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Integration of spatial maps in pigeons

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Abstract The integration of spatial maps in pigeons was investigated using a spatial analog to sensory preconditioning. The pigeons were tested in an open-field arena in which they had to locate hidden food among a 4×4 grid of gravel-filled cups. In phase 1, the pigeons were exposed to a consistent spatial relationship (vector) between landmark L (a red L-shaped block of wood), landmark T (a blue T-shaped block of wood) and the hidden food goal. In phase 2, the pigeons were then exposed to landmark T with a different spatial vector to the hidden food goal. Following phase 2, pigeons were tested with trials on which they were presented with only landmark L to examine the potential integration of the phase 1 and 2 vectors via their shared common elements. When these test trials were preceded by phase 1 and phase 2 reminder trials, pigeons searched for the goal most often at a location consistent with their integration of the L→T phase 1 and T→phase 2 goal vectors. This result indicates that integration of spatial vectors acquired during phases 1 and 2 allowed the pigeons to compute a novel L→goal vector. This suggests that spatial maps may be enlarged by successively integrating additional spatial information through the linkage of common elements.

Keywords Spatial · Pigeon · Map · Integration · Sensory preconditioning

Introduction

Since its introduction (Tolman 1948), the cognitive map has been a widely used conceptual tool for understanding spatial cognition and memory in both human and nonhuman animals (for reviews see Poucet 1993; Thinus-Blanc 1996). Spatial abilities are fundamental for navigating the world, avoiding dangers such as predators, and locating biological necessities such as food, shelter, and mates. A key property of any cognitive map is that it encodes the relations between environmental stimuli, such as landmarks and biologically significant outcomes like food. Within this framework, the spatial relationship between two or more external events is preserved as a vector that encodes the metric distance and direction between events (O’Keefe and Nadel 1978). An allocentric representation of the environment can then be constructed by connecting these elements together. This map can in turn be used to generate novel relationships between elements that have never been experienced or observed together, and given a subset of cues from the map can also be used to determine the location of absent cues. For example, a novel route between two spatial locations can be computed (i.e., a spatial inference) for use when learned routes become unavailable (e.g., Tolman 1948; see also O’Keefe and Nadel 1978; Ellen et al. 1984).

The main goal of the present research is to explore the acquisition processes underlying the formation of spatial cognitive maps. How are complex representations involving spatial information acquired and what are the mechanisms of encoding? In this article, we particularly investigate the mechanisms by which spatial maps between two items are acquired, and how independently acquired maps may be integrated into a larger, more complex, map.

Although less well known than its spatial application, the general notion of a cognitive map has also been extended to describing temporal relationships acquired in associative learning procedures (Honig 1981; Miller and Barnet 1993; Savastano and Miller 1998). In this context, it has been suggested that animals can integrate separate

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“temporal” maps by linking together their shared or common elements. The resulting higher-order map can be used to deduce new temporal relationships between events that had never been directly experienced together.

For instance, Miller and colleagues have used the Pavlovian sensory preconditioning and second-order conditioning procedures to explore how rats acquire and integrate simple temporal maps between paired events, such as conditioned and unconditioned stimuli (CSs and USs, respectively; Matzel et al. 1988; Barnet et al. 1991, 1997; Barnet and Miller 1996). Sensory preconditioning involves pairing a second-order CS A with a first-order CS B in the absence of reinforcement in phase 1 (i.e., $A \rightarrow B$) followed by pairing CS B with the US in phase 2 ($B \rightarrow US$). This procedure typically conditions a moderate response to CS A, which is thought to be mediated by an $A \rightarrow B \rightarrow US$ associative chain. This sensory preconditioning procedure is quite useful for establishing separate temporal maps in consecutive phases of training. Evidence for an integrated map then comes from the ability of the subject to use the associative chain to deduce a temporal relationship between the second-order CS A and the US, despite the fact that these two events had never been physically paired. That is, the rat acts as if it makes a temporal inference about the predictive relationship between events, such as a second-order CS and a US, that had never been physically paired. One important tenet of this temporal coding hypothesis is that the temporal inference between CS A and the US involves the integration of the $A \rightarrow B$ and $B \rightarrow US$ maps by way of super-positioning the common element in both maps, that is, CS B. Thus, CS B links the two memories into one at a specifically remembered temporal location, thereby allowing for computations of temporal vectors between any two events (e.g., CS A and the US) within the integrated map.

The experiment reported below explored whether spatial maps can be similarly integrated by the same common-element mechanism as previously established with temporal maps. Humans, for example, have a demonstrated ability to combine two spatial maps acquired during separate training experiences into a unified, higher-order map by superimposing the maps in memory via common elements shared among the maps (Hanley and Levine 1983). Given these considerations, we were interested in whether non-human animals could also integrate separately acquired spatial maps. To do this, we developed a spatial analog of the sensory preconditioning procedure (see below).

On a related front, a secondary goal of the present research was to possibly address some of the recent criticisms and questions generally raised concerning the cognitive mapping hypothesis (Bennett 1996; Shettleworth 1998). One criticism has been that the definition of a cognitive map is too vague (Thinus-Blanc 1996) or too broad (Bennett 1996) to generate clear, testable predictions or to illuminate psychological processes. Another criticism has been that simpler alternatives can often be proposed to account for most data that support cognitive mapping. In particular, experiments reporting spatial inferences (e.g.,

novel shortcuts) have been criticized on the grounds that it is difficult to prove that the novel route was truly novel, and for failing to control for processes like beacon homing or dead reckoning. It has turned out to be notoriously difficult to rule out these alternatives in experiments that purportedly show control by a cognitive map. In his critical review of the cognitive map literature, for example, Bennett concludes that none of the studies he reviews successfully eliminate alternative explanations, such as beacon homing, the use of visual “snapshots” (e.g., Cartwright and Collett 1983) or path integration (e.g., Wehner and Srinivasan 1981; Potegal 1982), to establish that the novel shortcut was truly novel.

There are two particular features of prior studies of cognitive maps that have made it difficult to rule out such alternatives. First, if the animal is allowed to navigate its environment during training so that it forms a cognitive map, it becomes problematic to determine whether a subsequent route was truly novel. Second, if the subject is prevented from traversing a particular route, such as by blocking the arm of a maze that will serve as a shortcut at test, how can we eliminate the possibility that the subject simply learned to navigate toward a cue near the goal? As a result, another goal of the current research was to use a design that might avoid many of the interpretational pitfalls encountered by previous demonstrations of spatial inferences.

In the experiment, pigeons (*Columba livia*) were tested in a landmark-filled arena using an analog of the sensory preconditioning integration procedure described above (e.g., Matzel et al. 1988). Pigeons were allowed to forage for food hidden on the floor of an arena. Landmarks were present in the arena, some of which bore a consistent spatial relationship to the location of the hidden food. These landmarks can be viewed as analogous to Pavlovian CSs and the food location as analogous to the location of the US. Pigeons were trained in separate phases on an $A \rightarrow B$ spatial vector and a $B \rightarrow \text{goal}$ vector, where A and B were visual landmarks (L and T, respectively; colored blocks of wood) and the goal was food hidden in a specific location (1 of 16 food cups; see Fig. 1). Thus, $L \rightarrow T$ and $T \rightarrow \text{goal}$ pairings were analogous to the preconditioning (top panel of Fig. 1) and conditioning (center panel of Fig. 1) treatments, respectively, of Pavlovian sensory preconditioning (note, food was also present in phase 1, but its role is explained in Methods). Following phase 2, pigeons were presented with landmark (LM) L (bottom panel of Fig. 1). If the pigeons were integrating the spatial vectors from prior training, then they could search at a novel location consistent with the integrated $L \rightarrow T$ and $T \rightarrow \text{goal}$ vectors experienced separately (see location “I” in the bottom panel of Fig. 1); an inferred $L \rightarrow \text{goal}$ vector that had never been directly experienced.

Besides the search for the integration of separately learned maps via the common-elements mechanism, this procedure controls for alternative explanations to that of forming a spatial inference in three ways: (1) the goal was presented at different locations in the search space across trials; (2) on test trials, we eliminated all potential spatial

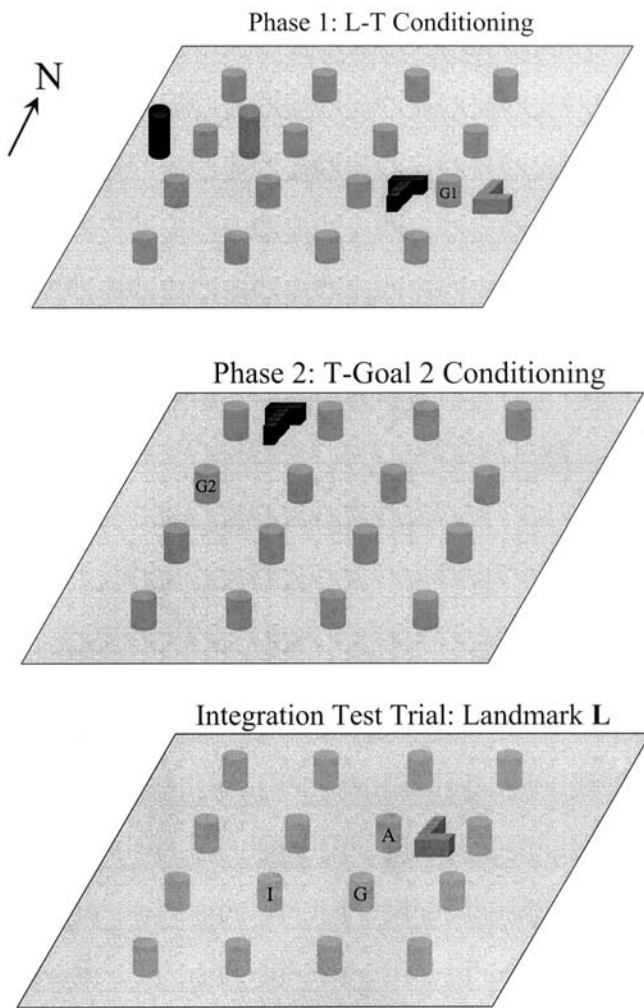


Fig. 1 Diagram of the experimental arena, showing the arrangement of the 4×4 grid of gravel-filled cups, the hidden food (*G*), and the landmarks (*T*, *L*, and two foils). The *top panel* shows the spatial arrangement of the consistent landmarks (*T* and *L*), goal 1 (*G1*), and inconsistent landmarks (*cylindrical foils*) during phase 1. The *middle panel* shows the spatial arrangement of LM *T* to goal 2 (*G2*) during phase 2. The *bottom panel* shows the spatial arrangement of LM *L* and the potential locations of search during the integration test. Letters on bottom panel: *I* = predicted cup for choices guided by the *L*→*T*→goal 2 hierarchical map, *A* = predicted cup for choices guided by the phase 1 *L*→goal 1 vector, and *G* = predicted cup for choices guided by a generalization to *L* of the *T*→goal 2 vector (see text for details)

cues to a hidden food goal that were present during training; and (3) the route (or vector) between the test cue and the goal was truly novel at test. As discussed below, these modifications help avoid the problems encountered by prior research and help to put the cognitive mapping concept on firmer ground.

Methods

Subjects

Three experienced male white carneau pigeons (*Columba livia*, Palmetto Pigeon Plant, Sumter, SC) were tested. They had prior experience with visual-choice discrimination touch-screen tasks (two from Cavoto and Cook 2001; one from Katz and Cook, unpublished data), but were naive to the task employed here. Subjects were maintained at 85% of their free-feeding weight during testing with free access to water and grit in their home cages, which were housed in a colony room with a 12-h light-dark cycle.

Apparatus

All experimental manipulations took place in a large room with a test area of 2.25×2.22 m. This test area consisted of three beige brick walls on the west, north, and east sides of the room and an opaque shower curtain hung wall-to-wall along the south side that partitioned the test arena from the rest of the room. A large clear plastic tarp was draped over the entire test area about 2 m above the floor to inhibit the pigeons from flying within the arena. Sixteen Tupperware cups, 6 cm in diameter and 6 cm high, were arranged on the ground in a 4×4 grid, centered in the test area (Fig. 1) and spaced 40 cm apart (center-to-center). Cups were attached to the ground of the experimental arena with Velcro, to prevent pigeons from knocking them over. Each cup was filled with plaster of Paris, except for the top 1.5 cm of the cup that was filled with small fish aquarium gravel (20% white and 80% black). Mixed grain could be hidden from view by being buried underneath the gravel, requiring the pigeon to sift through the gravel to obtain reinforcement.

Four objects that served as landmarks were used in this experiment. Object 1 was a blue wooden T-shaped object (20 cm long×20 cm wide×15 cm high) and object 2 was a red wooden L-shaped object (20 cm long×20 cm wide×15 cm high). Objects 3 and 4 were PVC pipe (15 cm diameter×30 cm high) painted orange and black, respectively. For phase 1B, objects 3 and 4 were repainted blue and red to match the color of objects 1 and 2. Objects 1 and 2 served as LMs *T* and *L*, respectively, whereas objects 3 and 4 served as foil landmarks that did not bear a consistent spatial relationship to the goal.

Procedure

Pre-training

During the first week of the experiment, pigeons were trained to search for hidden grain in a food cup. The pigeons were placed in a plywood box with an open window in the front panel allowing them access to a gravel-filled cup set in a shelf below the window. On the first few trials, a small amount of mixed grain was placed

on top of the gravel. Pigeons rapidly ate the visible grain. Over the next few trials, the grain was increasingly hidden below the gravel. This pretraining continued until all pigeons rapidly and successfully retrieved the hidden grain. This training was conducted in a different room from the one described.

Phase 1A: initial training

Beginning in the second week each pigeon received one three-trial session per day, 4 or 5 days per week in the open-field arena. At the beginning of each session, pigeons were placed in an opaque holding cage. This holding cage prevented subjects from observing activities of the experimenter before each trial. At the beginning of each trial, the pigeon was placed on the ground in the southeast corner of the arena with the room lights off. After release, the experimenter turned on the room lights, exited the testing area, and observed the trial from a monitor in an adjacent room. Only 1 of the 16 cups contained food on each trial. This food cup was randomly picked without replacement, assuring that each cup served as the goal once every block of 16 trials. The observer scored all cup choices by the pigeon during a trial. A cup choice was defined as the placement of the beak on or in the gravel of a cup (i.e., a dig). The termination of a choice occurred when the subject had moved approximately 10 cm away from the most recently chosen cup. If a pigeon dug in a cup, for example, then moved further than 10 cm from the cup, and returned and dug in the cup again, this was scored as two consecutive choices to the same cup. The trial ended when the bird had found the baited cup and consumed the food or the bird failed to make a cup choice for 15 min.

Two pairs of landmarks were present during phase 1A trials. The consistent landmarks (LMs L and T) were always placed 20 cm (center-to-center) to the east and west, respectively, of the baited food cup, while the inconsistent landmarks (the two foils) were similarly placed 20 cm to the east and west of a randomly-determined non-baited cup, with the constraint that two adjacent cups could not serve as the bait and foil cups (to prevent overlap between landmarks and foils). Thus, LMs L and T maintained a consistent spatial vector to the baited food cup, designated as goal 1 (phase 1A food goal; see top panel of Fig. 1), while the foils did not. During the first session the consistent landmarks, but not the inconsistent landmarks, were present. In addition, during the first session, the food was gradually hidden across trials. That is, on the first trial, the food was placed on top of the gravel, on the second trial, only some food was placed on top with the rest buried under the gravel, and on the third trial, all of the food was buried under the gravel. This strategy of again gradually hiding the food from view was to encourage the pigeons to transfer their digging behavior to the experimental context. The foils were introduced in session 2, and were present on all subsequent trials during phase 1A. The foils were included to encourage processing

of the individual features (e.g., shape and color) of LMs L and T, which would be evidenced by discriminating between the consistent landmarks and the foils. Note that, as an analog to phase 1A of sensory preconditioning, we were interested in the pigeons acquiring a spatial vector between LMs L and T. Unlike rats in a Pavlovian conditioning experiment, however, we were concerned that the pigeons might not incidentally acquire an association between two “neutral” stimuli, such as the landmarks, in the absence of motivation to actively process the arena’s contents.

Phase 1B: shape training

Beginning with the 11th session, the color of the inconsistent landmarks was changed to match the color of the consistent landmarks. Thus, the east and west foils were now red and blue, as were LMs L and T. Color-matched foils were introduced to further encourage processing of the individual shapes of the consistent landmarks, thereby reducing the potential for generalization between them during a subsequent test phase. In an attempt to improve performance, beginning with session 22 a correction procedure was implemented to discourage incorrect choices. If the cup between the inconsistent landmarks was chosen, the overhead room lights were extinguished for 45 s (i.e., a “time-out”), which inhibited the pigeon’s movement about the arena. This time-out procedure increased the costs of incorrect choices by delaying the time to the next reinforcement. The trial continued upon re-illumination of the room. Phase 1 consisted of 26 sessions.

Odor test

During the last session of phase 1B, the last trial was used to test for the possibility that the pigeons had learned to find the baited cup based on the odor of the hidden food. This trial was identical to the preceding trials of the session, except that (1) the cup that was typically baited during phase 1 (i.e., goal 1) was not baited, and (2) one of the typically non-baited cups (but not the cup between the inconsistent landmarks) was baited (pseudorandomly determined with the constraint that the cup must be at least 80 cm away from the nearest consistent landmark). We allowed the pigeons to make up to six choices on the odor-test trial. The trial ended when either the baited cup was chosen, goal 1 was chosen, or after the sixth choice if neither of these two cups were chosen. If the pigeons were using odor cues and not the landmarks to find the baited cup, they should choose the baited cup and not the one between the consistent landmarks.

Phase 2 training

During phase 2, LM L and the red foil were removed from the arena, and only LM T and the blue foil were present. LM T maintained a consistent relationship to the food cup at a new location (goal 2; see middle panel of Fig. 1), and the foil was randomly placed in the arena with the constraint that it could not occupy the same location as LM T. For two subjects LM T was placed 20 cm east and 40 cm north of goal 2, while for the third subject, LM T was placed 20 cm east and 40 cm south of goal 2. This LM→goal 2 vector served as the analog of a Pavlovian US in a sensory preconditioning procedure, and was used to assess the integration of the phase 1 and phase 2 vectors. To further facilitate acquisition during phase 2, the grain was again gradually hidden over the first two sessions. Beginning with session 5, the inconsistent landmark was removed from the arena; thus LM T was the only landmark present. Phase 2 lasted for 14 sessions.

Integration test

After phase 2 was complete, each pigeon received five test sessions. The first three test sessions each consisted of two reinforced phase 2 “warm-up” trials (i.e., T-goal 2; center panel of Fig. 1) followed by a nonreinforced test trial with LM L (bottom panel of Fig. 1). The inconsistent landmark was not present on warm-up trials, which were otherwise identical to phase 2 training trials. None of the cups were baited with food and no time outs occurred on test trials. The first six choices were recorded on each test trial, and the test trial ended after the subject’s 6th choice. The warm-up trials were scored normally (i.e., as in phase 2). Due to a large proportion of generalization errors during these initial test trials (further discussed in the Results), two further test sessions were conducted that added phase 1B warm-up trials. These sessions each consisted of one reinforced phase 1 warm-up trial (top panel of Fig. 1), followed by one phase 2 warm-up trial (center panel of Fig. 1), and followed by a test trial with L alone (bottom panel of Fig. 1). No inconsistent landmarks were present during the test sessions, but phase 1 warm-up trials were otherwise identical to phase 1 training trials, and phase 2 warm-up trials were otherwise identical to phase 2 training trials. All statistical tests were conducted using an alpha level of $P < 0.05$.

Results

Phase 1

Search behavior rapidly came under the control of the consistent landmarks. Mean number of choices to find the baited cup (goal 1) declined from mean = 5.5 choices at the beginning of training to the first choice (mean = 1) by session 10 (see Fig. 2). A one-way repeated measures analysis of variance (ANOVA) found a significant main

effect of session, indicating a reduction in number of choices to find the baited cup (goal 1) across sessions 2–10, $F_{(8,16)} = 5.32$, $P < 0.02$.

Inspection of Fig. 2 also reveals that introduction of the same-colored inconsistent landmarks in session 11 initially disrupted search accuracy, but it quickly recovered in subsequent sessions. This suggests that landmark color played a role during the initial phase. However, landmark shape acquired control over search by the end of phase 1B as evidenced by the drop in mean number of choices to locate goal 1 during phase 1B (indicated by the flattening of the slope of cumulative choices), $F_{(15,30)} = 2.24$, $P < 0.05$. By the end of phase 1B, the cup between the inconsistent landmarks was rarely chosen (mean = 0.11).

Odor test

None of the pigeons chose the baited cup on the odor test trial. Rather, all pigeons chose the cup associated with goal 1 on the odor test trial. Thus, cup choice was not influenced by the odor of the buried food, but was strongly controlled by the landmarks.

Phase 2

Performance declined (mean = 4.5) at the beginning of phase 2 (after the introduction of trials on which the food was completely buried) in which only one of the consistent landmarks (T) was present and it signaled a new vector to the baited cup (goal 2). With experience, accuracy improved over sessions as indicated by the flattening of the slope of cumulative choices in Fig. 3. By the last sessions of the phase the pigeons were taking a mean of 1.8 choices to find the hidden goal. A one-way repeated measures ANOVA conducted on choice data from the first three and last three sessions of phase 2 confirmed this

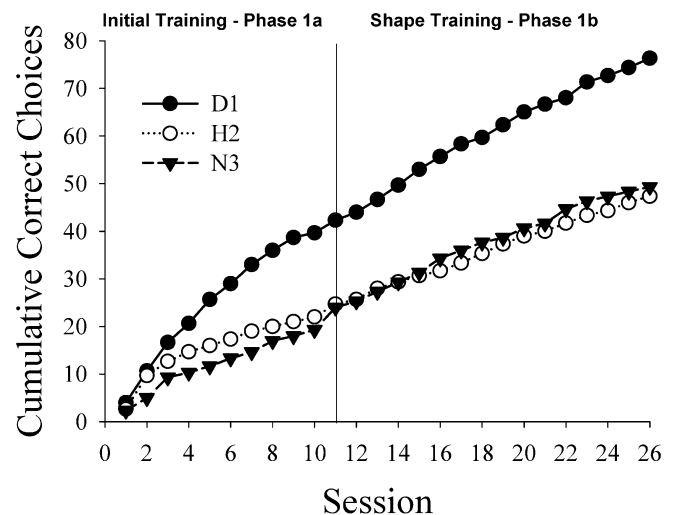


Fig. 2 Cumulative number of correct cup choices to select goal 1 during phases 1a and 1b

significant increase in search accuracy, $F_{(1,6)}=16.38$, $P<0.01$. This indicates the pigeons had learned the LM T→goal 2 vector by the end of phase 2.

Integration test

Three spatial choices were of particular interest in the integration test because they revealed the nature of the mechanisms guiding the pigeons' spatial behavior. First, if the pigeons were integrating the phase 1 L→T and phase 2 T→goal 2 vectors, they should infer an L→goal 2 vector and thereby make choices of cup location I (integrated associations; see bottom panel of Fig. 1). Second, if the pigeons' memory for the LM L→goal 1 vector acquired during phase 1 guided choices, one would expect visits to cup location A (association from phase 1; Fig. 1). Third, if the pigeons were generalizing the spatial control of responding between LM T and LM L, then one would expect visits to cup G (generalization) in Fig. 1. Location G (generalization) would be chosen if the T→goal 2 vector acquired during phase 2 generalized to LM L at test. The source of control for any other cup choices, of course, could not be determined.

The top panel of Fig. 4 reveals that the largest proportion of choices on the first three test trials were to cups G (mean =0.15) and A (mean =0.13), and very few to location I. Because over a month had passed between the end of phase 1 and the test sessions, we speculated that the large generalization effect may have been due to a failure to retrieve the L→T association established in phase 1. Failure to retrieve this association may have promoted generalization between LMs L and T (cf. the forgetting of stimulus attributes discussed by Spear and Riccio 1994). In particular, if the memory of phase 2 treatment predominated at test (i.e., a recency effect), and spatial control generalized from LM T to LM L, then cup choice to LM L may appear similar to that controlled by LM T during phase 2. Furthermore, generalization from LM T to

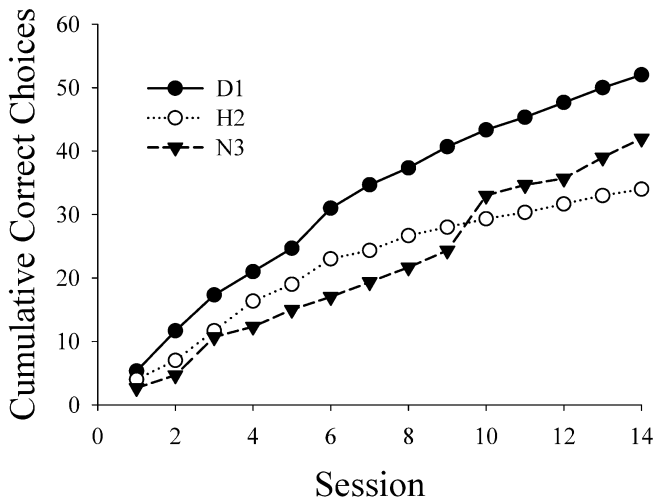


Fig. 3 Cumulative number of correct cup choices to find goal 2 during phase 2

LM L should have interfered with expression of spatial control by the L→T→goal 2 higher-order map produced by the integration of phase 1 and phase 2 learning.

In an attempt to enhance the detection of the inferred vector produced by an integrated spatial map, we conducted two test sessions during which subjects received one phase 1 warm-up trial, followed by one phase 2 warm-up trial, and followed by a test trial. During these sessions, cup I was the most frequently chosen (mean =0.22) cup (bottom panel of Fig. 4). By contrasting both panels of Fig. 4 it appears that the inclusion of the phase 1 warm-up trials during the test sessions was critical to expressing the integration of the L→T and T→goal 2 vectors at test.

A two-way repeated measures ANOVA on mean proportion of choices by location and test session (with and without phase 1 warm-up trials) as factors revealed a main effect of test session, $F_{(1,6)}=11.65$, $P<0.02$, and an interaction between test session and cup location, $F_{(2,6)}=37.56$, $P<0.01$. Planned comparisons were conducted to isolate the source of the interaction. Without the

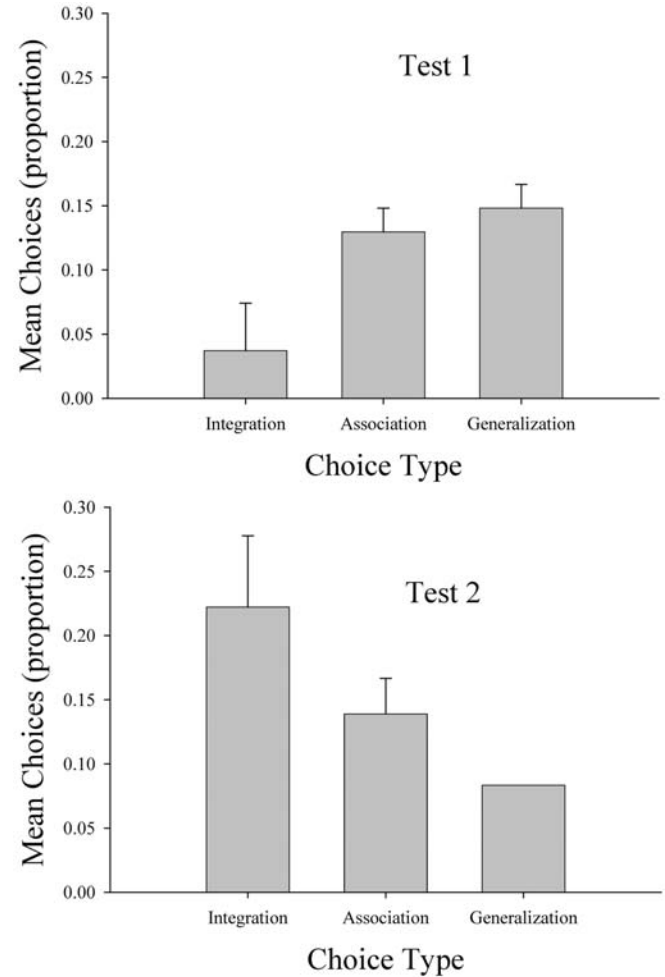


Fig. 4 Mean proportion of choices to cups integration (I), association 1 (A), and generalization 2 (G) for all subjects on the first three test trials (*top panel*) and the last two test trials (*bottom panel*). Error bars show the standard error of the mean

phase 1 warm-up trials (Fig. 4, top panel), cup I was chosen significantly less than cups A and G, $F_{S(1,2)} > 6.0$, $P_s < 0.05$. However, when a phase 1 warm trial was included in the test session (Fig. 4, bottom panel), cup I was chosen more frequently than cup G, $F_{(1,2)} = 8.23$, $P < 0.05$. No other comparisons within each type of test

session were significant. Finally, comparisons between the same cup location across session type (with and without phase 1 warm-up trials, bottom and top panels, respectively) revealed an increase in choices to cup I, $F_{(1,2)} = 75.88$, $P < 0.001$, and a drop in choices to cup G, $F_{(1,2)} = 10.67$, $P < 0.02$. There was no change in choices to

Table 1 Grid reflects the spatial distribution of all choices at test (series 1 and series 2) for all pigeons and for each pigeon separately. The distribution is centered around putative cup I, which places the test landmark (LM L) at the location indicated by the thickened cell

boarder between cells E3 and F3. Numbers represent proportion of choices across all three test trials in series 1 and the two test trials of series 2. (Note: the grid of response locations for pigeon N3 has been up-down reversed for expository purposes)

Pigeon

Test Series 1

Test Series 2

All Birds

	A	B	C	D	E	F	G
1	0	0	0.02	0	0	0	0
2	0	0	0.04	0.02	0.06	0.04	0
3	0	0	0	0.04	0.11	0.07	0
4	0	0	0.04	0.04	0.13	0.06	0
5	0	0	0.06	0.02	0.07	0.07	0
6	0	0	0.04	0.06	0.04	0.02	0
7	0	0	0	0	0	0	0

	A	B	C	D	E	F	G
1	0	0	0	0.03	0	0	0
2	0	0	0	0.06	0.03	0.08	0
3	0	0	0.03	0.03	0.14	0.03	0
4	0	0	0.06	0.22	0.08	0.03	0
5	0	0	0	0.06	0.06	0.03	0
6	0	0	0	0	0.03	0.03	0
7	0	0	0	0	0	0	0

Key
D4 = Integration
E3 = Association
E4 = Generalization
Increase by > 15%

D1

	A	B	C	D	E	F	G
1	0	0	0.06	0	0	0	0
2	0	0	0	0	0.06	0.06	0
3	0	0	0	0.06	0.17	0.11	0
4	0	0	0	0	0.11	0.11	0
5	0	0	0.06	0.06	0	0	0
6	0	0	0.06	0.06	0.06	0	0
7	0	0	0	0	0	0	0

	A	B	C	D	E	F	G
1	0	0	0	0.08	0	0	0
2	0	0	0	0.17	0	0.08	0
3	0	0	0	0	0.17	0	0
4	0	0	0.08	0.17	0.08	0	0
5	0	0	0	0.17	0	0	0
6	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0

H2

	A	B	C	D	E	F	G
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0.06	0
3	0	0	0	0	0.06	0.06	0
4	0	0	0.06	0.11	0.17	0.06	0
5	0	0	0.06	0	0.11	0.11	0
6	0	0	0.06	0.06	0	0.06	0
7	0	0	0	0	0	0	0

	A	B	C	D	E	F	G
1	0	0	0	0	0	0	0
2	0	0	0	0	0.08	0.08	0
3	0	0	0.08	0	0.08	0	0
4	0	0	0.08	0.33	0.08	0.08	0
5	0	0	0	0	0.08	0	0
6	0	0	0	0	0	0	0
7	0	0	0	0	0	0	0

N3

	A	B	C	D	E	F	G
1	0	0	0	0	0	0	0
2	0	0	0.11	0.06	0.11	0	0
3	0	0	0	0.06	0.11	0.06	0
4	0	0	0.06	0	0.11	0	0
5	0	0	0.06	0	0.11	0.06	0
6	0	0	0	0.06	0.06	0	0
7	0	0	0	0	0	0	0

	A	B	C	D	E	F	G
1	0	0	0	0	0	0	0
2	0	0	0	0	0	0.08	0
3	0	0	0	0.08	0.17	0.08	0
4	0	0	0	0.17	0.08	0	0
5	0	0	0	0	0.08	0.08	0
6	0	0	0	0	0.08	0.08	0
7	0	0	0	0	0	0	0

cup A across sessions. These data suggest that cup choice on tests without a phase 1 warm-up trial was guided in part by both the memory of the L→goal 1 vector and generalization from the T→goal 2 vector. However, including phase 1 warm-up trials during testing reduced generalization from T and increased control by the L→goal 2 vector inferred from the integrated L→T→goal2 spatial map.

Table 1 shows the spatial distribution of choices in test series 1 and 2 for all three pigeons combined and for each individually. The table shows that each of the three pigeons chose cup I more on test series 2 than on test series 1 (shaded cells). This increase was not accompanied by an increase in choices of other cups, except for subject D1 which showed an equal increase at one other location. For subjects H2 and N3, cup I experienced the greatest increase in choices relative to all other cup locations. In fact, cup I was the only cup location visited by each bird in every session of test series 2 further suggesting its increased salience. These changes in behavior towards cup I support the conclusion that the phase 1 reminder trials did specifically enhance control by the integration of the L→T and T→goal 2 spatial maps, rather than by generally increasing choices to cups distal to LM L at test. Otherwise, the distribution of remaining choices during testing shows a fair degree of scatter around the landmarks in general. This was likely due to the fact that any cup choice was relatively “cheap” as it took very little time and effort to quickly sift through a cup while just passing by.

Discussion

In this experiment, the pigeons appeared to integrate the spatial vectors acquired in two earlier training phases in a manner similar to that found by Matzel et al. (1988) in sensory preconditioning experiments with rats. At least when reminder trials were provided, this integration allowed subjects to compute a novel L→goal 2 vector. As such, these results extend the findings of Matzel et al. (1988) for the integration of A→B and B→US temporal vectors to the spatial domain, and suggest that similar mechanisms may govern temporal (e.g., the temporal coding hypothesis, Miller and Barnett 1993; Savastano and Miller 1998) and spatial processes.

These results add to the growing evidence that pigeons encode the spatial relationships between a hidden goal and individual landmarks near the goal (see reviews by Cheng and Spetch 1998, 2001). Pigeons have been shown to acquire separate landmark–goal vectors independently even in situations involving multiple landmarks (Spetch and Mondloch 1993; Spetch et al. 1996,1997). For example, after learning to find a hidden food goal in the presence of an array of landmarks, search locations on probe tests involving transformations of the landmark array (e.g., expansions of landmark locations or removal of individual landmarks) indicate that pigeons had encoded the vector between one or more individual landmarks and the goal.

In addition to encoding landmark–goal vectors, we found that pigeons also encoded landmark–landmark vectors. The fact that our pigeons searched most frequently at location I during the second series of tests suggests that they encoded the spatial relationship between LM L and LM T during phase 1 treatment. Furthermore, the difference in the pattern of search locations between the first and second series of tests indicates that retrieval of this L→T vector was necessary for pigeons to compute the L→goal 2 vector. The encoding of landmark–landmark and landmark–goal vectors allowed the pigeons to integrate these maps to construct a larger, higher-order map. The higher-order map can then be used to compute novel relationships between landmarks or between a landmark and a goal. These computed landmark–goal vectors can be used to guide a search in the presence of landmarks that had not been directly associated with the goal.

An interesting observation is that the integration effect required the presentation of phase 1 warm-up trials in addition to the phase 2 warm-up trials prior to testing. Without the phase 1 warm-up trials, subjects tended to be controlled by both the LM L→goal 1 association established during phase 1 and generalization of the LM T→goal 2 association to LM L. This shift suggests that there are several psychological strategies available to the animal in the test situation, and the strategies that exert control over behavior depend on experiences surrounding the test. For example, it is commonly observed that more recent experiences influence test behavior more than more remote experiences. Because more than a month had intervened between phase 1 training and test series 1, the effects of phase 2 training may have been more potent at the time of testing. However, phase 1 training did affect performance as well, as indicated by the proportion of choices to the location signaled by LM L during phase 1 (i. e., goal 1). The addition of phase 1 trials prior to testing may have increased the retrieval of both phase 1 and phase 2 associations, thereby allowing for their integration to subsequently influence search locations at test.

The integration of spatial maps and computation of novel spatial relationships would be an adaptive function allowing animals to respond flexibly in the natural environment. For example, the computation of a novel vector between a landmark and a goal would allow the animal to find the goal when it only has access to that landmark, or when visual beacons are obstructed from view (e.g., Brown et al. 1993; Brown and Bing 1997). Likewise, the ability to flexibly use novel routes while navigating may allow the animal to escape from dangerous situations, such as when a prey is faced with a predator, or allow it to navigate in less familiar terrain, as when a migrating bird has been blown off course. The ability to use novel routes would be dramatically enhanced by the ability to compute novel spatial vectors from a limited set of landmarks. We suggest that the ability to compute novel vectors requires the integration of landmark–landmark and landmark–goal vectors to form higher-order spatial maps.

Our emphasis on detailing the structural properties of a cognitive map process does not detract from the important role implicated for other mechanisms of pigeon navigation, especially at different spatial scales. Other implicated mechanisms include the use of a magnetic compass (e.g., Wiltschko and Wiltschko 2003), olfaction (e.g., Able 1996), and other uses for landmarks and environment geometry (e.g., Macphail 2002), to name a few. Many of these other abilities have been demonstrated in experiments involving pigeons homing over long distances. It is likely that the various navigational mechanisms contribute differentially to various parts of the homing journey, such as a compass mechanism guiding the bird over long distances, and cognitive maps, familiar landmarks, and beacon homing playing a larger role over shorter distances or in local settings. Ethological experiments conducted in naturalistic settings have been important in demonstrating the navigational prowess of the pigeon, and have helped elucidate the nature of the guiding mechanisms. However, well-controlled laboratory settings, such as those used for the current research, can establish the existence of important psychological mechanisms (e.g., the cognitive map) as a first step toward identifying their potential role in behavior in the natural world.

In addition to extending to the spatial domain, evidence for integration effects, these results provide stronger evidence for an integration process than has been shown in temporal maps in Pavlovian conditioning. For example, Matzel et al. (1988) provided only indirect evidence for the integration of separate temporal vectors by looking at the magnitude of conditioned suppression. However, in their paradigm responses were not timed to the CS in any meaningful way. In the current study of spatial integration, we have reported direct evidence that pigeons encoded specific spatial vectors in each phase of conditioning, and integrated those vectors. Rather than inferring acquisition and integration of associations based on the strength of responding, we were able to show acquisition and integration directly through the spatial location of subjects' choices themselves. Consequently, this study adds to the growing body of evidence that animals can integrate separately acquired vectors (maps) in both the spatial and temporal domains and compute novel relationships between elements that had not been directly paired.

Returning to an issue raised in the latter part of the Introduction, the utility of the cognitive map concept has been challenged on two fronts (e.g., Bennett 1996; Shettleworth 1998). First, the concept itself is poorly defined and inconsistently used throughout the literature. Second, it has proven notoriously difficult to effectively rule out alternative explanations for the hallmarks of cognitive mapping, such as the use of novel short cuts. As stated previously, we are restricting our use of the term to the most common feature of most of its various uses, that it encodes an allocentric representation of objects and places in space. Two limitations of earlier research on cognitive maps is that either (1) the animal is allowed to navigate its environment during training rendering uncertainty in whether "novel" routs are truly novel, or (2)

preventing the subject from traversing a particular route, such as a blocked maze arm, does not eliminate the possibility that the animal can use that shortcut because it can see a beacon located near or at the goal.

The current experiment eliminates these alternatives in three ways. First, the goal was presented at different locations in the search space across trials. This rendered useless the global room cues and features of the test arena. Second, on test trials we eliminated the only spatially consistent cue to the goal (LM T) that was present during phase 2 of training. Finally, by exposing the subject to the L→T and T→goal 2 maps in a piecemeal fashion, the target L→goal 2 vector was absent from training, and thus was truly novel at test. Thus, the only viable explanation for why the subject searched at location I at test is that the subject must have encoded the vector between LM L and LM T during phase 1, the vector between LM T and goal 2 during phase 2, and integrated these vectors so that it could compute the LM L→goal 2 vector at test. This may be the most conclusive demonstration to date that an animal can encode an allocentric representation of objects and locations in physical space, and use that representation to compute a novel spatial relationship. The study of the role of associative processes in establishing spatial (and temporal) relationships in conditioning experiments may be a fruitful method for studying allocentric spatial representations; a central feature of a cognitive map.

These results add to the growing corpus of evidence for the important role that associative learning plays in spatial behavior. There has already been a fair amount of research demonstrating cue-competition effects, such as overshadowing (e.g., Cheng et al. 1987; Cheng 1989; March et al. 1992; Spetch 1995; Roberts and Pearce 1999; Sanchez-Moreno et al. 1999) and blocking (Diez-Chamizo et al. 1985; Rodrigo et al. 1997), in the spatial domain (see reviews by Chamizo 2002, 2003). Other well-established associative phenomena, such as generalization and peak-shift, have been shown in the spatial domain as well (see review by Cheng and Spetch 1998). The current experiment adds to this evidence by demonstrating Pavlovian higher-order conditioning of associations between landmarks using a spatial task.

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References

- Able KP (1996) The debate over olfactory navigation by homing pigeons. *J Exp Biol* 199:121-124

- Barnet RC, Miller RR (1996) Second-order excitation mediated by a backward conditioned inhibitor. *J Exp Psychol Anim Behav Process* 22:279–296
- Barnet RC, Arnold HM, Miller RR (1991) Simultaneous conditioning demonstrated in second-order conditioning: evidence for similar associative structure in forward and simultaneous conditioning. *Learn Motiv* 22:253–268
- Barnet RC, Cole RP, Miller RR (1997) Temporal integration in second-order conditioning and sensory preconditioning. *Anim Learn Behav* 25:221–233
- Bennett AT (1996) Do animals have cognitive maps? *J Exp Biol* 199:219–224
- Brown MF, Bing MN (1997) In the dark: spatial choice when access to spatial cues is restricted. *Anim Learn Behav* 25:21–30
- Brown MF, Rish PA, VonCulin JE, Edberg JA (1993) Spatial guidance of choice behavior in the radial-arm maze. *J Exp Psychol Anim Behav Process* 19:195–214
- Cartwright BA, Collett TS (1983) Landmark learning in bees: experiments and models. *J Comp Physiol* 151:521–543
- Cavoto KK, Cook RG (2001) Cognitive precedence for local information in hierarchical stimulus processing by pigeons. *J Exp Psychol Anim Behav Process* 27:3–16
- Chamizo VD (2002) Spatial learning: conditions and basic effects. *Psicol Spec Issue Spatial Learn Cogn* 23:33–57
- Chamizo VD (2003) Acquisition of knowledge about spatial location: assessing the generality of the mechanism of learning. *Q J Exp Psychol* 56B:102–113
- Cheng K (1989) The vector sum model of pigeon landmark use. *J Exp Psychol Anim Behav Process* 15:366–375
- Cheng K, Spetch ML (1998) Mechanisms of landmark use in mammals and birds. In: Healy S (ed) *Spatial representation in animals*. Oxford University Press, Oxford, pp 1–17
- Cheng K, Spetch ML (2001) Landmark-based spatial memory in pigeons. In: Cook RG (ed) *Avian visual cognition*. <http://www.pigeon.psy.tufts.edu/avc/cheng/>
- Cheng K, Collett TS, Pichard A, Wehner R (1987) The use of visual landmarks by honeybees: bees weight landmarks according to their distance from the goal. *J Comp Physiol A* 161:469–475
- Diez-Chamizo V, Sterio D, Mackintosh NJ (1985) Blocking and overshadowing between intra-maze and extra-maze cues: a test of the independence of locale and guidance learning. *Q J Exp Psychol Comp Physiol Psychol* 37:235–253
- Ellen P, Soteres BJ, Wages C (1984) Problem solving in the rat: piecemeal acquisition of cognitive maps. *Anim Learn Behav* 12:232–237
- Hanley GL, Levine M (1983) Spatial problem solving: the integration of independently learned cognitive maps. *Mem Cogn* 11:415–522
- Honig WK (1981) Working memory and the temporal map. In: Spear NE, Miller RR (ed) *Information processing in animals: memory mechanisms*. Erlbaum, Hillsdale, N.J.
- Macphail EM (2002) The role of the avian hippocampus in spatial memory. *Psicologica* 23:93–108
- March J, Chamizo VD, Mackintosh NJ (1992) Reciprocal overshadowing between intra-maze and extra-maze cues. *Q J Exp Psychol Comp Physiol Psychol* 45:49–63
- Matzel LD, Held FP, Miller RR (1988) Information and expression of simultaneous and backward associations: implications for contiguity theory. *Learn Motiv* 19:317–344
- Miller RR, Barnet RC (1993) The role of time in elementary associations. *Curr Dir Psychol Sci* 2:106–111
- O’Keefe J, Nadel L (1978) *The hippocampus as a cognitive map*. Oxford University Press, Oxford
- Potegal M (1982) Vestibular and neostriated contributions to spatial orientation. In: Potegal M (ed) *Spatial abilities: developmental and physiological foundations*. Academic, New York, pp 361–387
- Poucet B (1993) Spatial cognitive maps in animals: New hypotheses on their structure and neural mechanisms. *Psychol Rev* 100:163–182
- Roberts ADL, Pearce JM (1999) Blocking in the Morris swimming pool. *J Exp Psychol Anim Behav Process* 25:225–235
- Rodrigo T, Chamizo VD, McLaren IPL, Mackintosh NJ (1997) Blocking in the spatial domain. *J Exp Psychol Anim Behav Process* 23:110–118
- Sanchez-Moreno J, Rodrigo T, Chamizo VD, Mackintosh NJ (1999) Overshadowing in the spatial domain. *Anim Learn Behav* 27:391–398
- Savastano HI, Miller RR (1998) Time as content in Pavlovian conditioning. *Behav Process* 44:147–162
- Shettleworth SJ (1998) *Cognition, evolution, and behavior*. Oxford University Press, New York
- Spear NE, Riccio DC (1994) *Memory: phenomena and principles*. Allyn & Bacon, Needham Heights, Mass.
- Spetch ML (1995) Overshadowing in landmark learning: touch-screen studies with pigeons and humans. *J Exp Psychol Anim Behav Process* 21:166–181
- Spetch ML, Mondloch MV (1993) Control of pigeons spatial search by graphic landmarks in a touch-screen task. *J Exp Psychol Anim Behav Process* 19:353–372
- Spetch ML, Cheng K, MacDonald SE (1996) Learning the configuration of a landmark array .1. Touch-screen studies with pigeons and humans. *J Comp Psychol* 110:55–68
- Spetch ML, Cheng K, MacDonald SE, Linkenhoker BA, Kelly DM, Doerkson SR (1997) Use of landmark configuration in pigeons and humans. Generality across search tasks. *J Comp Psychol* 111:14–24
- Thinus-Blanc C (1996) *Animal spatial cognition: behavioural and neural approaches*. World Scientific, Singapore
- Tolman EC (1948) Cognitive maps in rats and men. *Psychol Rev* 55:189–208
- Wehner R, Srinivasan MV (1981) Searching behavior of desert ants, genus *Cataglyphis* (Formicidae, Hymenoptera). *J Comp Physiol A* 142:315–338
- Wiltschko W, Wiltschko R (2003) Avian navigation: from historical to modern concepts. *Anim Behav* 65:257–272