ORIGINAL ARTICLE

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Evidence against integration of spatial maps in humans

Abstract A dynamic 3-D virtual environment was constructed for humans as an open-field analogue of Blaisdell and Cook's (2005) pigeon foraging task to determine if humans, like pigeons, were capable of integrating separate spatial maps. Participants used keyboard keys and a mouse to search for a hidden goal in a 4×4 grid of raised cups. During Phase 1 training, a goal was consistently located between two landmarks (Map 1: blue T and red L). During Phase 2 training, a goal was consistently located down and left of a single landmark (Map 2: blue T). Transfer trials were then conducted in which participants were required to make choices in the presence of the red L alone. Cup choices during transfer assessed participants' strategies: *association* (from Map 1), *generalization* (from Map 2), or *integration* (combining Map 1 and 2). During transfer, cup choices increased to a location which suggested an integration strategy and was consistent with results obtained with pigeons. However, additional analyses of the human data suggested participants initially used a generalization strategy followed by a progressive shift in search behavior away from the red L. This shift in search behavior during transfer was responsible for the changes in cup choices across transfer trials and was confirmed by a control condition. These new analyses offer an alternative explanation to the spatial integration account proposed for pigeons.

Keywords Virtual Environment · Human · Spatial · Cognitive Map · Integration

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Introduction

Since Tolman (1948), cognitive maps have been rigorously investigated in a variety of species including bees (Dyer 1991; Gould 1986; Wehner and Menzel 1990), chimpanzees (Menzel 1973, 1978), dogs (Chapuis and Varlet 1987), monkeys (Cramer and Gallistel 1997; Gallistel and Cramer 1996), pigeons (Cheng 1988), and rats (Keith and McVety 1988; Leonard and McNaughton 1990). Despite diverse differences in theoretical conceptions of a cognitive map (e.g., Gallistel 1990; O'Keefe and Nadel 1978; Thinus-Blanc 1988; Tolman 1948), novel short-cutting is generally taken as evidence of control by this representation. However, results in favor of a cognitive mapping hypothesis have been plagued by other explanations to novel short-cutting. These explanations generally fall into three categories (for a review see Bennett 1996): (1) the novel short-cut is not actually novel; (2) familiar landmarks are being recognized from a novel location; and (3) path integration is being used. Failure to rule out these alternatives to the cognitive mapping hypothesis has led some to suggest that no evidence exists in any species for the existence of cognitive maps (e.g., Bennett 1996; Shettleworth 1998, p. 317).

Recently, however, Blaisdell and Cook (2005) reported evidence for the integration of two independently learned spatial maps in pigeons while purportedly eliminating and/or controlling for alternate explanations. Using an open-field procedure, pigeons searched for a goal cup containing hidden food in a 4×4 grid of raised cups. The aforementioned alternatives to the cognitive mapping hypothesis were addressed by varying the goal location about the search space during training, eliminating training cues during testing, and testing for a novel landmark-goal vector. Specifically, in two separate training phases, differing landmarks were located in a consistent spatial relationship with food. During the first phase of training food was consistently located between two landmarks: a blue T and a red L (Map 1). During the second phase of training, food was consistently located down and left of a blue T (Map 2).

After initial training, transfer trials were conducted to test for integration of spatial information (i.e., combination of Map 1 and Map 2). Transfer trials consisted of presenting the red L from Map 1 training alone. Choices to the cup left of the landmark (i.e., Association cup) were interpreted as resulting from an association from Map 1 training because during Map 1 training the goal was consistently located to the left of the red L. Choices down and left of the landmark (i.e., Generalization cup) were interpreted as resulting from the generalization of Map 2 training to the red L because pigeons may have treated the red L as the blue T. Finally, choices down and two cups to the left of the landmark (i.e., Integration cup) were interpreted as resulting from an integration of Map 1 and Map 2 training because in the presence of the red L pigeons may have inferred the location of the blue T from Map 1 training and responded to the goal location predicted by this landmark from Map 2 training. By encoding landmark-landmark vectors during training, as suggested by Cheng (1995) and Spetch et al. (1996, 1997), and utilizing vector addition during testing, as suggested by Cheng (1989), pigeons may have been able to infer this novel spatial relationship between the red L and the "goal." Such a spatial inference based upon the integration of independently learned spatial maps would suggest the formation of an allocentric representation of space.

Initial results revealed pigeons utilized a generalization strategy that later shifted to an integration strategy. Specifically, in the first of two transfer tests, two Map 2 training trials preceded each of three separate presentations of red L transfer trials. Pigeons selected the Association and Generalization cups more than the Integration cup; thus, failing to provide evidence for integration. However, Map 2 pre-transfer trials may have controlled transfer performance because of their temporal proximity to the initial transfer trials. Because of the extended period of time between Map 1 training and initial transfer testing (i.e., a few months), a second test was conducted. In this second test, one Map 1 training trial (which served as a "reminder" trial to reactive the memory of Map 1) and one Map 2 training trial preceded each of two separate presentations of red L transfer trials. Pigeons then selected the Integration and Association cups more than the Generalization cup; the increased Integration cup choices from the first to second test provided evidence for integration.

Would humans, like pigeons, spatially integrate two independently learned spatial representations? The goal of the present study was aimed at conducting a conceptual replication of the procedure from Blaisdell and Cook (2005) with humans in a dynamic 3-dimensional (3-D) virtual environment. While numerous studies have been conducted using static 2- or 3-dimensional images to investigate spatial cognition in humans and/or pigeons (e.g., Cheng and Spetch 1995; Kelly and Bischof 2005; Kelly and Spetch 2004a, 2004b; Lechelt and Spetch 1997; Spetch 1992, 1995, 1996, 1998; Spetch and Mondloch 1993; Spetch and Wilkie 1994; for a review of the pigeon literature see Cheng et al. 2006) relatively few have employed the use of dynamic 3-D environments in testing humans. Dynamic three-dimensional environment-creating software has provided a new tool to fill this void (for review see Loomis et al. 1999; Stanney 2002). Research utilizing such software has been gaining in popularity because the resulting environments allow for ease in experimental manipulation, control of experimental design, and maintenance of ecological validity (for a review see Loomis et al. 1999; Péruch and Gaunet 1998). Further, the mechanisms used in navigating dynamic 3-D virtual environments have been argued to be similar to those used in navigating natural environments (Arthur et al. 1997; Hartley et al. 2003; Montello et al. 2004). Hence, dynamic 3-D virtual environments may be ideal for testing spatial mechanisms in humans and permitting comparisons across species.

In the present experiment, three separate groups of humans were tested: Reminder, No Reminder, and Integration Control. The Reminder group served as a replication of the procedure from Blaisdell and Cook (2005) in a dynamic 3-D virtual environment. The No Reminder group served to determine if reminder trials were necessary for humans to integrate spatial maps, as the initial transfer test with pigeons produced no evidence of spatial integration due to the presentation of only Map 2 training trials before transfer trials. Absence of an integration strategy was suggested to have resulted from an inability of the pigeons to retrieve the landmark-landmark vector encoded during Map 1 training which was in part due to the large length of time between Map 1 training and testing. Hence, "reminder" trials from Map 1 training, presented before each transfer trial, were necessary for pigeons to select the Integration cup. To test whether such reminder trials were necessary for humans to integrate spatial maps, Map 1 trials were replaced with Map 2 trials during testing for the No Reminder group. Humans will likely learn the training phases more rapidly than pigeons. If so, only minutes, as opposed to months, will elapse between training and testing for humans as compared to pigeons. As a result, human participants' memory of the Map 1 landmark-landmark vector should remain salient, and reminder trials should be unnecessary to reactive this memory from training. If rapid learning occurs humans may be guided by an integration strategy early during testing (i.e., transfer Trial 1), and reminder trials should only serve to strengthen the probability of the use of this strategy. The Integration Control group served to eliminate integration of spatial maps by presenting a novel landmark during testing (green X). A novel landmark could neither indicate a trained landmark-goal vector nor a trained landmark-landmark vector and therefore eliminated its individual or inferential use for determining accurate goal location. As a result, selection of the Integration cup by participants in this group could not be due to a spatial integration mechanism.

Method

Participants

Nine male Auburn University students (mean age = 25.5 years) were used as participants. Participants received extra credit for participation in the experiment.

Apparatus

A computer generated dynamic 3-D virtual environment was constructed and rendered using Valve Hammer Editor (Version 3.4) and run on the Half-Life Team Fortress Classic platform (Version 1.1.1.0). A custom-built personal computer with a 2.06-GHz processor (AMD 2600 +), 64MB video card (NVIDIA GeForce MX440), 17-inch flat-screen CRT monitor (KDS), optical mouse (Logitech), quiet-touch keyboard (Logitech), and speakers (Sound-Blaster) served as the interface for the virtual environment. The monitor (1152×864 pixels) provided participants with a first-person perspective of the virtual environment. In first-person perspective, the monitor represents a view from the perspective of the participant within the virtual environment; therefore, it represents a view of the virtual environment that is analogous to an individual's view of the natural environment. The arrow keys of the keyboard, the mouse, and the right mouse button served to navigate within the environment. Speakers emitted auditory feedback to participants.

An identical second personal computer was utilized as the server for the virtual environment. This computer recorded first- and third-person perspectives of the participants' movements within the virtual environment. In third-person perspective, the monitor represents an overhead view of the virtual environment. All experimental events were controlled and recorded using Half-Life Dedicated Server (Version 1.1.1.0) and Half-Life Television (Version 1.1.1.0) on this second personal computer.

Stimuli

All dimensions are length × width × height and measured in virtual units (vu). Virtual units are the unit of measurement used by the Valve Hammer Editor software. The virtual environment consisted of two rooms. The first room ($1280 \times 1024 \times 864$ vu) contained a raised path that participants needed to successfully traverse to an exit sign. The second room ($568 \times 544 \times 416$ vu) contained 16 raised cups ($58 \times 58 \times 40$ vu) in a 4×4 grid (see Fig. 1). The room was well-illuminated by an unseen light source located in the center of the room 64 vu below the ceiling. The wall opposite the start location (labeled S in Fig. 1) was noticeably darker than the other three walls of the room. A red L ($48 \times 48 \times 43$ vu), blue T ($48 \times 48 \times 43$ vu), green X ($48 \times 48 \times 43$ vu), red cylinder ($48 \times 48 \times 85$ vu), and blue cylinder ($48 \times 48 \times 85$ vu) were used as landmarks.
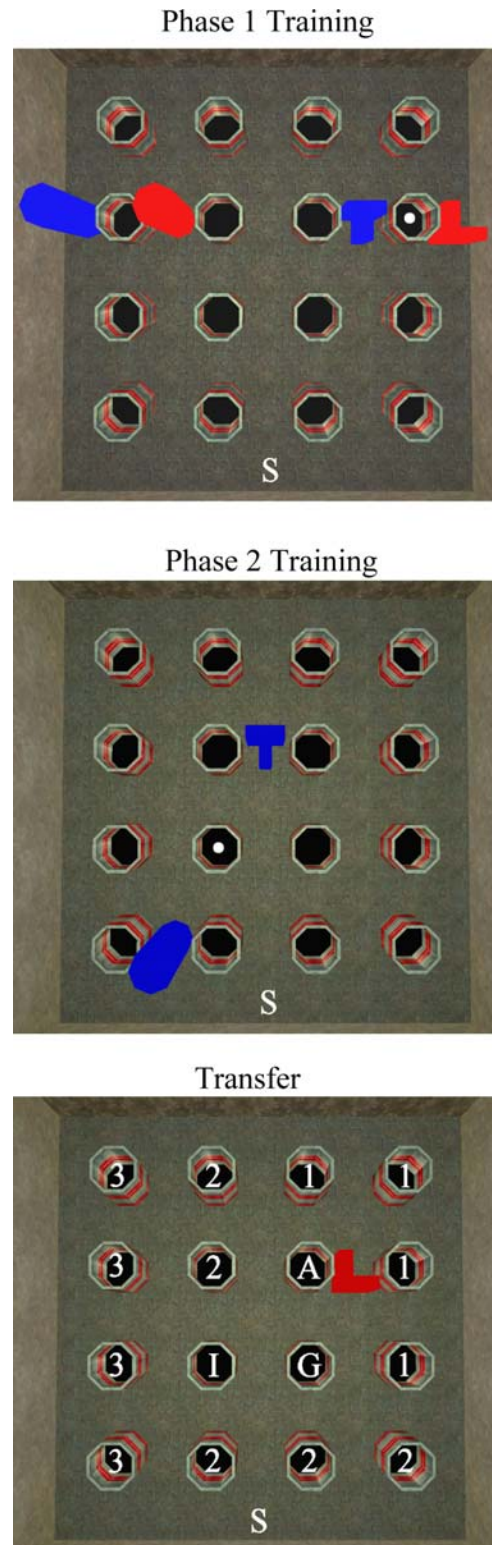
Fig. 1 An overview screen shot of the virtual open field for a possible trial from Phase 1 training (*top panel*), Phase 2 training (*middle panel*), and transfer (*bottom panel*). The S marks the position where participants entered the open field on all trials for training and testing. The white dot marks the location of the goal cup relative to the landmark(s). The positions of the landmarks were quasi-randomized across trials (see text for details). In the bottom panel locations for the Integration cup (I), Association cup (A), and Generalization cup (G) are marked. Also marked are cup distances from the test landmark.

Procedure

Participants were randomly assigned to one of three groups: Reminder, No Reminder, and Integration Control. Each group contained three participants. All participants began the experiment by sitting down at the computer in the testing room. The experimenter turned off the testing room lights and started the computer program. Participants were presented an instruction screen and could not proceed until clicking an OK box located in the lower left-hand corner of the screen. The instructions informed participants that they had 10 min to reach an exit sign and described the functions of the active keys and mouse buttons. The first room, which consisted of a narrowing and widening winding raised path, served to familiarize participants with the virtual environment and interface and was not used in any analyses. Participants moved via keyboard keys: ↑ (forward), ↓ (backward), ← (left), and → (right). Auditory feedback was provided to indicate movement within the environment (footstep sounds). Movement of the mouse served to change the view in a 360° sphere within the virtual environment. If participants fell off of the path during navigation of this room, there was a 2-s time-out (i.e., black screen), a message informing participants to stay on the path appeared on the screen, and they were returned to the start location. After participants completed the first room or 10 min elapsed, participants were presented with the instruction screen for the second room. The instructions informed the participants to locate the cup that transported them to the next room and again described the functions of the active keys and mouse buttons. After clicking an OK box located in the lower left-hand corner of the screen, the experiment proper began with the participants in the experimental room.

Participants began each trial at position S (Fig. 1) and were required to locate the goal cup. In order to select a cup (analogous to pigeons digging for seed), participants jumped into that cup. To jump into a cup, participants needed to simultaneously move forward (↑) and jump (right mouse button). Auditory feedback was provided to indicate a jump had occurred ("huh" sound). If the goal cup was selected, participants received "correct" auditory feedback consisting of a short sound clip (transport sound from Super Mario Bros.™) followed by a 1-s inter-trial interval (ITI) in which the screen was black. If a non-goal cup was selected, participants received "incorrect" auditory feedback consisting of a different short sound clip (game over sound from Super Mario Bros.™) and were not transported to the next trial. Participants were then required to jump out of the current cup and continue searching until the goal cup was selected.

All participants experienced two training phases followed by a testing phase. Training and testing were conducted in one continuous session. Only the testing phase differed across the three groups of participants. The testing phase consisted of two tests: Test 1 and Test 2. The experimental design and the landmarks used during training and testing are summarized in Table 1.

Table 1 Landmark presentations during training and testing by group

	Training		Testing	
Group	Phase 1	Phase 2	Test 1	Test 2
Reminder	T L	T	T, T, L	T L, T, L
No Reminder	T L	T	T, T, L	T, T, L
Integration Control	T L	T	T, T, X	T L, T, X

Note. Phase 1 and Phase 2 consisted of 16 trials each. Test 1 consisted of three blocks of three trials and Test 2 consisted of two blocks of three trials. One block from Test 1 and Test 2 is represented. Foils presented during Phase 1 and Phase 2 training are not included.

Phase 1 training

Phase 1 training consisted of 16 trials. For each trial, a goal cup was randomly assigned to one of the 16 cup locations. The blue T and the red L were then respectively positioned to the left and right of the goal cup (Fig. 1, top panel). The blue and red cylinders functioned as foil landmarks and were respectively positioned to the left and right of a randomly assigned cup (excluding the goal cup and cups directly to the left and right of the goal). See electronic supplementary material S1 for an example of a Phase 1 training trial, as experienced by the participants (i.e., first-person perspective).

Phase 2 training

Phase 2 training consisted of 16 trials. For each trial, a goal was randomly assigned to one of 12 cup locations. The cups in the top row were excluded as possible goal locations because of the landmark-goal relationship: the blue T was positioned up and right of the goal cup (Fig. 1, middle panel). The blue cylinder functioned as a foil landmark and was positioned to the left of a randomly assigned cup (excluding the location of the blue T) for the first five trials of training (as in Blaisdell and Cook 2005). The foil was absent in the remaining eleven trials. All other details were identical to Phase 1 training. See electronic supplementary material S2 for an example of a Phase 2 training trial, as experienced by the participants.

Reminder group testing

Test 1 consisted of three blocks of three trials. Each block consisted of two Phase 2 training trials followed by one transfer trial. For each transfer trial, a red L was randomly assigned to one of nine locations. The left column and bottom row of cups were excluded as possible goal locations because of the spatial locations needed to assess participant strategies. The three primary cups of interest were the Association, Generalization, and Integration cup (Fig. 1, bottom panel). Participants were required to make six choices in the presence of the red L alone to complete each trial. After each choice, participants received the same feedback as that

of selecting a non-goal cup in training. The sixth choice was followed by a 1-s black screen ITI. No foils were presented during testing. All other details of testing were identical to training. See electronic supplementary material S3 for an example of a transfer trial, as experienced by participants in the Reminder group.

Test 2 consisted of two blocks of three trials. Each block consisted of one Phase 1 training trial (i.e., the reminder trial), one Phase 2 training trial, and one red L transfer trial. All other details were identical to Test 1.

No reminder group testing

Test 1 was identical to Test 1 for the Reminder group. Test 2 was identical to Test 2 for the Reminder group with the exception that instead of reintroducing a Phase 1 training trial (i.e., the reminder trial) another Phase 2 training trial was presented in each block. Thus, for the No Reminder group a Test 2 block was composed of the same types of trials as used in a Test 1 block. See electronic supplementary material S3 for an example of a transfer trial as experienced by participants in the No Reminder group.

Integration control group testing

Test 1 and Test 2 were conducted identically to the Reminder group with the exception that a green X (i.e., novel landmark) was substituted for the red L during transfer trials. See electronic supplementary material S4 for an example of a transfer trial, as experienced by participants in the Integration Control group.

Results

Acquisition

Figure 2 (top panel) shows mean errors collapsed across groups for the 16 training trials of Phase 1 and Phase 2. Regardless of training phase, participants' search behavior rapidly came under the control of the consistent landmark(s) (blue T and red L during Phase 1 and blue T during Phase 2) at the same rate. A three-way mixed ANOVA on errors with Trial (1–16), Phase (1, 2), and Group (reminder, no reminder, integration control) as factors revealed a main effect of Trial $F(15, 180) = 14.1$, $p < 0.001$, $\eta^2 = 0.54$, power = 1.0. All other main effects and interactions were not significant, $Fs < 1$. As a result, there were no differences in acquisition between groups or training phases.

Trial 1 of Phase 2 training provided an opportunity to assess participants' strategies when presented the blue T and blue cylinder alone for the first time (i.e., a type of transfer trial). All participants initially selected a cup directly to the left or right of the landmark or foil. Figure 2 (bottom panel) shows the proportion of choices to these four locations for the first two choices during Trial 1 of
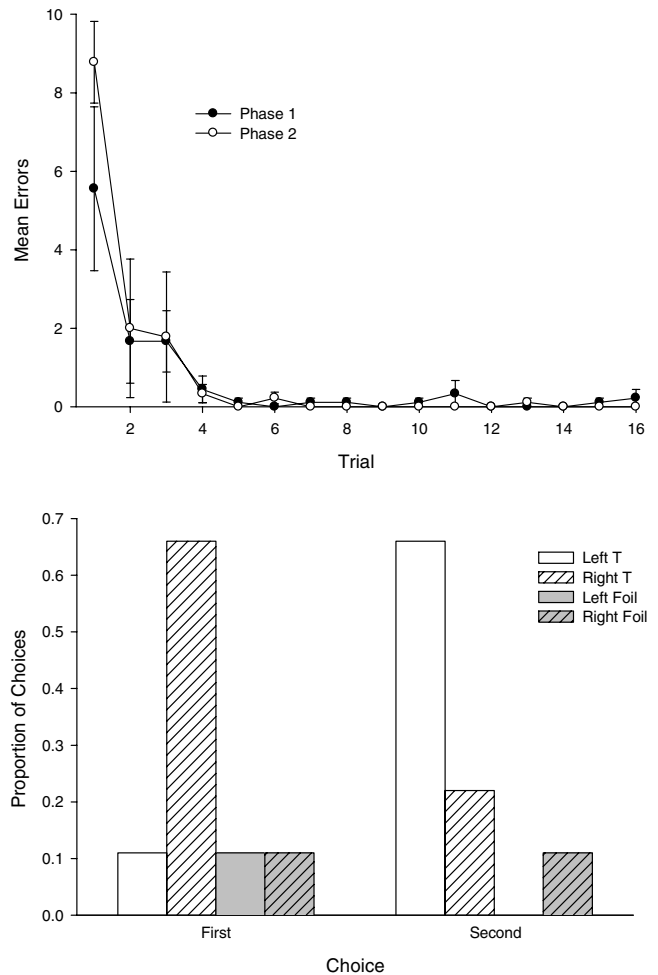
Fig. 2 Mean errors across trials collapsed over groups for Phase 1 and Phase 2 training (*top panel*). Error bars represent standard errors of the mean. Proportion of choices to the specified locations collapsed over groups for the first two choices of Trial 1 from Phase 2 training (*bottom panel*).

Phase 2 training. First choice analysis revealed that the majority of participants (66%) responded to the right of the blue T. Second choice analysis revealed that the majority of participants (66%) responded to the left of the blue T. These results were confirmed by Chi-Squares, $\chi^2(3, N = 9) = 9.22$, $p < 0.05$, and $\chi^2(3, N = 9) = 9.22$, $p < 0.05$, respectively. These analyses indicated that most participants' first choice was guided by an association strategy that, within a single trial, rapidly shifted to a generalization strategy.

In summary, all participants came under landmark control during both training phases within about five trials. The consistency of the acquisition functions suggests that any potential *a priori* participant differences resulting from previous experience (e.g., video game use) were unlikely factors in the present experiment. Moreover, all participants applied a rule learned during Phase 1 training when encountering a novel landmark configuration (i.e., first trial of Phase 2). This result indicates participants used search strategies learned within the present virtual environment.

Transfer

Choice type

The three cups of primary interest were the Association, Generalization, and Integration cup (see bottom panel of Fig. 1). Selection of the Association cup would provide evidence that choices were under landmark control from Phase 1 because the goal was located left of the red L and right of the blue T. Selection of the Generalization cup would provide evidence that choices were under landmark control from Phase 2 because of generalization from the blue T to the red L. Selection of the Integration cup would provide evidence that participants were integrating spatial information because they were able to combine the two spatial maps.

Figure 3 shows mean proportion of choices to the Integration, Association, and Generalization cups collapsed across the three transfer trials from Test 1 and the two transfer trials from Test 2 (as performed by Blaisdell and Cook 2005). In Test 1, more choices occurred to the Association and Generalization cups than to the Integration cup which suggested that humans failed to integrate spatial maps. In Test 2, however, choices decreased to the Generalization cup and increased to the Integration cup which suggested integration of spatial maps. Choices to the Association cup did not differ across tests. These results were confirmed by a three-way mixed ANOVA of Choice Type (integration, association, generalization) $\times$ Test (1, 2) $\times$ Group (reminder, no reminder, integration control) on mean proportions that revealed a significant Test $\times$ Choice Type interaction, $F(2, 12) = 10.38$, $p < 0.01$, $\eta^2 = 0.63$, power $= 0.96$. No other significant main effects or interactions were found. The absence of significant interactions indicated that all groups performed the same across tests. In order to isolate the source of the interaction, planned comparisons were performed. Across tests, choice responses significantly increased to the Integration cup, $F(1, 6) = 21.63$, $p < 0.01$, and significantly decreased to the Generalization cup, $F(1,$
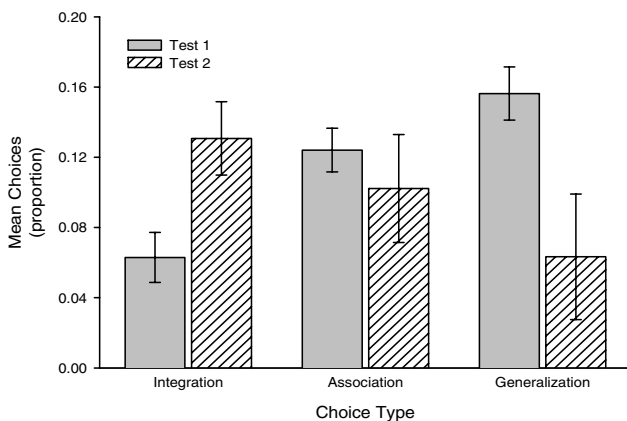
Fig. 3 Mean proportion of choices to the Integration, Association, and Generalization cups collapsed across groups and trials for Test 1 and 2. Error bars represent standard errors of the mean.

$6) = 5.95$, $p = 0.05$. Choices to the Association cup did not change across tests.

*Spatial distribution of choices*

To more fully illustrate the changes in cup choices across tests, Fig. 4 shows the spatial distribution of choices to each cup for each group (columns) across the five transfer trials. Transfer trials 1–5 appear consecutively in rows from top (Trial 1) to bottom (Trial 5). Choice distributions are centered at the Integration cup (4, 4). As shown, responding was concentrated around the test landmark (L or X) in transfer Trial 1 but began to spread with repeated presentations. Despite variability in the direction of the shift in search behavior, all groups moved away from the test landmark across transfer trials. This movement away from the test landmark could account for the increased choices to the Integration cup and decreased choices to the Generalization cup from Test 1 to Test 2, as shown in Fig. 3.

Distance analyses

To clarify the shifts in search behavior from Test 1 to Test 2, the mean response distance (in cups) from the test landmark (i.e., red L or green X) for each group (unfilled symbols) and meaned across groups (filled circles) was plotted across the five transfer trials in Fig. 5. Distances were calculated by counting the number of cups that each cup was displaced from the landmark (see the bottom panel of Fig. 1). For example, the Association and Generalization cups were one cup away from the landmark and the Integration cup was two cups away from the landmark. As shown, search behavior moved away from the landmark with the accumulation of choice responses. A two-way mixed ANOVA of Group (reminder, no reminder, integration control) $\times$ Trial (1–5) on distance revealed only a main effect of Trial, $F(4, 24) = 14.12$, $p < 0.001$, $\eta^2 = 0.7$, power $= 1.0$. The absence of a significant interaction indicated that all groups performed the same across transfer trials. A trend analysis on the Trial factor yielded only a significant linear component, $F(1, 6) = 103.7$, $p < 0.001$, $\eta^2 = 0.95$, power $= 1.0$, indicating that search behavior continued to move away from the test landmark across trials.

It is important to note that the Integration cup was two cups from the test landmark yet search behavior extended beyond this distance during transfer Trials 4 and 5. This result was confirmed by one-tailed, one-sample t-tests that compared mean distance in transfer Trial 4 (2.5 cups) and transfer Trial 5 (2.6 cups) to the distance of the Integration cup (2.0 cups), $t(8) = 2.11$, $p < 0.05$, $t(8) = 3.26$, $p < 0.01$, respectively.

Fig. 4 Spatial distribution of choices to each cup plotted for each group (columns) across the five transfer trials. Transfer trials 1–5 appear consecutively in rows from top (Trial 1) to bottom (Trial 5). The first three transfer trials formed Test 1 (*solid grid lines*), and the last two trials formed Test 2 (*dashed grid lines*). The size of a circle at an intersection is indicative of the mean proportion of choices to that spatial location. The distribution is centered at the Integration cup (4, 4). L or X = location of test landmark; ● Association cup choices (5, 5); ●Generalization cup choices (5, 4); ●Integration cup choices (4, 4).
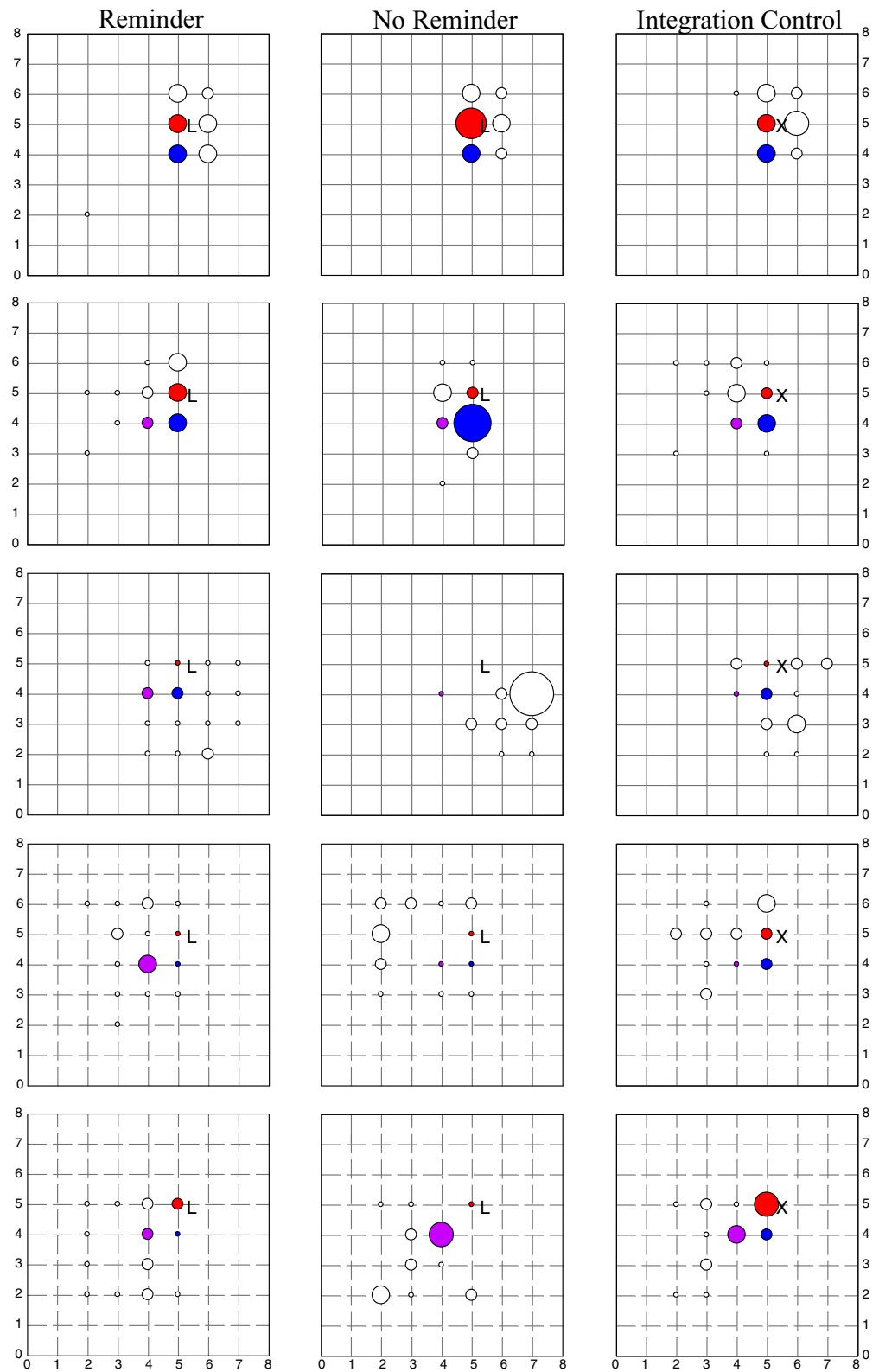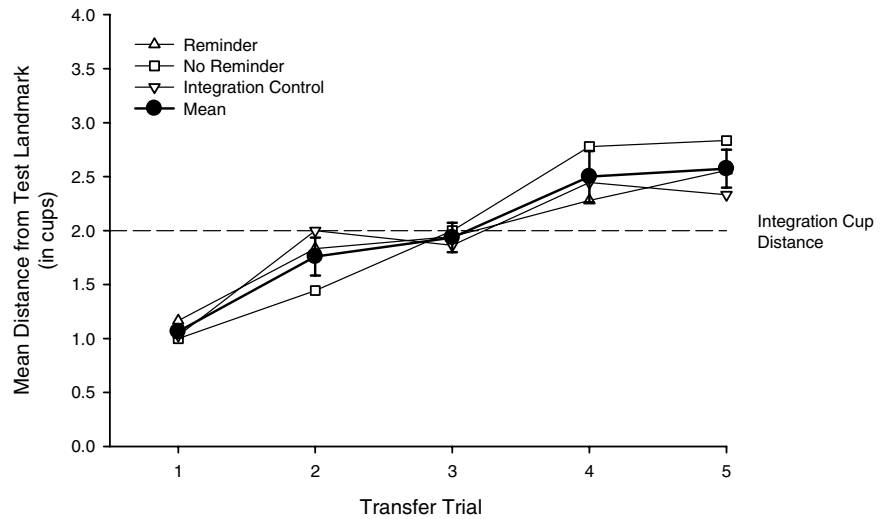

Transfer Trial 1 choices

Collectively, the prior results offer evidence that integration was not the mechanism responsible for the changes in cup choices across tests; however, it is possible that partic-

ipants integrated on their initial choice and then proceeded to shift their search as a result of the consequences of the choice responses. To assess the possibility of such early integration, each choice response during transfer Trial 1 was analyzed. Table 2 shows the number of participants

Fig. 5 Mean distance (in cups) from test landmark to choice location plotted for each group (*unfilled symbols*) and meaned across groups (*filled circles*) for each transfer trial. Error bars represent standard errors of the mean. The dashed line represents the distance of the Integration cup from the test landmark.

(Observed) choosing the Integration, Association, Generalization, and Other cups (parsed into distances of one cup or two or greater cups) for the six choices of transfer Trial 1 compared to the expected values. Expected values were calculated based on the probability of choosing a particular cup(s) multiplied by the total number of participants (9). For example, the probability of responding to the Integration cup was $1/16 = 0.0625$ multiplied by nine yielding an expected value of 0.5625. As shown, the majority of participants (56%) responded to the Generalization cup for their fist choice. This result was confirmed by a Chi-Square, $\chi^2(4, N = 9) = 40.07$, $p < 0.001$. An additional Chi-square ensured that this effect was not different across groups, $\chi^2(4, N = 9) = 2.4$, $p > 0.05$. Additionally, no participant responded to the Integration cup for any choice during transfer Trial 1. As a result, it is reasonable to conclude that during transfer Trial 1 participants did not integrate spatial maps but generalized from Phase 2 training.

Discussion

In the dynamic 3-D virtual open-field task humans rapidly acquired each training map. Transfer tests initially indicated that humans performed like pigeons; both species seemed primarily controlled by a generalization strategy during Test 1 but shifted to an integration strategy during Test 2. However, further analyses of the human data

suggested that integration was not the mechanism responsible for the participants' shift in search behavior. These more fine-grained analyses indicated that humans were progressively moving away from the test landmark with the accumulation of choice responses. A consequence of this movement away from the landmark was an increase in choices to the Integration cup. Without these additional analyses we may have prematurely concluded that humans were integrating independently learned spatial maps into a cohesive allocentric representation of space.

The search behavior of the Integration Control group also supported these findings. For this group, integration of the two independently learned spatial maps was not possible because a previously experienced landmark was unavailable for individual or inferential use during transfer trials. Yet, these participants showed increased choices to the Integration cup across tests and the same shift in search behavior away from the test landmark across transfer trials as the Reminder and No Reminder groups. Accordingly, there were also no differences between the Reminder and No Reminder groups with respect to shifts in search behavior. Finally, humans did not require the Map 1 reminder trials to produce the increased choices to the Integration cup across tests. However, given the shorter temporal difference between training and testing for humans (a few minutes) compared to pigeons (a few months), memories of previous training phases would likely serve a more powerful influence for humans compared to pigeons. That is, humans might not require reminder trials in order to ac-

Table 2 Observed and expected values for the six choices during transfer Trial 1 by choice type

Choice	Integration cup		Association cup		Generalization cup		Other 1 cup distance		Other 2 or > cups distance	
	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected	Observed	Expected
1	0	0.5625	2	0.5625	5	0.5625	2	2.25	0	5.06
2	0	0.5625	3	0.5625	1	0.5625	5	2.25	0	5.06
3	0	0.5625	1	0.5625	1	0.5625	7	2.25	0	5.06
4	0	0.5625	1	0.5625	0	0.5625	8	2.25	0	5.06
5	0	0.5625	2	0.5625	0	0.5625	7	2.25	0	5.06
6	0	0.5625	3	0.5625	1	0.5625	3	2.25	2	5.06

tivate a memory of Map 1 and, as a result, may be more likely than pigeons to integrate early during testing (i.e., transfer Trial 1); however, not a single choice occurred to the Integration cup during transfer Trial 1.

In comparing the present results with those of the pigeons, there are two possible interpretations. First, a qualitative difference may exist in the way pigeons and humans perform the open-field task; pigeons may integrate two independently learned spatial maps whereas humans do not. Such a difference would not be the first time species differences have been found in spatial tasks. However, it is usually found that humans use more complex navigational strategies than pigeons. For example, while both humans and pigeons are capable of utilizing landmark configurations to locate a goal location, pigeons utilize absolute distance from an individual landmark composing the configuration whereas humans apply an abstract rule to the relation between all landmarks composing the configuration (e.g., a middle rule; Spetch et al. 1996, 1997).

Second, there may be a qualitative similarity in the way pigeons and humans perform the open-field task. Such a conclusion would be reached if the pigeons and humans showed the same shift in search behavior across the transfer trials that could only be revealed with the more fine-grained analyses. In fact, based on prior research, one might expect to find such a similarity. Specifically, both humans and nonhumans have been shown to rely on landmarks in close proximity to a goal location (Bennett 1993; Cheng 1989; Cheng et al. 1987; Spetch 1995; Spetch and Wilkie 1994) and apply rules learned from training during testing (Mac-Donald et al. 2004; Spetch et al. 1996, 1997). In the current task, humans relied on landmarks in close proximity to a goal evidenced by the increased responding near any single landmark. Moreover, participants in the Reminder and No Reminder groups did not treat the test stimulus (red L) as an element from a previously experienced configuration and integrate spatial maps, but instead initially applied a rule learned from training; in the presence of a single landmark, participants selected the cup down and left of this landmark.

Investigating the applicability of general learning principles to the spatial domain is an important issue for comparative research (Cheng and Spetch 1998). For example, both blocking and overshadowing have been shown for humans and nonhumans in a variety of spatial tasks (Chamizo et al. 2003; Jacobs et al. 1997; Rodrigo et al. 1997; Spetch 1995). Blaisdell and Cook (2005) stressed the influence of associative conditioning in the process of building allocentric representations of space. However, the influence of other general learning principles, namely principles of operant conditioning, were not investigated as possible factors on the shifts in search behavior across transfer trials. Acquisition from training revealed that pigeons had learned the location of food relative to the landmark(s), and in both phases, the goal was located near the landmark(s). Thus, cup choices near the landmark(s) were reinforced while all others were non-reinforced, and spatial learning has been demonstrated following both outcomes (Olton et al. 1977a, 1977b; Olton and Samuelson 1976). Moreover,

during each of the five transfer trials (i.e., presentations of the red L alone), pigeons were allowed to make six choices before being removed from the apparatus. As all cups were non-baited during testing, there was an accumulation of non-reinforced choice responses across transfer trials (total of 30 non-reinforced responses). Due to the close proximity of food relative to a landmark(s) during training, initial transfer trials may have resulted in a concentration of search behavior near the test landmark. Absence of reinforcement for responses in the presence of the test landmark may have produced a progressive outward shift in search behavior across transfer trials that would remain undetected when choice responses were collapsed across tests. This progressive outward shift could result in an increase in responding to multiple displaced spatial locations isolated for analysis across tests (e.g., the Integration cup), as it did for humans.

Such an outcome would require pigeons to actively track previous cup choices and avoid return visits to these spatial locations. Studies of foraging behavior have shown that the selection of future foraging locations is largely influenced by the outcome (i.e., presence or absence of food) of previous foraging locations (e.g., Olton et al. 1977b; Real 1991; for a review see Shettleworth 1988). Formation of spatial memories for these previously visited foraging locations and their resulting outcome is critical for common foraging strategies (e.g., win-stay, win-shift, lose-stay, lose-shift; for a review see Olton 1979). Although forging strategy preference is species specific, pigeons tend to use a lose-shift as opposed to lose-stay rule (Plowright and Shettleworth 1990). Hence, pigeons' movement of their search behavior would be largely influenced by an avoidance of recently visited non-reinforced locations and could produce a progressive outward shift in the open-field foraging task.

For humans, the present results provided further evidence for rule learning in the spatial domain. Specifically, participants not only learned where the goal was located but also where the goal was not located. On two separate occasions in the presence of a novel stimulus configuration, participants initially applied a rule learned during training: they searched immediately left and right of the blue T during Trial 1 of Phase 2 training and down and left of the red L during Trial 1 of transfer. Failure of choice responses to yield reinforcement during transfer trials may have prompted participants to treat the red L as a novel stimulus with its own unique spatial relationship to a novel goal location and continue searching. Continued search for the goal location may have been guided by a lose-shift strategy, as participants made few repeated choices per transfer trial ($M = 0.76$, $SEM = 0.15$). Interestingly, this continued search for the goal location also resembled that of desert ants (*Cataglyphis*) attempting to locate their nest at the terminal point of a return trip which may indicate a similar search process characterized by Gaussian probability density functions (Wehner and Srinivasan 1981).

The current results also have comparative implications for the cognitive mapping hypothesis. Our results suggest that participants did not utilize a cognitive map in the present task. Instead, participants relied on a simple navigational strategy. This simple navigational strategy was

to apply spatial rules learned from training to novel landmarks. When this strategy failed, participants may have been guided by a lose-shift strategy. The use of a lose-shift strategy would explain movement away from the test landmark across transfer trials and increased choices to the Integration cup across tests. Such an alternative explanation of integration is congruent with extant animal research on cognitive mapping. Specifically, results have shown that animals do not utilize cognitive maps during navigation but instead rely on alternative navigational strategies (e.g., Gibson and Kamil 2001). Utilization of alternative navigational strategies to cognitive mapping has been found in recent human research as well (e.g., Foo et al. 2005; Gibson 2001; Waller et al. 2000; for a review see Wang and Spelke 2002). For example, Gibson (2001) found that humans did not utilize a cognitive map to locate a novel goal location but instead relied on current compass bearing and previously learned navigational vectors. Similarly, Foo et al. (2005) found that novel short-cutting by humans was not the result of an integration of learned routes into a cognitive map but instead was accounted for by landmark-based navigation.

In conclusion, humans did not integrate two independently learned spatial maps into a cohesive allocentric representation of space in the present virtual open-field task. Importantly, this is not to say that humans or pigeons are incapable of forming allocentric representations of space or inferring new spatial relationships; however, present results offer evidence to question the conclusion that pigeons did infer a new spatial relationship in the Blaisdell and Cook (2005) open-field procedure.

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