

Sensory Preconditioning in Spatial Learning Using a Touch Screen Task in Pigeons

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The authors used a touch screen-based visual-search task to investigate spatial integration in pigeons. First, pigeons were presented with a consistent spatial relationship between compound visual landmarks (LMs) A–X and B–Y, separately. Next, pigeons learned to find a hidden goal on the monitor in the presence of LMs A and B. The goal bore a consistent spatial relationship to LM A, but not to LM B. On nonreinforced probe tests, the peak and distribution of responses to LM X suggest that pigeons computed a novel X–goal spatial relationship on the basis of X–A and A–goal spatial vectors. Responses to LM Y, however, revealed no evidence of spatial integration. These results replicate and extend those of A. P. Blaisdell and R. G. Cook (2005) using an open-field task.

Keywords: Spatial map, sensory preconditioning, integration, spatial vector, associative, pigeon

It is important to the survival of many animal species that they accurately represent their world. Learning about the temporal and spatial texture of the environment enables them to track biologically important resources and events. For example, food-storing birds have been shown to remember “where” (Balda & Kamil, 1992; Shettleworth & Krebs, 1982) and “when” (Clayton & Dickinson, 1998) they stored food. Likewise, it behooves prey species to remember where they had previously encountered predators to better avoid them later. Tolman (1948) coined the term *cognitive map* to describe what animals learn about the space around them. According to Tolman, animals encode something like a topographical map of their surroundings. In their landmark book, *The Hippocampus as a Cognitive Map*, O’Keefe and Nadel (1978) expanded on Tolman’s definition by delineating two different spatial systems: the locale system for learning places and the guidance system for learning routes.

Recent studies of spatial learning suggest that associative processes play an integral role in spatial behavior. These demonstrations have typically used analogs to a Pavlovian conditioning procedure, in which an initially neutral conditioned stimulus (CS)

acquires the ability to elicit a conditioned response through pairings with a biologically significant unconditioned stimulus (US). Examples of associative phenomena that have been demonstrated in spatial tasks include cue–competition effects (see reviews by Chamizo, 2002, 2003; but see Hayward, McGregor, Good, & Pearce, 2003), latent inhibition (e.g., Prados & Redhead, 2002), and the peak shift effect (e.g., Cheng & Spetch, 2002). The parallels between associative processes in both conventional and spatial tasks support an important role for associative learning in the acquisition of spatial relationships.

If associative processes operate on spatial information, then how do they contribute to the development of cognitive maps? Higher-order conditioning is one candidate mechanism that has received empirical support for its role in building cognitive maps. Higher-order conditioning is the mediation of conditioning to one CS that has not been paired with a US by another CS that has been paired with the US. The two best-known examples of higher-order conditioning are sensory preconditioning and second-order conditioning. In a sensory preconditioning procedure, two neutral stimuli, CS2 and CS1 (e.g., audiovisual cues, flavors, etc.), are presented together to establish a CS2→CS1 association. Subsequently, one stimulus, CS1, is paired with a biologically significant US, such as food or shock. These pairings establish a CS1→US association. It is these CS2→CS1 and CS1→US associations that mediate the development of a conditioned response to CS2, despite never having been paired directly with the US (Brogden, 1939). The second-order conditioning procedure is similar except in that CS1 is paired with the US prior to CS2–CS1 pairings. These procedures allow CS1 to mediate an associative link between CS2 and the US.

A large body of evidence has accumulated supporting the notion that the association between a CS and a US encodes information about their temporal relationship. That is, the subject forms something like a temporal map between the CS and US, which includes the direction (e.g., forward or backward) and distance (how far) between them (i.e., a temporal vector). This temporal map allows the CS to serve as a temporal landmark (LM) for the US. Miller and his colleagues have established that novel temporal vectors

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can be computed through the integration of temporal maps. This evidence has been established using Pavlovian sensory preconditioning and second-order conditioning procedures in rats (Barnet, Arnold, & Miller, 1991; Barnet, Cole, & Miller, 1997; Barnet & Miller, 1996; Matzel, Held, & Miller, 1988) and humans (Arcedi, Escobar, & Miller, 2003). Miller and his colleagues derived strong evidence of temporal integration by manipulating temporal relationships among stimuli. For example, Matzel et al., 1988, explored temporal integration using a sensory preconditioning procedure. In Phase 1, two CSs were paired together with a forward (i.e., CS2→CS1) relationship. In Phase 2, rats received simultaneous (i.e., CS1–US, Experiment 1) or backward (i.e., US→CS1, Experiment 2) pairings of CS1 and the US. Rats that received simultaneous or backward conditioning in Phase 2 showed little conditioned responding to CS1 relative to control rats that were forward conditioned (i.e., CS1→US). However, CS2 evoked a strong conditioned response in all three groups, indicating that both CS2–CS1 and CS1–US associations were established. To explain the strong responding to CS2 but weak responding to CS1 in the simultaneous group and backward group, Matzel et al. hypothesized that rats formed a temporal map among paired stimuli (i.e., CS2–CS1 and CS1–US) and integrated separately acquired maps that contained a common element (i.e., CS1), thereby creating a CS2–US temporal map. These findings inspired the development of the temporal coding hypothesis (Savastano & Miller, 1998).

The goal of the current experiment was to determine whether higher-order conditioning, a well-established phenomenon of associative learning, provides a mechanism underlying the integration of spatial information into a map. Support for this mechanism would add to its role in the formation of temporal maps discussed above. The formation of mediated associations makes higher-order conditioning an attractive candidate mechanism for the linking together of LMs and goals into an integrated allocentric representation. For example, if on separate occasions LM1 becomes associated with a hidden food goal and LM2 becomes associated with LM1, then a higher order associative link between LM2 and the goal could be formed. If associations between LM2 and LM1 and between LM1 and the goal encode spatial information (distance and direction; i.e., a spatial vector), as associations between CS2 and CS1 and between CS1 and the US encode temporal information, then these associative links could be used to derive the spatial relationship between LM2 and the goal.¹ This would permit the subject to make a spatial inference and find the hidden goal in the presence of the novel situation of LM2 alone. Just such an inference is required to go from CS2→CS1 and CS1→US to CS2→US in a standard sensory preconditioning experiment. Furthermore, this type of spatial inference dovetails nicely with the important functional property Tolman (1948) ascribed to the cognitive map, that is, its role in allowing the animal to make a detour or novel shortcut.

Blaisdell and Cook (2005) explored the integration of spatial maps in an analog to the Pavlovian sensory preconditioning procedure using an open-field search task in pigeons. Hungry pigeons were trained to find food hidden in 1 of 16 food cups. Although the location of food varied randomly from trial to trial, a visual LM (LM1) was placed at a fixed distance and direction from the hidden food goal. The pigeons learned to use LM1 to find the location of a hidden goal, indicating that they had learned an association

between LM1 and the goal. This association included the spatial relationship between LM1 and the goal; that is, an LM1→goal spatial vector. A spatial vector is a spatial representation that includes the distance and direction between two objects or locations. Prior to establishment of the LM1→goal spatial vector, pigeons were presented with another LM (LM2) at a fixed spatial location relative to LM1 to establish an LM2→LM1 association. This experience should have resulted in the pigeons encoding the LM2→LM1 spatial vector. After both training phases were complete, pigeons received a test in which they were presented with only LM2. If they had encoded the LM2→LM1 and LM1→goal spatial vectors, they should have formed an LM2→LM1→goal higher-order associative chain. This higher-order chain would allow subjects to compute the novel LM2→goal spatial vector, which should then guide the pigeons to search at a specific predictable location within the arena. Blaisdell and Cook's results supported this prediction, suggesting that the pigeons had integrated two spatial vectors that shared a common element (LM1).

Our experiment replicates and extends Blaisdell and Cook's (2005) results by using pigeons in a spatial-search task presented on a touch screen-equipped monitor. Blaisdell and Cook reported only a single experiment; thus, a replication would place the phenomenon on firmer ground. The touch screen procedure provides distinct advantages over the open-field procedure for the study of associative processes of spatial cognition. The most important advantage for our purpose is that the touch screen task is virtually free of potential confounds that may be introduced by nonassociative spatial processes. In the real world, a full and diverse range of spatial processes has been shown to be engaged during navigation of three-dimensional space. Processes that use optic flow, dead reckoning, and motion parallax have been shown to play an important role in spatial behavior in natural settings (Gallistel, 1990; Healy, 1998; see also the *Journal of Experimental Biology*, Wehner, Lehrer, & Harvey, 1996, special issue on spatial behavior). These processes, however, are presumably not engaged in subjects' processing of spatial information on the two-dimensional surface of a touch screen. Thus, spatial learning tasks presented on a touch screen minimize these potential confounds, allowing for a purer assessment of the contribution of associative processes to spatial behavior guided by an allocentric representation. The touch screen task offers other advantages as well. It provides greater control over the presentation of stimuli and the recording of the spatiotemporal distribution of subject's responses. Many more trials can be conducted in each daily session, allowing for the accumulation of larger data sets and therefore more stable

¹ The view that associations encode more than a single value, such as the strength between the two associates, is unconventional. However, the results from research on the temporal coding hypothesis reviewed here, as well as the large body of work on interval timing, suggest that temporal information is encoded as part of the association. We are further suggesting that spatial information is also encoded as part of the association. An association that encodes temporal and spatial information not only allows the CS to elicit a conditioned response but also determines the temporal and spatial properties of the response itself. One could probably formulate an interpretation of these experiments in other ways, but we adopt this position as a heuristic by which to probe the nature of spatial and temporal learning. Heuristics are best evaluated in terms of their successes in driving the discovery of new behavioral phenomena.

behavior. Finally, a greater variety of experimental and control conditions can easily be conducted, which can include greater flexibility in using within-subject and between-subjects designs.

In the current experiment, pigeons were first trained on a spatial search task in which they were rewarded with mixed grain for pecking at a hidden goal location on the computer screen. A Pavlovian sensory preconditioning procedure was then used to explore the integration of spatial maps between visual LMs presented on the screen. In Phase 1, two visual LMs (LMs A and X), with a consistent spatial relationship to each other, were presented for 30 s without food reinforcement. Pigeons also received nonreinforced presentations of two other LMs (B and Y) in the same manner. In Phase 2, pigeons were reinforced for pecking at a hidden goal location that bore a consistent spatial relationship to first-order LM A but an inconsistent spatial relationship to first-order LM B. Pigeons then received separate 30-s nonreinforced probe tests of second-order LMs X and Y. The distribution of pecks on test trials with LM X indicated that pigeons had acquired $X \rightarrow A$ and $A \rightarrow$ goal spatial vectors that were used to compute (i.e., infer) an $X \rightarrow$ goal spatial vector. However, the distribution of pecks on LM Y probe-test trials did not provide evidence for integration, indicating that a consistent spatial relationship between reinforced LM A and the goal during Phase 2 was necessary for making a spatial inference. This experiment provides strong evidence that higher-order Pavlovian conditioning may serve as a mechanism by which an allocentric cognitive map is formed.

Method

Subjects

Three experimentally naive male white carneau and two experimentally naive male racing homing pigeons (*Columba livia*; Double T Farm, IA) served as subjects. Pigeons were maintained at 80% to 85% of their free-feeding weights. They were individually housed in a colony with a 12-hr light–dark cycle and had free access to water and grit. Experimental procedures occurred during the light portion of the cycle.

Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide \times 36 cm deep \times 38 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550M) visible through a 23.2 \times 30.5-cm viewing window in the middle of the front panel of the chamber. The bottom edge of the viewing window was 13 cm above the chamber floor. Pecks to the monitor were detected by an infrared touch screen (Carroll Touch, Elotouch Systems, Fremont, CA) mounted on the front panel. A 28-V house light located in the ceiling of the box was illuminated at all times, except when an incorrect choice was made. A food hopper (Coulbourn Instruments, Allentown, PA) was located in the center of the front panel, its access hole flush with the floor. All experimental events were controlled and recorded with a Pentium III-class computer (Dell, Austin, TX). A video card controlled the monitor in the super video graphics array graphics mode (800 \times 600 pixels).

Procedure

Stimulus displays. Five visual stimuli served as LMs. A white Z shape was used as the training LM for all subjects. A yellow I shape, an orange U shape, a gray double-dot, and a purple star served as visual LMs, counterbalanced across subjects. These stimuli were approximately 2.3 \times 2.3 cm in diameter. In addition, a 3-mm² dark-gray square marked the

center of each location on the 8 \times 7 grid of response locations (described below).²

Initial training. Subjects had previously been trained to retrieve mixed grain from the food hopper and had been autoshaped to peck a centrally presented white 2.5-cm circular ready signal. Once responding to the ready signal had been established, it was replaced with a 2.0-cm diameter white square goal marker and the response grid and training LM was introduced. A 20.3-cm wide \times 17.8-cm high search space on the computer monitor was divided into an 8 \times 7 grid. Each grid unit contained a 2-cm² response area that served as a possible goal location, with 0.5-cm space between adjacent grid units. On each trial, the goal was presented at 1 randomly determined location on the grid from the set of 56 grid locations. The goal location was visually marked with the 2-cm² white square that was gradually faded out as described below. The training LM bore a spatial location fixed 4 cm to the left and 2.5 cm above the goal. Initially, during each 100-trial session a single peck at the goal caused the hopper to be illuminated and raised for 2.5 s. During this phase of training, the response requirement was gradually increased over sessions, tailored to each pigeon's performance, from an FR-1 to a VR-3 schedule of reinforcement (range = 1 to 5). Each trial on which this requirement was met ended in 2.5 s of reinforcement. Alternatively, a trial ended without reinforcement and with a 30-s timeout with the house light extinguished if the pigeon met any of three conditions prior to reaching the requisite number of pecks at the goal: 3 cumulative pecks at the LM, 20 cumulative pecks at the set of nongoal locations, or 0 peck responses for 2 min consecutively. Both correct and incorrect trials were followed by a 10-s intertrial interval with the house light on. The larger, brighter goal marker was initially presented to facilitate acquisition of the task, but the size and brightness were gradually reduced until it matched the other response grid markers. This reduction was carried out within and between sessions by dimming and reducing the size of the marker depending on each pigeon's accuracy. Finally, subjects were required to search for the hidden goal location based solely on its spatial relationship with the training LM. By the completion of pretraining, the goal was marked with a 1-cm² medium-gray square for the first 5 trials of each 100-trial session. After the 5th trial, the goal marker was identical to those at all other grid locations (i.e., 3-mm² dark-gray square).

Phase 1: Sensory preconditioning treatment. After subjects performed at or above 80% accuracy on two consecutive sessions on which 5 trials contained a nondifferentially marked goal location we initiated sensory preconditioning treatment. Pigeons received three types of trials during each 100-trial session. Ninety trials involved the training LM as described above (with the first 5 trials of each session marked with the 1-cm² medium-gray square). The other 10 trials involved nonreinforced sensory preconditioning trials with either compound LMs AX or BY on separate trials. Preconditioning trials were embedded randomly within the session with the constraint that no preconditioning trial occurred prior to the 20th trial of the session. Five of the 10 daily preconditioning trials consisted of pairings between first-order LM A and second-order LM X. The other 5 preconditioning trials consisted of pairings between first-order LM B and second-order LM Y (see Figure 1A for examples of both trial types). The LMs were always placed with LMs A and B 4.5 cm (center to center) to the left of LMs X and Y, respectively. The location of the LMs on the screen

² We initially set out to train pigeons to peck at an unmarked screen location some distance away from the landmark. However, pilot studies conducted in our laboratory found that many pigeons were reluctant to peck at a location that was not visually marked in some manner. Marking the entire response grid with identical markers alleviated this problem by giving the pigeons a visible target to peck at. Because all of the response locations are marked in an identical fashion, finding the goal (i.e., choosing which marked location to peck at) could most optimally be solved through the use of the consistent landmark.

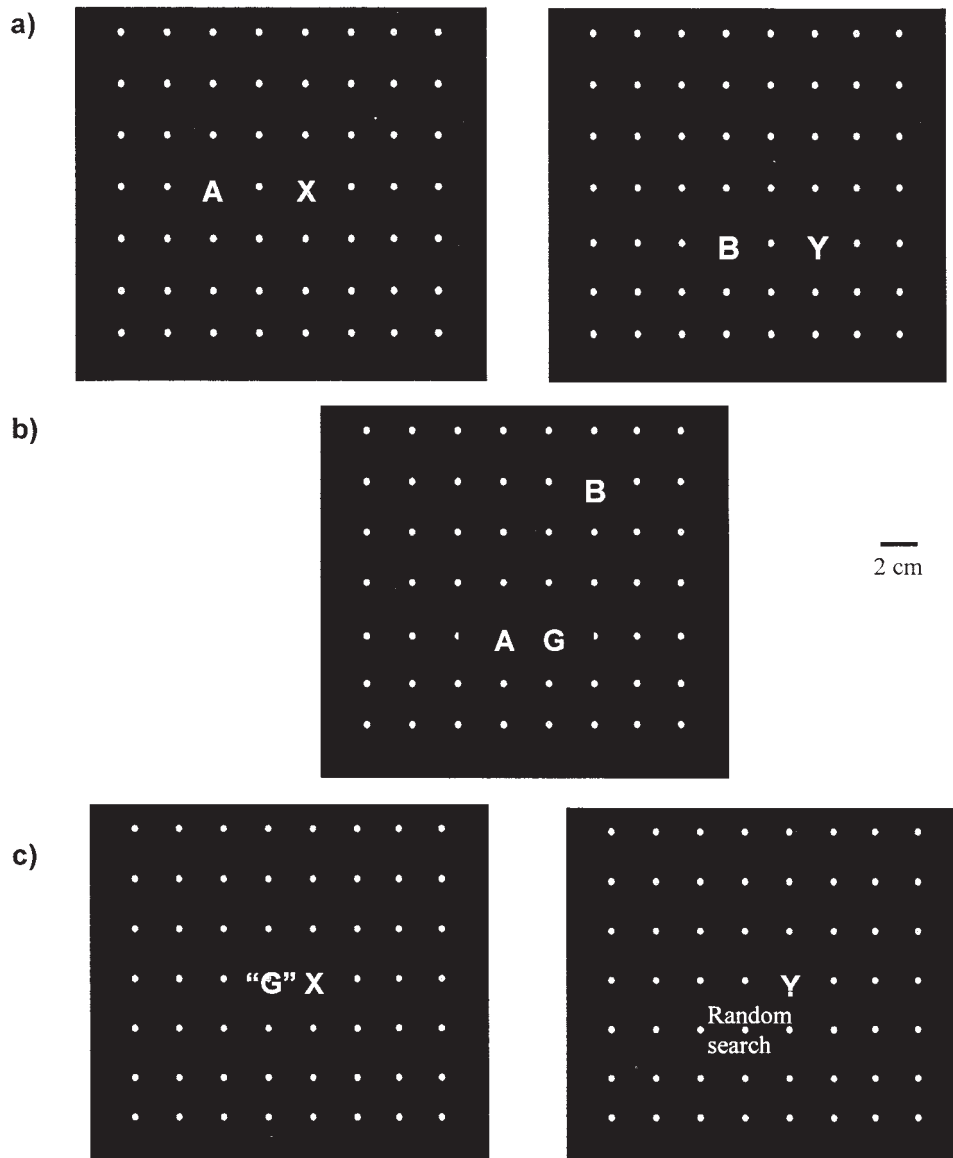


Figure 1. Diagrams of the landmark (LM) configuration on the touch screen. The circles denote the layout of the response grid. A: spatial relationship between LMs A and X and LMs B and Y during Phase 1 of sensory preconditioning. B: relationship between the consistent LM A to the goal during Phase 2; LM B was also present on Phase 2 trials, but its spatial relationship to the goal was randomly determined. C: predicted peak location of search on test trials with LM X and LM Y; “G” indicates the expected goal location based on the integration of the LM A–Goal and LM X–LM A spatial vectors. “Random search” indicates the expected pattern of search on LM Y trials.

was randomized across trials. Sensory preconditioning trials were 30-s in duration and ended without reinforcement. Pigeons received four daily Phase 1 sessions.

Phase 2: Acquisition of first-order conditioning. In Phase 2, subjects received simultaneous presentations of first-order LMs A and B with a hidden food goal. The goal was always located 2.4 cm to the right of LM A (see Figure 1B). LM B was presented at completely random locations relative to the goal, with the constraint that LM B could not overlap with LM A. Initially, a single peck at the goal was reinforced, but the response requirement was gradually increased to a VR 3 schedule (range = 1 to 5) depending on each pigeon’s accuracy. Initially, the goal was marked with

a 1-cm² medium-gray square for the first 20 trials of each 100-trial session to facilitate acquisition of the LM A–goal association. After the 20th trial, the goal marker was identical to those at all other grid locations (i.e., 3-mm² dark-gray square). The number of marked-goal trials was gradually decreased to the first 5 trials. A trial terminated in the same manner as described for initial training.

Testing and reminder treatment. Testing began for each pigeon when performance reached 80% accuracy on two consecutive Phase 2 sessions. Five nonreinforced test trials with LM X and 5 test trials with LM Y were randomly distributed among 90 Phase 2 trials, with the constraint being that test trials could not occur prior to the 20th trial in the session. On test trials,

the target LM (X or Y) was pseudorandomly presented at one of four grid locations, with the constraint that the LM would not appear farther than 5 cm from the center of the screen. This ensured that there were at least two grid locations in each direction surrounding the test LM at which peck responses could be collected. All test trials lasted for 30 s and ended without reinforcement. Six test sessions were conducted. A "reminder" session consisting of Phase 1 and Phase 2 treatments (but no test trials) intervened between the second and third test session and again between the fourth and fifth test session. On these reminder sessions, 5 nonreinforced A-X and 5 nonreinforced B-Y Phase 1 trials were interspersed among 90 reinforced Phase 2 trials, with the constraint that no Phase 1 trial occurred prior to the 20th trial of the session.

Data recording and analysis. Because the goal location was randomized on each trial from among the set of locations in the response grid, we transformed and standardized the peck location data onto a 17×17 -cell spreadsheet centered one grid unit to the left of the test LM, the location corresponding to that at which responding was expected on the basis of the integration of the A-X and A-goal spatial vectors (i.e., the spatial inference location).

Results

All subjects learned the task involving the pretraining LM in a mean of 54 days (range = 48 to 60 days) and were able to peck the unmarked goal location at above 80% accuracy on a VR3 schedule of reinforcement. Following Phase 1 of sensory preconditioning treatment, 4 of the pigeons rapidly reached criterion performance during Phase 2 treatment ($M = 10$ days; range = 8 to 12 days), whereas 1 pigeon took 38 days to complete Phase 2. This suggests that pigeons had associated the goal with a view of LM A with the spatial relationship of being one grid location to the left of the goal.

Neither main effects of reminder treatment nor interactions with other factors were found; thus, all subsequent analyses were conducted on data pooled across all test sessions. Figure 2A shows the proportion of pecks for all pigeons along the x - and y -axes on test trials with second-order LM X (left panel) and LM Y (right panel). Although response distributions on the y -axis were practically identical for both LMs, separate peaks are evident along the x -axis for LMs X and Y. The response peak (i.e., location pecked most frequently) was one grid location to the left of LM X (see Figure 2, Coordinate 9 on the x -axis), which had been paired with a first-order LM (LM A) trained with a consistent relationship to the goal. This grid location corresponds to the goal location computed from the addition of the X→A and A→goal spatial vectors. Thus, a response peak at this location indicates that pigeons made what can be described as a spatial inference on the basis of an allocentric X→A→goal map. On LM Y test trials, however, the response peak was located one grid unit to the right of LM Y (see Figure 2, Coordinate 11 on the x -axis). LM Y had been paired with a first-order LM (LM B) that did not bear a consistent spatial relationship to the goal. This observation is interesting because, even when there was no consistent spatial relationship between a test cue and the goal, responses still conformed to a unimodal distribution. Furthermore, the location of the peak to the right of LM Y suggests that peck location was controlled by generalization from LM A. The difference between LMs X and Y in response distributions in the x -axis is reliable, $\chi^2(16, N = 100) = 37.52$, $p < .01$, but no difference was found in y -axis distributions, $\chi^2(16, N = 100) = 3.93$. These results suggest that pigeons integrated the X-A and A-goal spatial maps, allowing them to compute an X-goal spatial relationship, which guided search at test.

The results suggest that two different processes influenced pigeons' responding on probe test trials with second-order LMs. When tested on LM X, which had been paired with a LM (LM A) that bore a consistent spatial relationship to the goal, pigeons showed evidence of computing a novel X-goal spatial vector. This novel X-goal spatial vector allowed them to "infer" the location where the goal should be. This novel spatial vector must be based on the integration of the X-A spatial vector acquired during Phase 1 with the A-goal spatial vector acquired during Phase 2. Moreover, the X-goal spatial vector depended on LM A, the first-order LM, having a consistent spatial relationship to the goal. LM B did not have a consistent spatial relationship to the goal, and therefore, a consistent spatial vector between LM Y and the goal could not be computed. As a result, LM Y did not support a spatial inference, despite the fact that the first-order LM with which it was paired (LM B) was temporally (and, to a lesser degree, spatially) contiguous to the goal. This suggests that both spatial contiguity and consistency appear to be necessary for behavior indicative of a spatial inference.

LM Y provided no information about the location of the hidden goal because its associate, LM B, had been paired with the goal without a consistent spatial relationship in Phase 2. Thus, we predicted that search in the presence of LM Y would be random. However, to our surprise, search was not random and appeared to be controlled by generalization from LM A to LM B. Phase 1 treatment should have established a reliable Y→B spatial vector. During Phase 2, LM B was paired with the goal and with LM A but in a spatially inconsistent fashion. Despite the lack of a consistent spatial relationship, pigeons may have formed B-goal and B-A associations that lacked a spatial component. The B-goal association may have motivated pigeons to respond to LM Y (i.e., conventional sensory preconditioning), though they should have been uncertain as to where to respond. To explain the nonrandom nature of responding to LM Y, it is possible that a functional equivalence developed between LM B and LM A because both had been paired with the goal.

Our results indicate that two processes, spatial inference and generalization, contributed to the spatial distribution of search. Additional support for this interpretation can be found by looking at the total number, rather than proportion, of responses generated on test trials with LMs X and Y (see Figure 2B). Responding was marginally higher on trials with LM X than with LM Y, $t(28) = 1.98$, $p = .057$. This difference may also reflect a conventional sensory preconditioning effect. In addition to measures of central tendency (e.g., response peak), measures of variability in response distributions may also be informative about the nature of the underlying processes guiding search. To assess response variability, we calculated the mean distance of pecks around the peak for test trials with LM X and LM Y. This measure reflects the variability in the distribution of responses around each LM. There was less dispersion in responding around LM X ($M = 2.17$, $SE = 0.09$) than around LM Y ($M = 2.90$, $SE = 0.15$), $t(185) = 9.20$, $p < .001$. Thus, computation of an X→goal spatial vector resulted in a more concentrated search around the peak at the "inference" location. Search on LM Y trials, however, was more variably distributed around the "generalization" location. One potential explanation for the observation of marginally less responding and greater dispersion in search around the response peak on LM Y trials than on LM X trials is that pigeons were less certain as to

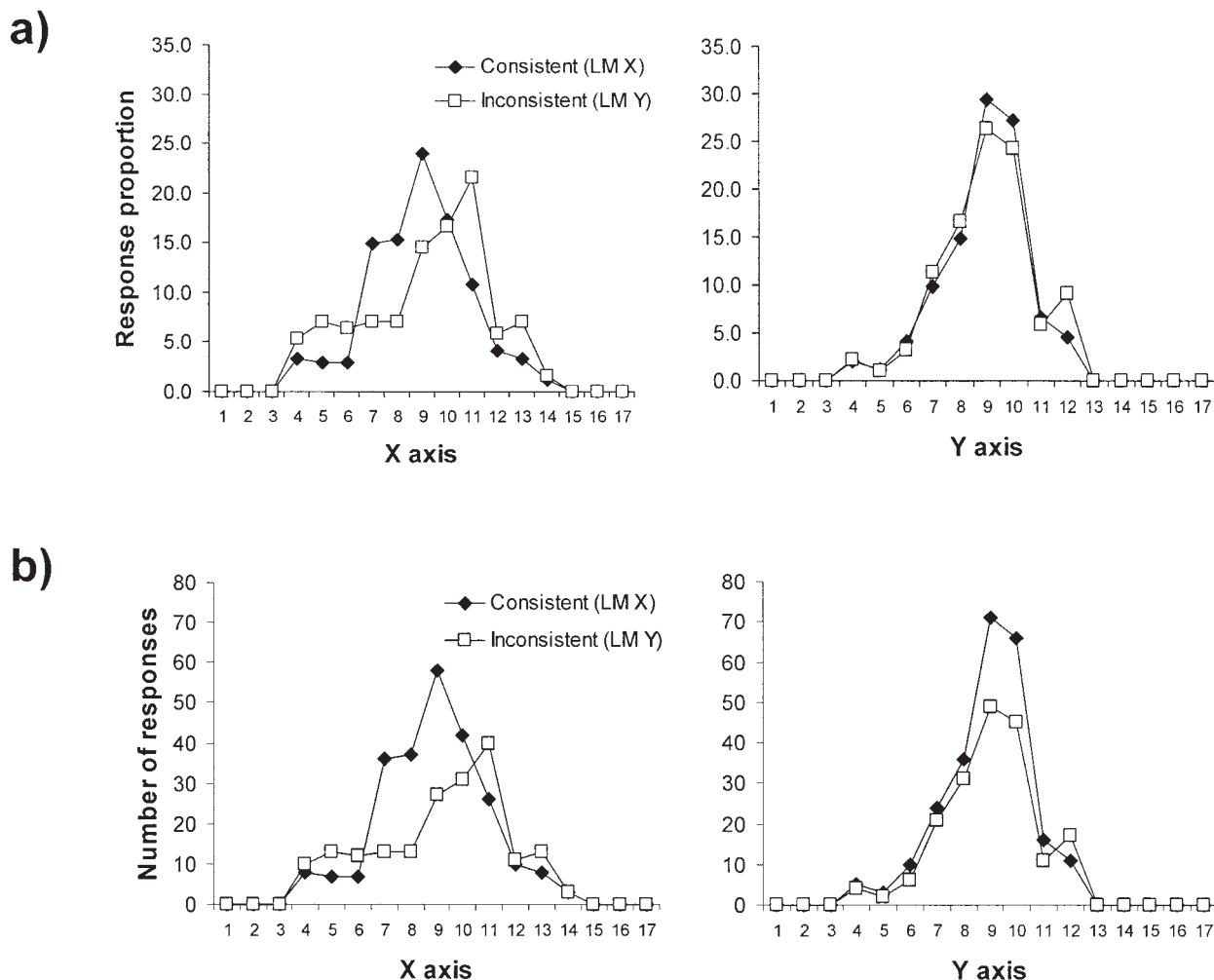


Figure 2. A: proportion of searches for all pigeons along the x-axis (left) and y-axis (right) for the consistent landmark (LM) X and inconsistent LM Y test trials. B indicated the sum total of searches for all pigeons along the x-axis and y-axis for the consistent LM X and inconsistent LM Y test trials. For both A and B, x-axis Location 9 is the expected goal location computed by the integration of the $X \rightarrow A$ and $A \rightarrow$ goal vectors, and x-axis Location 11 is the expected goal location relative to LM A. The y-axis Location 9 is the expected goal location based both on the integration of the $X \rightarrow A$ and $A \rightarrow$ goal vectors and relative to LM A.

where to peck in the presence of LM Y than LM X (cf. confidence measures of human decision performance). Further studies would need to address this more directly to evaluate this interpretation.

Discussion

We found evidence that pigeons can integrate two independent spatial maps acquired through Pavlovian sensory preconditioning using a touch screen-based spatial-search task. Beyond merely replicating Blaisdell and Cook's (2005) results with a new procedure, the current experiment improves on their study in a number of important ways. First, in their task, pigeons searched for a food goal during the Phase 1 preconditioning trials. Not only was this a departure from conventional sensory preconditioning, in which no inherently biologically reinforcing stimulus (e.g., a US) is present during compound trials, it complicates the interpretation of re-

sponding at test by introducing multiple sources of control over search. That is, in addition to showing evidence of the integration of Phase 1 and Phase 2 spatial vectors, pigeons showed evidence of control by Phase 1 LM-goal learning. The current experiment used a conventional sensory preconditioning procedure, in which no reinforcement was provided on Phase 1 sensory preconditioning trials, obviating the problem encountered by Blaisdell and Cook. Second, the current experiment included a variant of the unpaired control condition typically used in Pavlovian conditioning experiments. Unpaired controls are important in that they demonstrate the necessity of CS-US pairings for learning and performance. In the current experiment, LM B served as a variant of an unpaired control cue. However, rather than being temporally unpaired with the goal (US), LM B was paired with the goal, but with a nonconsistent spatial relationship. That is, an association

could have formed between LM B and the goal, but that association could not have contained reliable information about the spatial location of the goal. Thus, if a stable spatial relationship between the first-order LM and the goal is necessary to support the computation of a second-order LM–goal spatial relationship, then LM Y (which was paired with LM B) should not have been able to guide search to an “integration” location. Indeed, we found that LM Y did not support behavior indicative of a spatial inference. Rather, pigeons seemed to generalize from LM A, although the spatial variability around this peak location suggests generalization was a weaker effect.

Our results, along with those of Blaisdell and Cook (2005), suggest that Pavlovian conditioning may be a mechanism by which spatial relationships among LMs and between LMs and goals can be acquired. Furthermore, such spatial associations can be integrated into a more complex allocentric map via higher-order Pavlovian conditioning (e.g., sensory preconditioning). These results also support the more general notion that associative learning may underlie the building of allocentric representations of space, such as Tolmanian cognitive maps. In this view, allocentric spatial (or temporal, Honig, 1981; Savastano & Miller, 1998) representations preserve both metric distance and direction among stimuli (O’Keefe & Nadel, 1978); that is, a spatial vector. One of the more interesting and useful features of a cognitive map is that it can be used to generate novel relationships between events or locations that had not been experienced together. For example, given a cognitive map containing spatial vectors between Events A and B and B and C, an individual should be able to calculate the novel spatial vector between Events A and C.

The reliable effect of spatial integration shows clearly that the pigeons encoded two different spatial vectors: $X \rightarrow A$ and $A \rightarrow \text{goal}$. Our results add to the growing body of evidence that animals learn to use $LM \rightarrow \text{goal}$ spatial vectors to locate hidden goals. This has been most thoroughly explored in pigeons using LM-based spatial search tasks by Spetch, Cheng, and their colleagues (see review by Cheng & Spetch, 2001). Their experiments generally reveal that individual LM–goal relationships determine where in an arena or on a touch screen pigeons search for a hidden goal. Our findings go beyond this by establishing the mechanism by which LM–LM and LM–goal spatial vectors become bound into a higher-order spatial map. The spatial map can be used to guide search by allowing the animal to compute novel relationships between elements of the map. These novel relationships can then be used to infer the location of a hidden goal, even in the absence of any cues that had been physically paired with the goal. The behavioral flexibility conferred by a cognitive map seems to hold self-evident functional utility.

Blaisdell and Cook (2005) reviewed the contention surrounding the concept of a cognitive map (Bennett, 1996; Shettleworth, 1998). One hallmark of a cognitive map is the ability to make a novel shortcut (Tolman, 1948). However, it is this central feature that has faced the most severe criticism. The experiments providing evidence for novel shortcutting have been criticized because they failed to establish that the “novel” route was truly novel, a beacon or other goal marker directly led the animal down the shortcut (see also Mackintosh, 2002), or path integration was used to allow the animal to find the goal by dead reckoning (see Bennett, 1996, for a discussion of these experimental flaws). The sensory preconditioning procedure used in the current experiment

and by Blaisdell and Cook avoids these problematic confounds. In these procedures, subjects never experienced the novel $X \rightarrow \text{goal}$ spatial relationship during training. Furthermore, neither the goal nor any of the training LMs were present on the critical test trials with LM X. Because the location of the goal was randomly placed among the entire set of search locations, neither the search locations themselves nor the surrounding environment (e.g., touch screen or operant chamber in the current experiment or the walls and other room cues in Blaisdell & Cook’s experiment) could cue the subject to the goal location. Therefore, search at the computed “inference” location could only have been guided by the integrated representation forged between LM X and the goal mediated by LM A: That is, the X –goal spatial vector was truly novel at test and is best interpreted in the framework of a cognitive map.

Although we have ruled out common alternative explanations for spatial inferences, there is one recent suggestion that we must deal with. Mackintosh (2002) suggested that animals can find hidden goals through a combination of beacon homing and random searching when a LM or a beacon is close to the hidden goal. Is it possible that such a strategy could account for our results? In the current experiment, the “inferred” goal location was 2.4 cm to the left of LM X. If the pigeons were using a process like the one described by Mackintosh, then searches should have been distributed randomly and evenly around LM X. However, Figure 2 reveals that search on test trials with LM X was concentrated around the location derived by computing the integration of the X –A and A–goal spatial vectors and not at other locations around LM X. Thus, pigeons were not merely homing in on LM X and searching randomly around it. Rather, they searched around the area where the goal would be expected on the basis of an integrated map. The current data (to the extent that they generalize to three-dimensional situations) and the results of Blaisdell and Cook (2005) suggest that animals can form a cognitive map of their environment. Furthermore, we demonstrated that cognitive maps can be formed by associative learning. To what extent do cognitive maps actually contribute to spatial behavior in the wild? The answer to this question is still in its infancy and can only be answered with techniques (such as those developed here) that can effectively dissociate the various other spatial processes that have confounded previous research.

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