participants passively learned the spatial layout. Indeed, orientation-specific encoding has been shown in an orientation procedure using a survey task with passive navigation (Kelly & Spetch, 2004). However, our study differed from the typical survey approach in several ways that may have encouraged an orientation-free representation. First, our images were detailed pictorial representations of an environment, not schematic or line drawing representations of the spatial layout. Second, participants were asked to locate a goal in an environment with a very simple geometry, a rectangle. Perhaps, the combination of pictorial richness and environmental simplicity may have allowed the participants to more easily form an allocentric representation of the environment.

4.3. Cue weighting

Previous studies have shown that human and non-human animals may encode several types of cues when remembering the location of a goal. However, these cues tend to be relied upon in a weighted fashion. In this study, we found that adults encoded featural and geometric cues when searching for a hidden goal in a virtual environment. Through the use of cue manipulation tests, we found that participants showed primary control by the featural cues. However, the arrangement of the featural cues relative to the goal location during training (i.e., Beacon vs. Landmark) influenced the relative cue weighting when the featural and geometric cues provided conflicting information regarding the goal location (Cue Conflict tests, Experiment 2). This result is particularly informative considering that the two groups required a similar number of training trials to learn the task and did so to similar accuracy levels. These results support previous research showing that the nature of the representation formed depends on whether a beacon homing strategy or a landmark piloting strategy is adopted.

An intriguing question arises from our study: could the participants have encoded the local *geometric* information (i.e., the angular information of the corners, see Tommasi & Polli, 2004) using a beacon homing strategy or a landmark piloting strategy? Although our study aimed at investigating how the featural cues were encoded, similar questions could have been asked about how the geometric information was represented. Although the participants showed a strong encoding of the featural cues, it is possible that the participants in group Landmark may have encoded the local geometry using a beacon homing strategy (i.e., search at a corner) – this explanation may account for the secondary search peaks directed to the two corners on either side of the correct feature during the Cue Conflict tests in Experiment 2. This question could be addressed by adopting similar training procedures to those used in our study, but designed to investigate the encoding of geometric information using a beacon homing strategy or a landmark piloting strategy.

Our study was designed to examine the relative importance of featural and geometric information for men and women orienting in a virtual environment. We found that although featural information is weighted more heavily than geometry, geometry still plays a critical role. Indeed the relationship between geometric and featural information depends strongly one's initial experience with an environment and relative cue informativeness. We also found that men and women rely on featural and geometric information to differing degrees. Although this is a robust result reported in many studies of human navigation, our results are particularly unique because they show that sex differences, in preferred cue use, are present at the very initial step of navigation – orientation. However, our study goes beyond a simply geometric–feature categorization of cue use by men and women, and shows how the reliance on these cues is dynamically influenced by other variables. We are encouraged that the adoption of similar fine-grained analyses in studies of spatial cue use will be an important, and necessary, step for understanding the complex relationship of human spatial navigation.

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