



## Factors that influence negative summation in a spatial-search task with pigeons<sup>☆</sup>

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### ABSTRACT

A variant of the standard conditioned inhibition procedure was used to evaluate landmark-based spatial search in a touchscreen preparation. Pigeons were given compound trials with one landmark (A) positioned in a consistent spatial relationship to a hidden goal and another landmark (B) positioned randomly with respect to A and the hidden goal (AB+). On half of the non-reinforced inhibitory trials, A was paired with landmark X (AX−) and on the remaining trials B was paired with Y (BY−). All subjects were also given reinforced trials with a transfer excitator (T+). During conditioned inhibition training, subjects showed no change in overall responding during AX− trials but did show a decrease in the number of pecks to the goal location signaled by A. During non-reinforced summation tests with landmark T, X had a greater suppressive effect than did Y on overall responding but the percentage of pecks at the goal did not differ unless X was positioned near the expected goal signaled by T. These data demonstrate that the effectiveness of a stimulus trained as an inhibitor is dependent on the strength of the association between its training excitator (A) and the US, as well as, the spatial arrangement of stimuli during testing.

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### 1. Introduction

Investigating the conditions for stimulus control of behavior has driven research in the field of associative learning since Pavlov's seminal studies on the salivation reflex of dogs. Of the possible factors influencing stimulus control, Pavlov was the first to empirically test how the spatiotemporal contiguity between stimuli would impact conditioned behavior (Pavlov, 1927). Despite the accumulated evidence for its importance, many of the most influential models of associative learning do not incorporate temporal and spatial factors in their predictions of stimulus control (e.g., Mackintosh, 1975; Pearce and Hall, 1980; Rescorla and Wagner, 1972). One of the major developments in the study of associative learning in the last 25 years has been a fuller appreciation

for the impact of spatiotemporal relationships among stimuli on both the magnitude AND form of the response. In particular, theoretical advances such as behavior systems theory (Timberlake, 1983, 2001), temporal coding hypothesis (Matzel et al., 1988; Savastano and Miller, 1998), rate expectancy theory (Gallistel and Gibbon, 2000; Gallistel, 2003), and packet theory (Kirkpatrick and Church, 2000a,b) provide better explanations of how temporal contiguity influences stimulus control. Spatial contiguity, however, has received relatively less attention.

Not surprisingly, researchers studying spatial learning have reported many of the same effects while manipulating spatial contiguity as have been reported in the timing literature (see Chamizo, 2002; Cheng, 1992 for a review). Of these, the influence of spatial contiguity on the development of conditioned inhibition has received the least attention. In a standard conditioned inhibition procedure, a conditioned stimulus (CS A, also called a training excitator) is followed by an unconditioned stimulus (US) on some trials but not on other trials when it is presented in compound with a putative inhibitor (X). Assuming X has been learned as a signal for US omission, its inhibitory power should transfer to conditioned responses to other stimuli that signal the occurrence of the US. Thus, inhibitory control by X is commonly assessed using a summation test in which X is presented in compound with a second, independently trained conditioned stimulus (T), or transfer excitator. A proper inhibitor should result in negative summation, or attenuated conditioned responding during the test. Missing from this

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description, however, is a prediction of stimulus control that incorporates the temporal information provided by each cue (excitators and inhibitors) – which can have dramatic effects on the magnitude and form of the response elicited during the summation test. Previous research indicates that an inhibitor does not uniformly disrupt responding, but rather, exhibits its inhibitory control during an interval of time derived from the temporal configurations of stimuli encountered during training (Barnet and Miller, 1996; Burger et al., 2001; Denniston et al., 1998a,b, 2004; Maier et al., 1976). These temporal effects have been reported in aversive and appetitive preparations (e.g., Williams et al., 2008; Suits, 2009).

Barnet and Miller (1996) found evidence that temporal relationships among stimuli are encoded in the associations formed during conditioned inhibition and alter the effective transfer of inhibitory control to a transfer excitator. The novel prediction is that the effectiveness of an inhibitor is modulated by the temporal relationship between the training excitator and the US. Barnet and Miller manipulated the temporal specificity of an inhibitor by pairing it with an excitator that was either trained simultaneously (SIM) or serially (SER) with the US (for simplicity we discuss only a subset of conditions). The transfer excitator was always serially paired with the US. Consequently, only in Group SER did the expectation of shock omission evoked by the inhibitor match the same temporal interval in which the US was expected based on the transfer excitator (i.e., the interval following the transfer excitator). As predicted, the summation tests indicated more inhibition of conditioned responding to the transfer excitator in Group SER than SIM. Subsequent studies manipulating the temporal relations among stimuli support the hypothesis that an inhibitor exhibits a period of maximal inhibition during summation tests (e.g., Barnet and Miller, 1996; Burger et al., 2001; Denniston et al., 1998a,b, 2004) and conditioned inhibition training (e.g., Suits, 2009; Williams et al., 2008).

Beyond providing a demonstration of the role of temporal information in stimulus control, the findings of Barnet and Miller (1996) also highlight the crucial role of the integrity of the A-US association to an effective inhibitor (X). In fact, its role is so crucial that the only successful procedure for extinguishing an inhibitor's control is not through post-conditioning extinction trials of the inhibitor but by extinguishing its training excitator (A). Lysle and Fowler (1985) describe the modulation of X by A as a "slave" process, whereby inhibitory control by X is dependent on the excitatory strength of the training excitator A. In their experiments investigating post-conditioning extinction of X, common explanations for the protection of X during extinction were controlled; however, X maintained its inhibitory control throughout the extinction treatment.<sup>1</sup> On the contrary, when A was extinguished the effectiveness of X was reduced. A performance-based model, the comparator hypothesis (Miller and Matzel, 1988; Miller and Schachtman, 1985), provides one theoretical account of the connectivity between stimuli that allows A to modulate the effectiveness of X. The comparator hypothesis describes conditioned responding as the result of an interaction among CS–CS and CS–US associations. The behavioral effect of inhibition is the result of a negative response potential generated by the product of the strong A–X and A–US associations down-modulating the effectiveness of the weak or non-existent X–US association. If A is extinguished, then the product of the A–X and A–US associations will be greatly

reduced, as will their ability to modulate the effectiveness of the X–US association (see Denniston et al., 2004, for details).

The comparator hypothesis can be combined with the temporal coding hypothesis to predict the role of temporal relationships in stimulus control. The temporal coding hypothesis suggests that associative relationships automatically capture not only the strength between two paired events (i.e., whether or not one will occur given the occurrence of the other), but also the temporal information between them (Barnet and Miller, 1996). This prediction has received support in both aversive (see Savastano and Miller, 1998 for a review) and appetitive preparations (Leising et al., 2007). In a similar fashion, it is likely that the spatial relationships between stimuli encountered during conditioned inhibition training, including that of the training excitator to the inhibitor (A–X) and to the US (A–US), influence the effectiveness of an inhibitor.

Conditioned inhibition in the spatial domain can be studied by using a landmark, or training excitator, that signals the distance and direction to a hidden goal (A+). On other trials, the training excitator may be paired with another landmark, an inhibitor, with no opportunity for reinforcement (AX–). To the best of our knowledge, the only study demonstrating inhibitory control of search behavior has been conducted recently by Sansa et al. (2009). In their study, rats were trained in a Morris water pool to locate a hidden platform (the goal) in the presence of a single landmark (A+, Experiment 1) or a configuration of landmarks (Experiment 2). On other trials, the same training landmark was presented with a second landmark but with no hidden platform (AX–). Rats were then tested during summation tests with a transfer excitator and with a retardation of acquisition test in which the inhibitory landmark now signaled the location of a hidden platform. Passing both tests for conditioned inhibition has become the standard convention for demonstrating conditioned inhibition (Cole et al., 1997; Rescorla, 1969). Sansa et al. conducted summation and retardation tests and found reduced search behavior within the quadrant of the pool where the hidden platform had been during excitatory training. Sansa et al. also reported a withdrawal effect, characterized by reduced search in the area of the hidden platform, during AX– trials across sessions of conditioned inhibition training. Withdrawal from a stimulus has also been used as evidence that a stimulus has acquired inhibitory control (e.g., Wasserman et al., 1974). Not surprisingly, evidence from Sansa et al. suggests that inhibitory control by a landmark is functionally equivalent to that of non-spatial inhibitory cues (e.g., an auditory CS).

Previous experiments have shown that the effectiveness of a stimulus trained as an inhibitor is dependent on the strength of the association between its training excitator (A) and the US, as well as, the temporal relationships between stimuli encountered during training and testing. The current experiment seeks to extend the investigation of conditioned inhibition in the spatial domain by using a procedure that manipulates both the spatial relationships between A and the US, and between the inhibitor (X) and the transfer excitator (T). All pigeons received search training with two landmarks trained as excitators (A and B) and two trained as inhibitors (X and Y). A hidden goal was randomly selected from among 56 possible locations and pigeons were given access to mixed grain when the location of the goal was pecked. On training excitator trials A signaled the position of the hidden goal while B was randomly positioned on the screen (AB+). On separate trials, pigeons were given AX– and BY– with no goal. After conditioned inhibition training, X was expected to be a more effective inhibitor. Subjects were then given separate summation tests with X and Y placed near (X–near or Y–near) or far (X–far or Y–far) from a goal signaled by T. We predicted that summation tests with X would reveal greater negative summation effects (i.e., fewer pecks to the goal) than Y irrespective of the position of the inhibitor. Furthermore, we expected to find greater negative summation in the presence of

<sup>1</sup> Two processes were thought to maintain the effectiveness of an inhibitor (X) during extinction. The first was the association between A–US, which was evoked into memory when X was presented during extinction and provided the expectation of the US necessary to maintain X as an inhibitor. The second was the association between the context and the US, which was also present during extinction of X. The A–US and context–US associations were predicted to endure throughout the extinction treatment as a result of the successfully predicted omission of the US by X.

X when positioned nearer to the goal, but no difference in performance between tests of Y at the near and far positions.

## 2. Experiment

The influence of the spatial relationship between the training excitator and the hidden goal (i.e., A→US) on the effectiveness of negative summation can be studied by training two excitators which vary in their predictive utility (see Fig. 1a). To achieve this two training excitators (A and B) were present on the display during AB+ trials but A was positioned in a consistent spatial relationship to a hidden goal while B was positioned randomly with respect to A and the goal. On inhibitory trials, each training excitator was independently paired with an inhibitory landmark (AX– or BY–) and no opportunity for reward. Additionally, all subjects received reinforced trials with a transfer landmark (T+). The location of landmarks on the screen varied across trials, but the A-goal and T-goal spatial configurations remained stable. Thus, reliable performance required pigeons to use the spatial information provided by the landmarks to locate the goal. Inhibitory stimulus control by X and Y was assessed through summation tests with T (see Fig. 1b–e). The summation tests included trials with each landmark (X or Y) placed directly adjacent to the hidden goal (i.e., near), and trials with each landmark positioned at greater than twice the distance from the goal as the near position (i.e., far).

In this experiment, both excitators (A and B) predicted the presence of the hidden goal, but only one excitator (A) signaled its exact location in space. A variant of this type of training procedure in the Morris water maze has shown that, as expected, A acquires better spatial control than B (Roberts & Pearce, 1998). Consequently, we predicted that the landmark (X) which was trained as an inhibitor in conjunction with A will more effectively disrupt responding during the summation tests than the landmark (Y) paired with B. As previously discussed, the temporal relationships between stimuli encountered during training and at the time of testing influence the effectiveness of an inhibitor. Thus, we predicted that the spatial position of the inhibitor during summation testing would have similar effects. It is hypothesized that the proximity of X and Y to the predicted hidden goal will influence the degree to which X and Y disrupt responding during testing. Specifically, we expect X to more effectively disrupt responding during summation testing, and particularly so when X is placed closer to the predicted goal (based on the transfer excitator).

### 2.1. Method

#### 2.1.1. Subjects

The subjects were three male White Carneaux and two male Racing Homing pigeons (*Columba livia*) supplied by Double T Farm, Iowa. They had previously participated in an appetitive spatial sensory preconditioning experiment (Sawa et al., 2005) in which they had been reduced to 80–85% of their free-feeding weights. The stimuli used in this procedure are the same as those used by Sawa et al. Pigeons were individually housed in a colony with a 12-h light–dark cycle and had free access to water and grit. Experimental procedures occurred during the light portion of the cycle.

#### 2.1.2. Apparatus

Testing was conducted in a flat-black Plexiglas chamber (38 cm wide × 36 cm deep × 38 cm high). All stimuli were presented by computer on a color LCD monitor (NEC MultiSync LCD1550M) visible through a 23.2 cm × 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 touchscreen (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, with 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 SVGA graphics mode (800 pixels × 600 pixels).

### 2.2. Procedure

#### 2.2.1. Stimulus displays

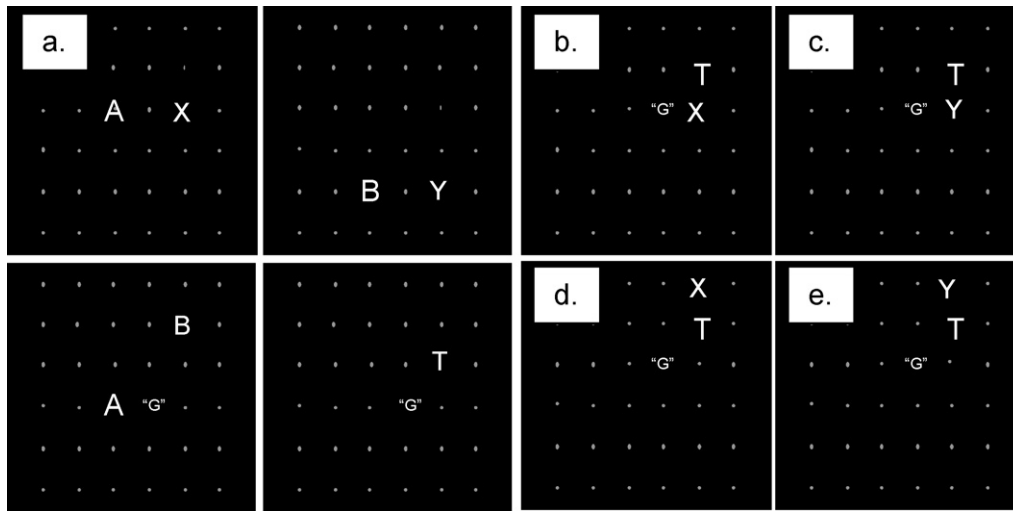
Five visual stimuli served as spatial discriminative stimuli (i.e., landmarks). A white “Z”-shape was used as the training landmark for all subjects. A yellow “I”-shape, an orange “U”-shape, a gray “double-dot”, and a purple “star” served as visual landmarks, which were counterbalanced across subjects. Each stimulus was approximately 2.3 cm × 2.3 cm in diameter. In addition, a 3-mm<sup>2</sup> dark-gray square marked the center of each location on the 8 × 7 grid of response locations. Each grid unit contained a 2-cm<sup>2</sup> response area that served as a possible goal location, with 0.5-cm space between adjacent grid units.

#### 2.2.2. Pretraining

All subjects received 100-trial sessions with a transfer landmark (T). The hidden goal was located one grid location to the left and down from T. On each trial, the goal was presented at a randomly determined location within the 8 × 7 grid. The goal location was visually marked with a white square that was gradually faded out. Initially, a single response to the hidden goal was followed by 3-s access to mixed grain and a 10-s intertrial interval (ITI). 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 1–5). 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 non-goal locations, or 0 pecks for 2 min consecutively. After subjects showed accuracy above 80% for two consecutive sessions with the transfer stimulus, they proceeded to conditioned inhibition training.

#### 2.2.3. Conditioned inhibition training

Conditioned inhibition training consisted of 28 days of 100-trial sessions with three types of trials (see Fig. 1a). On AX– trials, X was paired to the right of A in a consistent spatial relationship with no goal location. On BY– trials, Y was paired to the right B with no goal. LMs were aligned in the Y-axis but spaced 5.0 cm apart in the X-axis, center to center. Trials of AX– and BY– terminated after 30 s. The displayed locations of these paired visual stimuli were selected from among the potential grid coordinates, with the constraint that all landmarks be visible within the 8 × 7 grid (i.e., 40 possible locations). On AB+ trials, the hidden goal was located 2.5 cm to the right of A. LM B, however, was positioned randomly with respect to both the ‘goal’ and A. As in pretraining, correct responses were initially reinforced on a continuous reinforcement schedule with 2.5-s access to mixed grain. 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 1–5). A trial would terminate after incorrect responses in the same manner as described above for T. All three types of trials were interspersed randomly within a session with the constraint that a non-reinforced trial could not occur prior to the 10th trial of the session. The first 10 trials of each session incorporated a 1-cm<sup>2</sup> grey marking stimulus at the goal—a technique also utilized in Sawa et al. (2005) to establish baseline responding. Each session



**Fig. 1.** An illustration indicating the spatial relationships between visual stimuli, and between visual stimuli and a hidden goal (“G”, see text for details) during training (a) and testing (b)–(e). The small grey circles denote the layout of the response grid. (a) During training, AX and BY were paired with no opportunity for reinforcement. On reinforced trials, A was trained as a reliable predictor of the goal while B was positioned randomly with respect to A and the goal. The transfer excitator (T) was also trained as a reliable predictor of the hidden goal. Panels (b)–(e) illustrate each of the different summation tests: (b) Near-X, in which X is positioned adjacent to the expected goal, (c) Near-Y, in which Y matches the position of X, (d) Far-X, in which X is positioned at the same distance from T as in Near-X, but further from the expected goal, and (e) Far-Y, in which Y matches the position of X.

consisted of 25 trials of AX– and BY–, and 50 trials of AB+. Subjects were required to achieve 80% accuracy for two consecutive sessions on AB+ trials before proceeding to testing.

During conditioned inhibition training, one subject gradually decreased responding over sessions. To restore responding to appropriate levels, the ratio of reinforced to non-reinforced trials was adjusted as follows. Initially, the sessions were reduced to a ratio of 90 reinforced trials and 10 non-reinforced. This was maintained until accuracy increased to 80%. Once achieved, the ratio was adjusted by replacing 10 reinforced trials with 10 non-reinforced trials to achieve a ratio of 80 reinforced to 20 non-reinforced trials. The ratio of reinforced to non-reinforced trials was continually adjusted in increments of 10, in this manner, until the training ratio of 50 reinforced to 50 non-reinforced trials was re-established.

#### 2.2.4. Testing

Before testing began, subjects were given additional 100-trial sessions with T to reestablish baseline responding. Testing began after subjects achieved an accuracy of 80% or above for two consecutive sessions. Subjects were then given one test session with 120 trials, of which 95 were reinforced trials of the transfer landmark (T+) and the remaining 25 consisted of five types of non-reinforced tests. On transfer tests, T was presented alone with no opportunity for reinforcement (see Fig. 1b–e). On Near-X summation test trials, X was positioned 2.5 cm to the right of the goal signaled by T. On Far-X summation test trials, X was positioned 5 cm above and 2.5 cm to the right of T’s goal. On Near-Y summation trials, Y was in the same position relative to T’s goal as X in Near-X trials, and on Far-Y trials Y was in the same position relative to T’s goal as X in Far-X trials. Test trials lasted for 30 s with no opportunity for reinforcement.

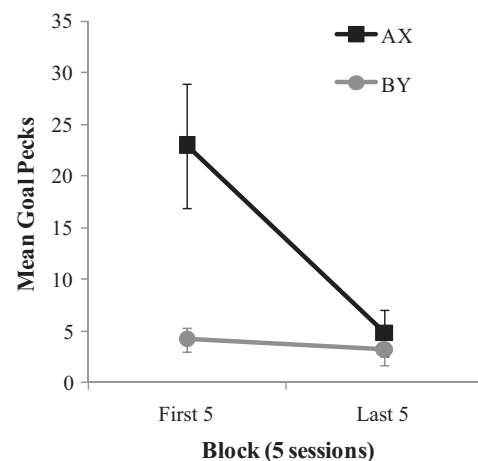
### 3. Results

All statistics are reported at the level of  $p < .05$  unless otherwise specified. The sum of all recorded responses during a trial is referred to as overall pecks, whereas, all responses recorded within the region defined as the hidden goal are referred to as goal pecks.

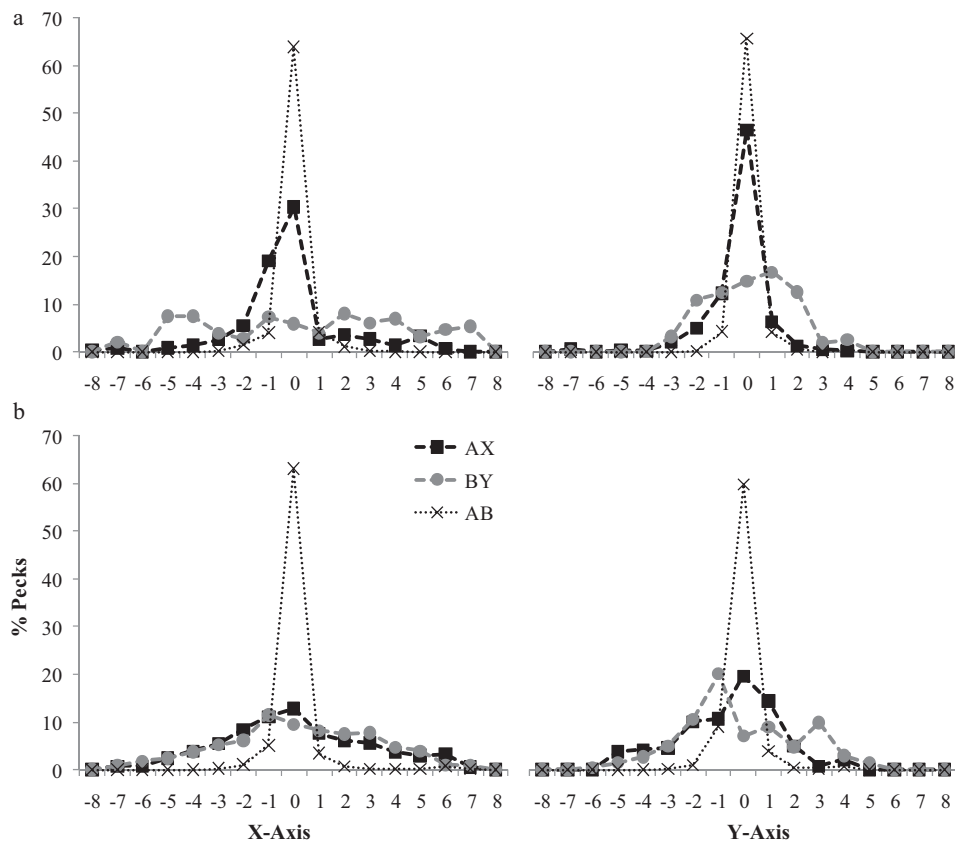
#### 3.1.1. Training

The data from conditioned inhibition training were blocked across Days 1–5 and 24–28, representing the first and last five days of conditioned inhibition training, respectively. A repeated-measures analysis of variance (ANOVA) conducted on overall pecks with Landmark (AX or BY) and Block (first or last) as repeated measures failed to find any main effects or the interaction,  $F_s(1, 4) < 1$ . Fig. 2, however, displays a decrease in goal pecks during trials of AX but not BY. These observations were confirmed by an ANOVA conducted on goal pecks, which revealed a marginal main effect of Landmark,  $F(1, 4) = 5.76$ ,  $p = .07$ , a main effect of Block,  $F(1, 4) = 11.06$ , and the interaction,  $F(1, 4) = 7.92$ .

Fig. 3 shows the distribution of responses for each trial type. At each location in the X- and Y-axis a percentage was calculated for each bird by dividing the number of responses at that location by the total number of responses for that trial type. The values in Fig. 3 are the mean percentage of total pecks for trials with AB+, AX–, and BY–. A Chi-square analysis was used to compare the expected



**Fig. 2.** Mean number of pecks at the goal location during conditioned inhibition training from the first 5 to the last 5 sessions. Error bars indicate the standard error of the mean.



**Fig. 3.** Distribution of searches for all pigeons along the X-axis (left panels) and Y-axis (right panels) from the first 5 (a) to the last 5 (b) sessions of conditioned inhibition training. Responses have been standardized such that the expected goal is at 0 in both the X- and Y-axis. AX- and BY- trials were non-reinforced, whereas AB+ trials were reinforced. On AB+ trials, the goal was at a consistent spatial location with respect to A, but selected randomly with respect to B.

vs. observed frequency of pecks at each location in the X and Y axis of the display. This analysis found a significant difference in the distribution of responses on AX and BY trials on both the X- and Y-axis during the first 5 sessions,  $X^2s(16) \geq 91.54$ . By the end of training (i.e., last 5 sessions) differences in the X-axis had been eliminated,  $X^2s(16) = 9.95$ ,  $p > .05$ , but remained in the Y-axis,  $X^2s(16) = 45.77$ .

### 3.1.2. Testing

#### 3.1.2.1. Overall responding

In order to better compare data collected across five different testing conditions (Near-X, Far-X, Near-Y, Far-Y, Transfer alone), we transformed overall pecks for each bird by dividing the number of responses during each trial by the total number of responses across all trial types. To test whether performance during each summation test differed from that of the transfer excitator alone, a repeated-measures ANOVA was conducted on percent overall pecks with test (Near-X, Far-X, Near-Y, Far-Y, Transfer) as a repeated factor. This test revealed a main effect of test,  $F(4, 16) = 7.10$ . Tukey's honestly significant difference (HSD) statistical post hoc test compared Near-X ( $M = 9.80$ ,  $SD = 3.90$ ), Far-X ( $M = 12.40$ ,  $SD = 6.58$ ), Near-Y ( $M = 18.60$ ,  $SD = 8.79$ ), and Far-Y ( $M = 16.40$ ,  $SD = 4.04$ ) to transfer excitator alone trials ( $M = 40.20$ ,  $SD = 16.04$ ) and found differences between each comparison,  $ps < .05$ .

A separate repeated measures ANOVA was conducted on percent overall pecks during the four summation tests with Landmark (X or Y) and Proximity (Near or Far) as repeated factors and revealed a main effect of Landmark,  $F(1, 4) = 11.27$ , such that fewer overall responses were emitted on trials with X than Y. No other differences

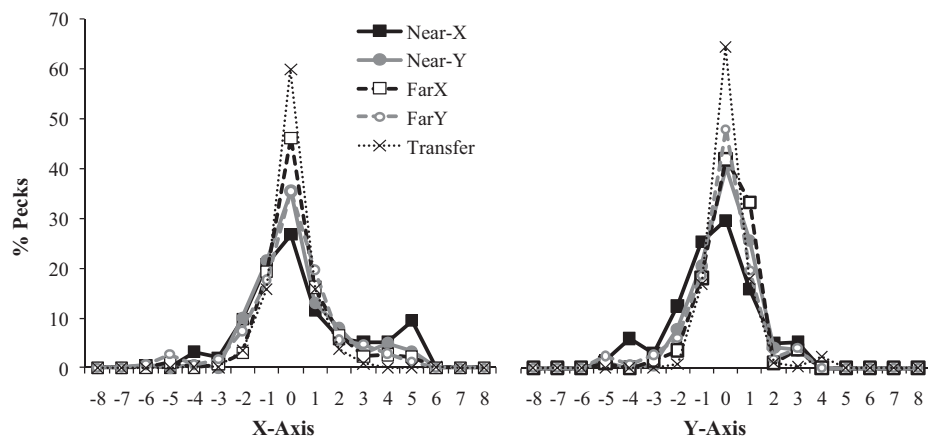
were found,  $Fs(1, 4) < 1.63$ ,  $ps > .05$ . Given our a priori prediction, planned comparisons were conducted and revealed that Near-X differed from Near-Y,  $F(1, 4) = 7.79$ , and no other differences,  $Fs(1, 4) < 1$ .

#### 3.1.2.2. Responses to goal

Responses to the goal were also converted to a percentage for each bird by dividing the number of pecks to the goal during each trial type by the total number of pecks for that trial type. A repeated measures ANOVA conducted with test (Near-X, Far-X, Near-Y, Far-Y, Transfer) as a repeated factor revealed the main effect,  $F(4, 16) = 5.40$ . Tukey's HSD compared Near-X ( $M = 13.24$ ,  $SD = 12.17$ ), Far-X ( $M = 20.65$ ,  $SD = 18.76$ ), Near-Y ( $M = 19.46$ ,  $SD = 11.76$ ), and Far-Y ( $M = 23.31$ ,  $SD = 11.89$ ) to transfer excitator alone trials ( $M = 43.16$ ,  $SD = 16.78$ ) and found differences between each comparison,  $ps < .05$ , except for that between Far-Y and transfer excitator alone.

A separate ANOVA was conducted on percent goal pecks during the four summation tests with Landmark (X or Y) and Proximity (Near or Far) as repeated measures. This test revealed a marginal main effect of Proximity,  $F(1, 4) = 6.57$ ,  $p = .06$ , but no other effects or the interaction,  $Fs(1, 4) < 1.95$ ,  $ps > .05$ . Planned comparisons revealed that Near-X differed from Near-Y,  $F(1, 4) = 62.68$ , but no other differences,  $Fs(1, 4) < 3.93$ ,  $ps > .05$ .

Lastly, we again used a Chi-square analysis to compare the percentage of pecks at each location in the X and Y axis separately. Comparisons of responding during each summation test to that of the transfer alone revealed that Near-X, Near-Y, and Far-Y all differed on the X-axis from tests of the transfer excitator (see Fig. 4),  $X^2s(16) \geq 34.71$ . On the Y-axis, all trial types differed from that of the



**Fig. 4.** Distribution of searches along the X- and Y-axis for all summation tests and non-reinforced tests of the transfer excitator alone. Responses have been standardized such that the expected goal is at 0 in both the X- and Y-axis.

transfer excitator,  $X^2s(16) \geq 67.88$ . These findings add confidence to the results obtained from the previous analysis that used just percent goal pecks. Similarly, consistent with previous analysis the Chi-square test revealed a difference between pecks during Near-X and Near-Y trials,  $X^2s(16) = 31.55$  (in the X-axis), but no difference in either axis between Near-Y and Far-Y,  $X^2s(16) < 15.17$ , or Far-X and Far-Y,  $X^2s(16) < 13.53$ . The analysis of percent goal pecks, however, was unable to reveal a difference between Near-X and Far-X, but this difference was found in both the X-axis and Y-axis with a Chi-square analysis,  $X^2s(16) > 54$ .

### 3.2. Discussion

Using a variant of the standard conditioned inhibition procedure, we found negative summation effects depend both on a landmark's spatial relationship to the goal signaled by a transfer excitator (T) and the spatial relationship of the training excitator to a hidden goal (A-goal). During training, pecks to the goal signaled by A were suppressed during trials with AX– but overall pecks (i.e., to all locations) did not change across trials. Summation tests revealed the importance of the training excitator (A and B), such that having X anywhere on the display disrupted overall responding more than Y, though the presence of Y did reduce responding compared to trials with the transfer excitator alone. Spatial relationships also played a role in negative summation; a marginal stimulus non-specific proximity effect was also observed during summation tests, such that placing either X or Y nearer the goal signaled by T reduced percent goal pecks, but not overall pecks. The interaction of these two factors is apparent on summation tests in which X and Y were positioned near the goal signaled by T. On these trials the presence of X resulted in fewer overall pecks and fewer percent goal pecks than Y. Moreover, comparisons of response distributions from the summation tests revealed differences only between Near-X and Near-Y and Near-X and Far-X. These results represent the most thorough demonstration of negative summation in the spatial domain.

Maier et al. (1976) argued that although conditioned inhibition has received much theoretical and empirical attention, “little is known about the conditions which produce it and which control its strength” (p. 217). Subsequent work has resulted in a better understanding of these conditions. For example, Lysle and Fowler (1985) found that the effectiveness of an inhibitor is dependent on the strength of the association between the training excitator and the US. The importance of temporal relationships has been shown most recently by Denniston et al. (2004), who used post-training manipulations of an excitator's temporal relationship to the US to reveal the temporal specificity of inhibition. To the best of our knowledge, no

study has evaluated these conditions within the spatial domain. In our experiments, the presence of X resulted in both a greater overall suppression of pecks, as well as a suppression of pecks at the goal signaled by T. Tests with inhibitory landmark Y failed to reveal spatial precision of inhibition as strong as did X. These results extend the importance of the training excitator-goal spatial relationship in determining the effectiveness of an inhibitor to the spatial domain.

It is conventional to use a combination of both a summation and retardation test to evaluate the effectiveness of an inhibitor (Rescorla, 1969). We were unable to complete a retardation test. In our spatial-search task there is little exploration in the absence of direct reinforcement, thus it would be difficult to train a specific reinforced location. One alternative may have been to introduce a prompt cue, like a large gray dot at the goal location. However, pecking to a previously reinforced, large gray dot introduces its own complications. Sansa et al. (2009) represents the only other report of conditioned inhibition in the spatial domain and did conduct a retardation test in the Morris pool. In the Morris pool, searching in the absence of a hidden platform is motivated by the aversive nature of the cold water. In discussing their results, Sansa et al. conclude that withdrawal from the area of the expected goal on AX– trials during training and the traditional tests of condition inhibition (summation and retardation) seem to measure the same thing. In our experiment, evidence for withdrawal from the area of the expected goal during AX– trials comes from an analysis of pecks at the goal, which decreased across trials while total pecks during a trial were unaffected by additional training.

The exact nature of conditioned inhibition, including the label of “inhibitor” itself is still a matter of debate (Rescorla, 1985, 1991). Research which reveals the conditions that produce inhibitory-like behavior and/or influence its effectiveness are critical to evaluating and revising competing theories of conditioned inhibition. Here we report the first attempt to manipulate (a) the strength of an inhibitor by influencing the reliability of spatial information provided by its excitatory training associate and (b) the spatial proximity of the inhibitor to a rewarded location during summation tests. Consistent with previous literature from non-spatial tasks, we found modulation of the effectiveness of an inhibitor by the training excitator with which it was paired. Additionally, we found that the proximity of X and Y to the hidden goal had a non-specific influence on negative summation. These findings should encourage additional research into the roles of predictive validity and proximity in the development of conditioned inhibition, and consequently, theories which incorporate both the spatial and temporal relationships encountered during conditioning.

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