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The dynamics of spatial anticipation in pigeons and rats

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University of Iowa

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THE DYNAMICS OF SPATIAL ANTICIPATION IN PIGEONS AND RATS

by

Daniel Ian Brooks

An Abstract

Of a thesis submitted in partial fulfillment
of the requirements for the Doctor of
Philosophy degree in Psychology
in the Graduate College of
The University of Iowa

July, 2010

Thesis Supervisor: Professor Edward A. Wasserman

ABSTRACT

The analysis of the pre-choice behaviors in an operant conditioning task led to the observation that pigeons often produced *anticipatory* pecks that were directed at the location of their next response. Despite the possible utility of this behavior for understanding basic behavioral processes in animal learning and the widespread use of touchscreen displays to present pictorial stimuli, there has been little evaluation of the spatial distribution of touchscreen responding. So, we sought to investigate the mechanisms that account for this anticipatory behavior, whether this behavior changes over time, and how general this phenomenon might be. To answer these and other related questions, we report in a series of eleven studies and two re-analyzed datasets a detailed characterization of this anticipatory discrimination behavior in both pigeons and rats.

In the first chapter, we review relevant literature related to the phenomenon of anticipatory behavior and prospective coding. In the second chapter, we outline a basic three-link discrimination paradigm, which we adapted from a procedure originally developed to study spatial anticipation in autoshaping. This simple procedure afforded us the ability to measure responses during a task that engages prospective processing.

In the third chapter, we evaluate two possible mechanistic explanations for this anticipatory behavior; namely, that animals are motivated to produce anticipatory responses because of a shorter temporal route to reinforcement or because of the spatial and temporal contiguity of the stimuli used in the task. In the fourth chapter, we evaluate several spatial parameters that might importantly influence the distribution of these anticipatory responses. In the fifth chapter, we re-evaluate data from two previously published projects to assess the generality of

the observed phenomenon and to evaluate the possibility that the anticipatory responses are a fractional reproduction of the terminal response.

Finally, in the sixth chapter, we discuss the implications for the presented work in several fields. We also sketch a computational framework for the presented data using a Dynamic Field Theory model, attempting to show how the prospective representation of an upcoming spatial location might guide anticipatory behavior.

Abstract Approved: _____
Thesis Supervisor

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CERTIFICATE OF APPROVAL

PH.D. THESIS

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has been approved by the Examining Committee
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To Marilyn.
Why do birds suddenly appear
Every time you are near?
Just like me
They long to be
Close to you.

Baseball is a game of anticipation. There are always hundreds of permutations and combinations about what might happen next. It's always about anticipation.

That's what the true baseball fan understands.

William Patrick Kinsella

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ABSTRACT

The analysis of the pre-choice behaviors in an operant conditioning task led to the observation that pigeons often produced *anticipatory* pecks that were directed at the location of their next response. Despite the possible utility of this behavior for understanding basic behavioral processes in animal learning and the widespread use of touchscreen displays to present pictorial stimuli, there has been little evaluation of the spatial distribution of touchscreen responding. So, we sought to investigate the mechanisms that account for this anticipatory behavior, whether this behavior changes over time, and how general this phenomenon might be. To answer these and other related questions, we report in a series of eleven studies and two re-analyzed datasets a detailed characterization of this anticipatory discrimination behavior in both pigeons and rats.

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CHAPTER 1

LITERATURE REVIEW

General introduction: Choice Before the Moment of Choice

Consider the following situation: you are driving north on I280 in Iowa, in the middle of three lanes of traffic. When you near the northern terminus of I280 (which intersects with I80), the road narrows to two lanes and you must quickly choose between going west or east. About two miles before you reach this choice point, and while the highway is still three lanes wide, there are signs saying, “bend left to go west” and “bend right to go east.” If you are a good driver, then you will put some thought into this decision and merge left or right well before the point where the two-lane road forks.

So, where are you headed? Perhaps you want to return to Iowa City or to visit the World’s Largest Truck Stop (both destinations west). Or, perhaps you plan a drive across the Mississippi river on your way to Moline or Chicago (both destinations east). Either way, you will make your lane choice having suitable information about the destination.

We might conduct an experiment in which we measure this lane-choice behavior by watching only at the fork in the two-lane road. From those behavioral measurements, we might conclude that the drivers had a good idea about their destination. Sure, a sad few might have been lost and made the wrong turn; but, the vast majority of drivers traveling on I280 who navigate that fork in the road will likely have chosen correctly much earlier, when the road was still three lanes wide.

The behavior of pigeons in operant chambers is not so very different. In many experiments, the pigeon starts a trial, is presented with some discrete, discriminative stimulus, and makes a choice between a set of available

alternatives. We measure the ability of the pigeon to solve a particular discrimination by recording a binary behavior (“correct key choice”), which is not so different from recording the direction of cars on the multi-lane road.

But, the actual behavior of choosing a road or choosing a key is only one behavioral product of the cognitive process that precedes it. And, there may be other behavioral products of this decision process which provide key insights into the mechanics of this process.

For example, if we were to expand our car-navigation study to include other variables, then we might measure the speed of the cars as they approach the fork in the road. Are some cars more “hesitant” than other cars when their drivers first notice the road signs? Do some cars speed up or slow down as they approach the fork in the road? We might also measure other behaviors: Do some cars change lanes before they reach the fork? How far in advance do they do so? Do the cars suddenly switch lanes or do they gracefully glide from one lane to another?

These additional types of performance measures provide a different type of behavioral index for this decision process. Because they occur well before the actual moment of choice, but they are antecedent behaviors which may rely on the same cognitive process of directing the car, they might provide fresh insights into when drivers decide to turn or they may reveal the decisiveness of some drivers and the uncertainty of others.

Critically, certain variables, such as car speed or spatial position, can be measured continuously throughout the period before the choice is made. In a sense, these types of variables can provide a *dynamic* perspective on the decision process; indeed, they may also reveal that certain aspects of the decision process were initiated far in advance of the actual choice behavior that we originally measured.

These types of response dynamics have been studied in experimental situations which are far removed from driving cars. As an example, consider the behavioral paradigm that was utilized by Tenenhaus, Spivey, Eberhard, and Sedivy (1995), in which participants were asked to retrieve a target object while their eye movements were being tracked. Although the participants were highly accurate at the behavioral task (i.e., they rarely failed to identify a simple object), information about the way that they processed these stimuli was gained by examining how they moved their eyes before they made their choice response. Because eye movements were required for selecting the appropriate object, the eye movements that occurred in advance of target selection could reveal how fully each participant entertained the possible options. The researchers found that items with a close phonological relationship to the target item were more likely to be fixated than were other possible alternatives, revealing an important aspect of decision behavior which was not well captured by the choice response alone.

As an example of the utility of this paradigm beyond simple phonological effects, Dahan and Tanenhaus (2005) found that conceptual, visual competitors garnered more attention than did non-conceptual competitors (e.g., “snake” was confused with “rope,” but not with “couch”). These anticipatory eye movement tasks have also been successfully deployed with infants (McMurray & Aslin, 2004) to study both categorization and other aspects of visual perception.

Although eye movement paradigms provide a strong index of prechoice behavior in adult and infant humans, they offer little utility for research with a favorite experimental animal, the pigeon, because no suitable method has yet been devised to track pigeon gaze. This technical problem is complicated by a number of anatomical and visual system disparities which make eye movements in pigeons difficult to interpret: pigeons are “multifoveal,” having one area that serves central vision and another area that serves lateral vision; in addition,

pigeons' saccades often occur within head-thrusts or in only one eye (see Dittrich, Rose, Buschmann, Bourdonnais, & Gunturkun, 2010).

However, a second kind of behavioral task has also been deployed to measure pre-choice behavior in people. For example, Spivey, Grosjean, and Knoblich (2005) asked participants to make a binary choice between phonological competitors by performing a mouse click on the appropriate target. After being presented with a target word (e.g., "candle"), participants were asked to choose between pictorial alternatives, one of which was always the target word; the other alternative might be phonologically related (e.g., "candy") or it might be unrelated (e.g., "pasta"). Rather than examining only the binary choices made by their participants, Spivey et al. (2005) tracked the *trajectory* of participants' mouse movements en route to making their binary decision. Behavioral analyses disclosed that participants made faster, more direct mouse movements toward the correct items when they were presented with a non-phonologically-related competitor than when they were presented with a phonologically-related competitor.

Therefore, at least in people, pre-choice behavior can be successfully measured without recording such behaviors as eye movements. Critically, similar measures may also provide valuable information about cognitive processes in pigeons. The challenge lies in isolating a similar period of pre-choice behavior in which to measure responding. Unlike people, pigeons cannot move manual mice to select between response alternatives; instead, they make only short, bursts of ballistic pecking motions. Yet, despite the fact that pigeons do not make direct analogs of mouse movements, many experimental designs call for a period of stimulus observation and concomitant responding which provides just such an opportunity to measure pre-choice behavior.

In one example of such a design, the pigeon is presented with a single stimulus (such as an array of icons to be categorized as “same” or “different”) and it must complete an FR schedule (Fixed Ratio; a constant number of responses to the stimulus) before being presented with two choice keys, only one of which is correct (e.g., one key corresponds to “same” and one to “different”). Typically, as in human studies, measures related to the choice keys are taken: the accuracy with which the pigeon pecks the correct key or the speed with which it does so. In addition, one might also measure the spatial distribution of pre-choice pecks as a proxy for the kinds of anticipatory behaviors that have been measured in people.

Previous Peck Location Analysis in Pigeons

We are not the first to suggest that measuring the location (or the intensity) of pecking responses during operant conditioning experiments may yield interesting results; several studies have tracked the distribution of pecking at pictorial stimuli. Researchers as early as Skinner (1965) tracked responding by inserting carbon paper between the pecking surface and the discriminative stimuli. Using this simple method, Skinner discovered that pigeons preferentially pecked at particular places on items in a discrimination task. Indeed, Skinner (1960) notes in his declassified description of “Project Pigeon” that “a simple device using carbon paper to record the points at which a pigeon pecks a figure showed a promise which has never been properly exploited” (p. 29).

Even in a three-key operant chamber which provides no way to precisely track the location of the pigeon’s peck, recording to which of two keys the bird responded during certain autoshaping designs provided critical information about the way in which pigeons were processing the conditioned stimuli. This idea will be more fully developed in the later section on autoshaping.

Beyond using simple methods such as carbon-paper tracking or tracking which of three keys a pigeon might peck, newer technology allows for the

automatic localization of the pigeon's response. These "touchscreen" devices permit tracking the response on a pixel-by-pixel basis, with data output as if the pigeon's beak were a mouse cursor on a computer screen. This technological development was critical for the emergence of experimental designs such as visual search as a methodology to be used with the pigeon. By experimentally tracking the pigeon's response using a touchscreen (or similar device), researchers could determine if the pigeon had pecked the target or a distracter item in a visual search task (Blough, 1977; Katz & Cook, 2003).

Response location has also been tracked in a limited set of pigeon categorization and conceptualization tasks. Allan (1993) reported that pigeons tend to peck at the discriminative features of stimuli in a naturalistic image categorization task which entailed the discrimination of humans from nonhuman stimuli. In this experiment, pigeons were presented with a set of slides, half of which contained people and half of which did not; the birds were reinforced for pecking at pictures of humans but not for pecking at pictures without humans. The data showed that pigeons quickly learned to respond to pictures with humans, preferentially pecking at the regions of the pictures that contained human figures. Importantly, this preference transferred to new pictures, indicating that peck location tracked the category "human" rather than being the result of a pecking preference only for the specific set of training images.

Recently, a more detailed experiment replicated key aspects of the Allan (1993) study (Dittrich et al., 2010). Dittrich et al. not only found that pigeons tracked particular features in the discriminative stimuli, but that the birds suffered greater decrements in discrimination performance when those features were removed than when other features in the objects were removed. Specifically, Dittrich et al. taught pigeons to discriminate pictures of people from pictures without people. By tracking the location of the response, Dittrich et al. found that

pigeons again preferentially pecked at the areas of the pictures that were occupied by the human figures—particularly the heads of these people. When the heads (or the bodies) of the people were removed in a subsequent test, Dittrich et al. found more control by the heads of the people, indicating that these were the areas that the pigeons used to categorize the objects.

Further types of analyses have tracked the emergence of discriminative responding within the course of individual go/no-go trials. In go/no-go experiments, pigeons make a “go” response by pecking to some types of stimuli, whereas they make a “no-go” response by withholding pecks to other types of stimuli. Because pigeons do not completely withhold responding on “no-go” trials and because even “go” trials have some fixed duration (typically go/no-go experiments are conducted with an FI [Fixed interval; a response is required after a set amount of time has elapsed] or a VI [Variable interval; a response is required after a variable amount of time has elapsed] reinforcement schedule), the temporal distribution of responses over the course of the trial can be analyzed.

One example of this type of study was conducted by Cook, Kelly, and Katz (2003). In that experiment, pigeons were presented with a sequence of pictures; the birds had to peck only at “same” sequences while withholding pecks at “different” sequences. For example, the sequence of pictures might be “AAAAAA” (same), “ABABAB” (different), or “ABCABC” (different). If the pigeons compared the current item to previous items, then although the “ABABAB” sequence and the “ABCABC” sequence are each nominally “different” sequences, the temporal distribution of pecking responses might differ for these two sequences, because the first sequence is less varied than the second. Indeed, pigeons pecked more at “ABABAB” sequences than at “ABCABC” sequences, perhaps indicating the greater similarity of the “ABABAB” sequences to the “AAAAAA” sequences. Relatedly, the results of Cook and Brooks (2009)

and Brooks and Cook (2010) confirmed that within-trial pecking distributions in an auditory discrimination task also change over time as a function of stimulus similarity.

These experiments on peck location are all somewhat different from the studies of dynamic decision processes that were reviewed with humans because none ended in a spatial choice response. This disparity may heighten the propensity of the pigeons to peck at particular diagnostic features in the stimuli rather than to direct their pecks at a particular location in space. Alternatively, the types of feature-rich displays that are typically presented to the birds in these experiments may increase the likelihood of preferential pecking at a particular set of diagnostic features. Although the stimuli and behavioral tasks in these prior pigeon experiments are different than those presented in this dissertation, these experiments all provide an interesting, complementary set of data regarding peck location.

Nonetheless, for the purposes of the set of experiments in this dissertation, we will be primarily concerned with the case in which arbitrary report responses are ultimately used to indicate a choice. In the forced-choice task, rather than in the go/no-go task or the single-response visual search task that have previously been presented, the pigeon is presented with a discriminative stimulus and it is required to make an “observing response” prior to its being given a set of keys which symbolically represent a set of answers (see Wasserman, 2002). For example, the stimuli might be arrays of identical and nonidentical objects, and the choice keys might represent “same” or “different” responses; or, the stimuli might be pictures of cats, cars, chairs, and flowers, and the keys might correspond to their category membership.

Here, the “observing response” is the aforementioned FR schedule that precedes the choice response. The observing response (e.g., Wyckoff, 1952;

Roper & Zentall, 1999) was, historically, a response which an animal might produce to “observe” a set of discriminative stimuli that are associated with different schedules of reinforcement. In the classic case (Wyckoff, 1952), the pigeon was presented with a single white keylight that was reinforced on a mixed FI-30/Extinction schedule (i.e., one that did not allow the pigeon to predict the delivery of reinforcement for responding on any given trial). At the same time, a treadle was available which the pigeon could press to change the stimulus from white to either red or green. Importantly, this also changed the information that the pigeon had about the response contingencies present on any given trial; green samples were associated with FI-30 access to grain whereas red samples were associated with extinction. Wyckoff reasoned that while producing this response did not change the frequency of reinforcement delivery, it gave the animal additional *information* (though, this information gathering hypothesis has received conflicting support in the years since; see Dinsmoor 1983). The “observing response” that we will be discussing is of a similar nature; here, the animal is required to complete an FR response to the stimulus in order to produce a second set of discriminative stimuli (i.e., the report keys). The requirement of this latter kind of an observing response, which produces choice or other discriminative stimuli, is now a standard feature in most animal cognition studies.

In our first attempt to measure the pre-choice behavior that occurs during the observing response phase of discrimination learning tasks, we studied pigeons which had been taught a trial-unique same/different discrimination (Brooks & Wasserman, 2008; Brooks & Wasserman, 2010). In the same/different discrimination, the pigeon is presented with an array of 16 items. On Same trials, the pigeon is shown 16 identical items; on Different trials, it is shown 16 nonidentical items. After completing an observing response to this array, the pigeon is presented with two choice keys to the left and right sides of the display:

one of these keys is to be pecked on Same trials and the other is to be pecked on Different trials. If the pigeon is correct, then it receives food and advances to the next trial; if the pigeon is incorrect, then it is given a dark timeout and it must proceed to one or more correction trials. This particular task is difficult to master, but after extensive training, pigeons routinely approach 90-100% correct key choice.

What we found when we measured pre-choice pecks during this task was surprising: even during the observing response period, the pigeons responded differently to the Same and Different arrays (Brooks & Wasserman, 2010). At first, it seemed as though the pigeons made spatially directed responses toward the location of their impending choice response, but closer inspection of the data revealed that this trend was only robust on Different trials, not on Same trials. So, although there was a clear disparity between these conditions and although the pigeons' final choice responses were well above 90% correct on both Same and Different Trials, their FR responses were not symmetrically distributed. We reasoned that this might be because the birds were using a specific strategy to solve the task; namely, they were sensitive to the array variability or detecting differences in the display (Young, Ellefson, & Wasserman 2003; Young & Wasserman, 2001).

Furthermore, this distributional disparity did not appear to be constant through time. To evaluate this possibility, we calculated the disparity in the distribution of Same and Different trials for each peck position in the FR by using a non-parametric statistic called Rho, which was initially derived by Herrnstein, Loveland, and Cable (1976) to measure the differences in peck rates during go/no-go experiments. We confirmed that this measure can also serve as an index of the disparity between overlapping spatial distributions. More importantly, we found that the disparity in the spatial distribution of pecks increased as a function

of the number of pecks in the FR, but that this disparity reached its maximum at about 5 or 6 pecks into the trial.

We next performed an interesting experimental manipulation: rather than presenting pigeons with either 16 identical or 16 nonidentical items, we presented them with *mixtures* of 16 items that were partly identical and partly nonidentical on nondifferentially reinforced test trials (i.e., trials in which the birds were given reinforcement no matter what they chose). For example, we showed the birds displays of 8S/8D (i.e., 8 identical and 8 nonidentical) items or 12S/4D items. Presenting the birds with mixtures of identical and nonidentical items changes the variability of the array; pigeons have previously been shown to dimensionalize the categorical Same/Different task into a continuous variability discrimination task (Young, Wasserman, & Garner, 1997; Young, Ellefson, & Wasserman 2003). Therefore, by manipulating variability, we should systematically affect pigeons' choice responses. The birds showed highly systematic choice behavior as a function of the variability of the array. As well, their pre-choice pecking behavior also spatially shifted when we manipulated the variability in the stimulus array, pecking more similarly to Different trials than to Same trials when the arrays were more variable than when they were less variable.

Current Aims

Despite these interesting observations of the pigeons' behavior during the FR in this purportedly "cognitive" task, we knew little about the basic mechanics of this behavior. How reliable is the measurement of spatially directed, pre-choice pecking behavior? What are the mechanisms that account for this anticipatory behavior? Does this behavior change over time, both across learning and within individual trials? To answer these and other related questions, we have prepared a set of experiments using a more basic discrimination paradigm, adapted from an

autosshaping study that was conducted 3 decades ago by Wasserman, Carr, and Deich (1978).

The organization of this dissertation is as follows. In the first chapter, we present a review of the literature relevant to the current project. In the second chapter, we outline the basic anticipation procedure which will form the foundation for the bulk of the experiments and present data from three experiments on pigeons and rats.

In the third chapter, we evaluate two possible mechanistic explanations for this anticipatory behavior; namely, that animals are motivated to produce anticipatory responses because of a shorter temporal route to reinforcement or because of the spatial and temporal contiguity of the stimuli used in the task. In the fourth chapter, we evaluate several spatial parameters that might importantly influence the distribution of these anticipatory responses.

In the fifth chapter, we re-evaluate data from two previously published projects. This was done for two reasons: first, to assess the generality of the observed phenomenon, and second, to evaluate the particular interpretation that the anticipatory responses are some kind of fractional reproduction of the terminal response.

Finally, in the sixth chapter, we discuss the implications for the presented work in several fields. We also sketch a computational framework for the presented data using a Dynamic Field Theory model, attempting to show how the prospective representation for an upcoming spatial location might guide anticipatory pecking behavior.

Autoshaping

The Discovery and Importance of Autoshaping. Autoshaping is a behavioral phenomenon at the crossroads of Pavlovian and Operant conditioning. In a typical autoshaping experiment, a key is lighted immediately before the

delivery of food. Although no pecks to this keylight are required, pigeons will reliably come to peck at it. The term autoshaping is a portmanteau derived from “automatic shaping”, used to describe what is essentially a “hands free” way of reliably getting birds to peck at a keylight (a requirement in the operant lab, so that birds might be trained to do other, more complex tasks). The initial report of autoshaping (Brown & Jenkins, 1968) described a number of parameters which affected the likelihood of the pigeon producing autoshaped responses: forward and backward contingencies, light only trials or constant light, shorter trials or longer trials, and others. The basic phenomenon of autoshaping was highly replicable; of 36 subjects trained with an 8-s lighted key followed by presentation of food, all pecked the key in an average of only 45 trials. But, the discovery of autoshaping was essentially a methodological advance; indeed, Brown and Jenkins (1968) immediately delivered food reinforcement contingent on a peck to the keylight (a contingency which, if absent, makes the autoshaping procedure considerably more interesting!).

Williams (1981) begins one of his chapters on autoshaping in a particular way which bears paraphrasing here. In short, he remarks that the phenomenon of autoshaping might be considered one of the most serendipitous scientific discoveries in animal learning. Considering the circumstances in which a punctate visual cue is presented immediately before the onset of food, it is unremarkable or unsurprising that *something* would be conditioned. But, consider the extreme luck that that conditioned *something* just so happens to be a “skeletal behavior, directed at the response key, and apparently identical to the behavior that constitutes the classic example of the free operant!” (p. 58).

But, as noted by Locurto (1981), it was not until the advent of a second autoshaping procedure—in which food was withheld after responding—that autoshaping truly became theoretically important. Whereas early explanations of

autoshaping tended to focus on the instrumental contingencies built into the procedure—in which pecking the keylight was immediately followed by food (Brown & Jenkins 1968, Locurto 1981)—later procedures discounted the involvement of this instrumental contingency in favor of a Pavlovian contingency.

The important paradigm in this shift was the *omission* procedure; originally developed by Sheffield (1965) to study conditioned salivary responses in dogs. Sheffield deployed the omission procedure to see whether the salivation CR (Conditioned response) was due to Pavlovian or operant contingencies. The operant contingencies in the case of salivation might be the relative ease of eating following salivation, which would lubricate food prior to chewing and swallowing.

In Sheffield's procedure, dogs were first trained to salivate to an auditory CS (Conditioned stimulus). They were then given a new contingency in which food was withheld if the dogs salivated. Nevertheless, the dogs continued to salivate to the tone, even when doing so cost them food reinforcement, showing that salivation was under Pavlovian, not operant control.

Williams and Williams (1969) applied this procedure to pigeons, in which making autoshaped responses to the lit key led to the *omission* of food reinforcement. In this study, autoshaped responses continued to occur even in particularly maladaptive situations; pigeons pecked even when it cost them food to do so! These results have been replicated numerous times (see Killeen, 2003); the phenomenon is now generally known as *negative automaintenance*, referring to the fact that a behavior under presumptive operant control is maintained by the animal even in the face of a *negative* contingency. In a dramatic example of the maladaptive behavior expressed by autoshaping, Schwartz (1973) arranged an omission schedule in which green keylights were followed by food and red keylights were followed by electric shock. As this was an omission procedure,

food presentation occurred if a keypeck was not produced; likewise, shocks were given if a keypeck was not emitted. An operant analysis would suggest that pigeons should emit relatively few keypecks when the keylight was green (as doing so would cost the pigeons food) and peck vigorously when the keylight was red (as doing so would prevent the electric shock). But, the exact opposite result occurred: pigeons pecked often to the green key and almost never to the red key, despite this behavior costing valuable reinforcement and resulting in persistent shocks! This is a most peculiar behavior that made some researchers reconsider “the power of instrumental contingencies” (Killeen, 2003), or at the very least, consider the power of non-instrumental contingencies present in the learning environment.

At its heart, the autoshaping procedure essentially breaks the link between the sign and the significante of food reinforcement (see Hearst & Jenkins, 1974). In normal settings, both the signal for food (the sight of food) and the significante of food (its nourishing properties) are contiguous in time and space; they are integral cues. Responding to a signal for food by approaching and contacting it generally results in the animal receiving its reinforcing properties (Wasserman, 1981). Thus, autoshaping or sign-tracking is, naturally, quite a beneficial reaction to stimuli. Because in the natural setting the sign and significante are integral cues, sign-tracking prompts the approach of reinforcers and the avoidance of punishers. But, in the laboratory, these two properties can be unhooked so that the signal for food (the keylight) occurs in a different spatial location than the receipt of food, creating what appear to be strange or stupid behaviors under omission contingencies (see Blumberg & Wasserman, 1995).

This omission procedure has special relevance for this dissertation; the omission procedure involves the comparison between the *temporal contiguity* at work in standard autoshaping with a *differential contingency* between response

and food delivery. Similarly, some of the experiments in this dissertation directly pit *spatial contiguity* against *differential contingency*—either by an increased work requirement (large FR) or by an increased delay to reinforcement. These experiments will allow us to see whether spatially-directed responses in anticipation of an upcoming stimulus are caused by the mere spatial coincidence of two events or are determined by the differential reward for making those types of responses.

Autoshaping has also been used to study reinforcer expectation or anticipation (Jenkins & Moore, 1973). It happens that pigeons peck differently at an autoshaped keylight when the reinforcer will be food than when it will be water. This fact has been used to leverage autoshaping to study the pigeon's expectation of which reinforcer will follow a particular stimulus. For food reinforcers, pigeons make large beak gapes and biting motions toward the key; for water reinforcers, pigeons make gentle pecks with a closed beak. Utilizing these differential peck behaviors, Allan and Zeigler (1994) found that when pigeons were presented with two different sizes of pellets, they pecked these stimuli with two different gape sizes. If the pigeons expected a smaller pellet, then they made smaller gape pecks; if they expected a larger pellet, then they made larger gape pecks. Therefore, we have a distinct behavioral marker that pigeons anticipate a particular reward.

Given these findings, one might question whether the propensity to make autoshaped responses to the keylight is caused by “stimulus substitution,” in which animals would respond to the key as if it were reinforcer (Garcia-Hoz, 2003). Two sets of experiments are directly relevant in this case. The first involves the removal of the peck-like responses to the reinforcer by directly inserting the reinforcer into the pigeon's bill (e.g., Woodruff & Williams, 1976; Lucas, Vodraska, & Wasserman, 1979); in this case, rather than requiring water-

deprived pigeons to engage in the peck-like motion to consume water at the end of each trial, water was directly injected into the bill. Despite the fact that there was no overt pecking response required to obtain the reinforcer, pecks to the keylight still developed.

The second set concerns the use of reinforcers that do not engender pecking behavior, for example, the use of diffuse heat as a reinforcer for chicks in a cooled experimental chamber. Although the onset of heat in these cases can serve as a reinforcer and although chicks come to make certain responses to heat onset (such as “head lowering” and “napping”; see Wasserman, 1981), none of these heat-onset reactions involve directed pecking. Nevertheless, virtually all of the subjects that received heat-keylight pairings came to peck at the keylight, with some also making “snuggling” responses toward the light.

Secondary Reinforcement in Autoshaping. In the traditional autoshaping task, only one stimulus (i.e., the keylight) precedes food delivery. In a second-order conditioning task, two keylights precede the delivery of food. In one type of second-order task, serial conditioning, food is presented following both, in the following manner: CS2-CS1-Food. In the classical second-order conditioning task, food is given on first-order trials (e.g., CS1-Food), but not on second-order trials (e.g., CS2-CS1).

The studies of Rashotte (1981) provide a good demonstration of how a basic second-order relationship might be established in autoshaping. In the basic task, animals in the Experimental group were given a number of CS1-Food pairings before a second phase in which CS2-CS1 pairings were given. Control groups were also run in which animals received two experiences that might inhibit the formation of CS2-CS1 associations. The first control was one in which the birds received normal CS1-Food pairings but only random CS2-CS1 pairings (insufficient for conditioning to occur). Thus, these birds could learn something

about CS1, but were unlikely to learn to peck at CS2. A second Control group received CS2-CS1 pairings as in the standard experimental group, but had only been given randomly presented CS1-Food pairings (again, insufficient for conditioning to occur). The critical data (pecks to the CS2 stimulus) showed very weak pecking in both control groups but very strong pecking in the experimental group, demonstrating the formation of a CS2-CS1 association. Other examples of second-order conditioning in autoshaping (e.g., Rescorla & Cunningham, 1979) will be more fully discussed later in the text.

Spatial Anticipation in Autoshaping. Autoshaping has also been used to study spatial anticipation as well as reward anticipation. For example, in Wasserman, Carr, and Deich (1978), two sequentially presented CSs in a serial conditioning paradigm (CS2 and CS1) were followed by food. Each trial proceeded with the presentation of CS2, then CS1, then food.

In Experiment 1, CS2 consisted of the two outside keys lit in either a green-red or a red-green configuration. For some pigeons, CS1, a white light, always appeared on the side that had been lit red; for other pigeons, CS1 always appeared on the side that had been lit green. When peck distributions were measured, Wasserman et al. (1978) found that pigeons not only pecked at the key (CS1) that immediately preceded food, but they also pecked at the keys that preceded it (CS2). Interestingly, the pigeons overwhelmingly pecked at the colored key that was in the upcoming location of CS1.

In Experiment 2, rather than both colors being present during CS2, only one color was present. For example, both keys might be lit green or both lit red. If both were lit green, then CS1 would be on the left; if both were lit red, then CS1 would be on the right. Again, a strong likelihood for the pigeons to peck at CS2 was observed; and, again, the pigeons preferentially pecked at the key location on which CS1 would appear.

One critical feature of these two spatial discrimination tasks is that in neither case was pecking at CS1 or CS2 differentially rewarded; because the study involved an autoshaping procedure, no behavior at all was necessary for the pigeons to receive food. Thus, it is possible to study these spatial anticipation effects without explicitly training this type of behavior.

Theoretical Considerations

The Origins of Anticipation. “Anticipatory” responses have been a well-recognized behavioral phenomena in psychology. In some sense, the study of learning can be said to be the study of anticipation: in order to survive in a complex and dangerous world, organisms must react effectively to a variety of signals, some of which indicate that they should prepare to eat, some of which signal that they should prepare to run. Indeed, psychologists as early as James (1890) recognized the value of anticipating future events; his theory of “ideo-motor action” held that anticipating the outcome of actions or situations provided the basis for voluntary thought.

Early learning theorists were particularly captured by the fact that not only humans, but animals too seemed to make responses which suggested that they “anticipated” the outcome of a situation; for example, rats might make chewing motions as they approached the end of a runway or they might turn in a given direction too soon before the upcoming choice point in a maze. These responses were originally termed *fractional anticipatory goal responses* by Hull (1931), a name which denoted three qualities of the response: (a) it was often “fractional,” or incomplete, in nature, (b) it was “anticipatory,” in that although the response might be situationally appropriate (e.g., chewing motions before the presentation of a to-be-chewed food), it occurred before the response was required, and (c) it was often a “goal directed” response which would eventually be directed toward the goal of the behavioral sequence that was being performed.

These fractional anticipatory goal responses were assumed to be generated in the same way as Pavlovian CRs (see Amsel & Rashotte, 1984). Just as a tone might precede a puff of air to the eye and reflexively trigger an eyeblink, Hull reasoned that the state of hunger would precede the act of eating food. After learning, hunger would therefore evoke components of the behaviors associated with eating, which would be triggered during the behavioral chain that led to feeding (e.g., making a number of turns in a maze before arriving at the goal box). The subset of these responses that did not compete with the overt behavior (maze running) would appear as fractional anticipatory goal responses.

But, there were complications from the analysis of fractional goal responses as well: for example, how can one explain *anticipation* without *cognition*? Here, Hull viewed anticipatory behaviors as nothing more than behavioral sequences which were emitted faster than the occurrence of stimuli in the environment:

Sequences in the outer world evoke parallel reaction sequences in sensitive organisms... [The] organismic sequences acquire a tendency to run off by themselves, independently of the original world sequences. The organism has thus acquired an intimate function copy of the world sequence, which is a kind of knowledge.

In the case the two sequences begin at the same time but the organismic or behavior sequence runs off at a faster rate, the knowledge becomes fore-knowledge or foresight. This has great significance in terms of biological survival. (1930/523)

Despite this seemingly behavioristic analysis of anticipatory behavior, there was still something decidedly non-behavioristic in Hull's *fractional anticipatory goal response* (MacCorquodale & Meehl, 1948). An "internal representation" was generated because the fractional response elicited an internal "interoceptive cue," *sg*, which could then be linked to a number of other responses, such as turning or moving toward a particular goal location. As well,

the term “anticipatory” itself was cognitive. This fact did not escape Hull’s notice; by his last book, he had abandoned the term entirely for the more neutral “antedating,” which did not carry the same nominal baggage.

There were further doubts about the explanatory value of the fractional anticipatory goal response and about the internal states that it created. For one, Skinner (1953) wrote a critique not of fractional anticipatory responses directly, but rather of the common practice of using any sort of internal states to explain behavior. He noted that “the practice of looking inside the organism for an explanation of behavior has tended to obscure the variables which are immediately available for a scientific analysis.” (1953, 31).

Although the *fractional anticipatory goal response* may no longer be in common use in experimental psychology or even in basic learning texts, several “orphans” of this realm of research remain. One of the most well-studied of these is the *differential outcomes effect* (Trapold, 1970). The basic rationale is as follows: on the receipt of a particular stimulus, the expectation of a particular reward (rather than of simply reward in general) is generated due to the differential pairing of those two events.

Trapold devised an experimental situation in which the reinforcer following S_1 (Stimulus 1) and R_1 (Response 1) was either the same as or different from the reinforcer following S_2 and R_2 . If the expectation of the unique reinforcer can serve a signaling value, then discriminations with differential outcomes ought to be learned faster than discriminations with nondifferential outcomes. Indeed, this result is what occurs.

The inclusion of differential outcomes also facilitates certain types of memory processes, presumably because of the extra signaling value that the expected outcomes might provide. For example, DeLong and Wasserman (1981) trained two groups of pigeons with either nondifferential (Group NDO) or

differential (Group DO) probabilities of reinforcement for responding to the test stimulus in a successive matching design. [Successive matching is an experimental design in which two stimuli are presented in the same spatial location and one schedule of reinforcement is in effect on trials in which these stimuli match and another is in effect on trials in which they do not.] Under these contingencies, pigeons in Group NDO performed poorly with delays of only 5-s between the sample and test stimuli; but, Group DO performed well with long retention intervals (of up to 10s). Thus, the added cue from differential outcomes for particular samples may serve to increase memory for an item across a delay.

Prospective and Retrospective Coding. Modern theories of anticipation and animal memory have more strongly considered the role that “anticipation” in the cognitive sense might play in explaining behavior. The concept of “prospective” memory derived from an analysis of animal memory by Konorski (1967; see Wasserman, 1986) is an example of such a construct. This analysis suggests the use of two types of memory systems: one component (“prospective memory”) is used to efficiently execute behaviors in the service of upcoming goals or events, whereas the other component (“retrospective memory”) is used as a store of information about past events. For example, if one’s goal is to visit Iowa City, then the choice to move to the left lane on I280 after seeing the Iowa City road sign might reflect usage of the prospective component of memory. Conversely, memory for the color of that road sign after having passed it might reflect usage of the retrospective component of memory.

Wasserman (1986) described two paradigms that may differentially call on the two memory processes in animals. The first of these is a *simple discrimination* task. Here, a set of two or more sample stimuli is followed by a set of two or more test stimuli; correct responses are determined solely by the sample stimuli. For example, a red triangle might require a left response and a yellow triangle might

require a right response, regardless of the test stimuli, vertical and horizontal lines, that are presented during the test in randomized spatial locations. In this type of task, the animal could store a prospective code about where to respond after seeing the sample. The second type of task is a *conditional discrimination* task. Here, a set of two or more sample stimuli is followed a set of two or more test stimuli; correct responses are determined by specific sample-test stimulus combinations. For example, to receive reinforcement, a blue square sample stimulus might require a peck to a horizontal line test stimulus, whereas a green square sample stimulus might require a peck to a vertical line test stimulus; the sides on which the horizontal and vertical lines appear is counterbalanced. In this type of task, the animal must store a retrospective code about the kind of sample that it saw in order to respond correctly in the test.

Despite the fact that critical behavior (a peck to one of the two side keys) is dependent on prior sample information in both cases, these two experimental methods produce very different results. For example, prospective memory has been experimentally shown to be more resistant to the deleterious effects of delayed testing than retrospective memory (Smith 1967, Honig & Wasserman 1981). In Honig and Wasserman (1981), pigeons were placed in a go/no-go task in which a sample was presented, followed by a delay interval, followed by a test stimulus. Certain sets of stimuli were followed by food, whereas others were not; if pigeons learn the go/no-go discrimination, they peck vigorously on reinforced trials and withhold responses on nonreinforced trials.

Two types of trials were given. In one type of trial, a simple discrimination task, the first stimulus (e.g., a colored key) would signal whether the pigeon should respond to the test stimulus (e.g., a line orientation), irrespective of the test stimulus value; one stimulus always signaled the delivery of reward, whereas another stimulus always signaled nonreward. In the other type

of trial, a conditional discrimination task, the color of the first stimulus served as a conditional cue, such that the pigeon should respond only if one of the two line orientations was subsequently presented. The first stimulus therefore only signaled reward if it was followed by a particular second stimulus; otherwise, it signaled nonreward. Thus, in the first task, the animal can prepare a response and anticipate reinforcement (i.e., engage in prospective coding), whereas in the second task, the animal must wait to compare the test stimuli to memory of the sample stimulus (i.e., engage in retrospective coding). When tested with various delays (0-s to 25-s) inserted between the sample and the test stimuli, performance dropped much more rapidly in the conditional discrimination than in the simple discrimination.

Still, it is uncertain if the memory code in the Honig and Wasserman (1981) study was a prospective code for the upcoming *response* or a prospective code for the upcoming *outcome*. Each of the two samples in the simple discrimination of Honig and Wasserman (1981) entail a different outcome; one sample always signals the delivery of food, whereas the other always signals the non-delivery of food (cf. DeLong & Wasserman, 1981).

The role of outcome expectancy was tested in a follow-up study by Urcuioli and Zentall (1990). To control for the effect of differential outcomes, all trials ended with food presentation if the correct response was given. To this end, the nonrewarded trials in Honig and Wasserman (1981) were replaced by trials involving a DRO5-s schedule (DRO; Differential Reinforcement of Other [Behavior], a schedule in which the bird is reinforced for doing something other than responding), in which reinforcement was given if the bird withheld pecking for 5-s. In that way, the prospective response account (“respond” vs. “don’t respond”) can be separated from the prospective reward (differential outcomes) account.

After being trained on the Urcuioli and Zentall (1990) task, pigeons did not show the simple discrimination advantage in delay testing; instead, the pigeons responded similarly during both simple and conditional trials after equivalent delays. This result suggests that the findings of Honig and Wasserman (1981) were primarily mediated by the differential outcomes (food vs. no food) that were associated with the first stimulus in the simple discrimination rather than the prospective coding of “respond” vs. “don’t respond.”

A second type of conditional discrimination to study prospective coding was designed by Pontecorvo (1985) and replicated and extended by Urcuioli and DeMarse (1997). The methodological change in these studies was to require a spatially directed response on every trial, rather than to use a go/no-go design. In these two studies, pigeons were shown two centrally presented sample and test stimuli and, rather than responding to that central key, the birds had to make a left or right key choice. The task was either true matching task with colored keys (Pontecorvo, 1985) or symbolic matching (Urcuioli & DeMarse, 1997) [Symbolic matching is an experimental procedure similar to true matching, but involves training arbitrary associations, e.g., “A” matches “1”, “B” matches “2”, rather than truly matching associations, in which “A” matches “A”]. For example, pigeons in Pontecorvo (1985) might be required to peck the left key after seeing the sequences “Red-Red” or “Green-Green” on the center key, but they might be required to peck the right key after seeing the sequences “Red-Green” or “Green-Red” on the center key.

Two groups of pigeons were trained in the critical conditions in each experiment. One group received a delay between the sample and the comparison stimulus (Group Retrospective); a possible trial sequence might proceed as “Red-DELAY-Green-Response.” The other group received a delay between the matching information and the response (Group Prospective); a possible trial

sequence might proceed as “Red-Green-DELAY-Response.” Because pigeons in Group Retrospective had delays inserted between the sample and the comparison stimuli, they must store a retrospective representation about the kind of sample given. Conversely, pigeons in Group Prospective had delays inserted between the entire stimulus sequence and the choice response; so, they may store a prospective representation about the kind of response they would make at the end of the delay.

Pontecorvo (1985) and Urcuioli and DeMarse (1997) reported effects of increasing delays that mapped onto those reported by Honig and Wasserman (1981). For group Prospective, longer delays had a much less deleterious effect on behavior than for group Retrospective, suggesting that prospective cues may have mediated performance in Group Prospective, whereas retrospective cues may have mediated performance in Group Retrospective.

But, Urcuioli and DeMarse (1997) took the additional step of recording behavior during the delay period for Group Prospective. These recordings revealed that the animals in Group Prospective engaged in particular behaviors during the delay which were consistent with their next response, such as shifting toward the location of the next key or biting in its direction before its appearance. These behaviors might serve as mnemonic cues for the animal, although those behaviors were not unrelated to the final choice responses in the task [see next section].

Response Mediation. Response mediation is the idea that, rather than storing a neural signal for a to-be-remembered event, animals or people engage in an overt behavior to help them remember. Conventionally, a behavior like vocal rehearsal is often given as an example of a response mediation; rather than passively storing a sequence of digits to be remembered in a test of short term memory, human subjects will often engage in a type of response mediation in which they repeat the sequence to themselves.

Hunter's (1913) experiments involving rats and dogs are some of the first appearances of this kind of mediation in animal behavior. In his delayed response paradigm, Hunter trained animals to select from a number of food wells; the animals were allowed to watch as one of these wells was baited with food. Hunter found that only those animals that maintained a positional fixation on the baited well were able to effectively choose the baited well after a long delay. He reasoned that, rather than storing a mnemonic code for which food well to visit, these animals immediately oriented toward the food and remained stationary throughout the delay period in order to code the location of the food by using an overt behavior.

Such effects have also been observed in monkeys. For example, Kojima (1980) taught rhesus monkeys a similar delayed response task. He observed highly stereotyped delay behavior that was consistent with monkeys' responding to the anticipated location of reward during the delay period. The task used by Kojima (1980) may have strongly promoted this form of responding; when a second task was used which required that the animal respond on the center key during the delay, memory performance suffered.

Despite the history of research on response mediation, both Eckerman (1970) and Kojima (1980) noted that response meditation strategies have rarely been observed in action, because few experimenters studying operant behavior have ventured inside the box or measured responding during the delay interval. As a counterexample, Blough (1959) reported that some of his subjects in a delayed matching design were able to maintain very high levels of accuracy at delays far beyond what other pigeons could handle. From direct observation of the pigeons' behavior, he concluded that the different pecking behaviors in which they engaged during the retention interval acted as a kind of rehearsal cue.

To test whether these mediating responses could facilitate retention behavior in the case that they existed, several studies have explicitly required the production of differential sample behaviors which might facilitate the use of response mediational strategies. Many of these studies have used non-spatial manipulations (see Urcuioli, 1985, for a review), choosing instead to program different schedules to the samples such as DRL (DRL; Differential Reinforcement of Low [Rates of Behavior]; i.e., produce responses, but slowly) vs. FR schedules (e.g., Urcuioli, Pierce, Lionello-DeNolf, Friedrich, Fetterman, & Green, 2002). At least two studies (Eckerman, 1970; Zentall, Hogan, Howard, & Moore, 1978) have used explicit spatial manipulations.

Eckerman (1970) studied the effect of differential sample behavior by explicitly requiring that pigeons respond to different sides of a long strip of keys before being tested in a conditional matching task. He found that accuracy and acquisition were fastest in groups trained to respond at different locations for different samples. Similarly, Zentall et al. (1978) required four groups of pigeons to respond in one of four ways to two sample stimuli in a conditional discrimination. In the first group, pigeons were required to respond in a different spatial location for each sample; in the second, pigeons were required to respond to one sample, but not the other; in the third, pigeons were required to respond to neither sample; and, in the fourth, pigeons were required to respond in the same spatial location for both samples. Zentall et al. found a clear acquisition benefit for the birds required to peck different spatial locations to the two samples, suggesting that different types of sample responses could facilitate learning.

However, in a separate analysis by Zentall et al. (1978), delays were inserted between the sample and test stimuli for these same four groups of pigeons. During the delay, Zentall et al. observed the behaviors of the pigeons and classified the types of behaviors that were displayed during the delay as either

under control of the sample (“When the Red sample was shown, the pigeon pecked the top key during the delay”) or not under control of the sample (“Regardless of the sample shown, the pigeon pecked the top key during the delay”). These behavioral classifications during the delay actually correlated more strongly with choice performance than did group assignment, suggesting to Zentall et al. that “delay behavior is a better predictor of performance than experimental treatment (p. 215).” In other words, different types of spatial responses to the sample stimuli could facilitate learning, but the response mediations that the pigeons adopted were more important for accurate delay performance.

Other Tests for Prospective Coding. Studying conditional discrimination tasks is not the only way to test for the kinds of memory codes that animals might utilize. A further observation (Cook, Brown, & Riley, 1985; Grant & Kelly, 2001; Zentall, Steirn, & Jackson-Smith, 1990) is that certain types of spatial discriminations that involve multiple choices afford researchers a good opportunity to test for prospective or retrospective coding.

One such discrimination is the radial arm maze, in which baited food wells are located at the ends of each of eight arms and the rat’s task is to run down each arm to collect food without making repeat trips. In this task, the memory demands change as each choice is made; but, they change in opposite directions for retrospective and prospective memory stores. For example, consider the situation immediately after the rat’s first choice: it might code one arm retrospectively (“I have visited arm A”) or seven arms prospectively (“I still need to visit arms BCDEFGH”). If we were to insert a long delay between this choice and subsequent choices (after Cook, Brown, & Riley, 1985), it should be much easier for the rat to remember a retrospective code than a prospective code. But, consider what happens after seven choices have been made and the rat must make

its eighth choice: a retrospective code (“I have visited arms ABCDEFG”) is much more cumbersome than a prospective code (“I still need to visit arm H”). If we were to insert a delay between the seventh choice and the final choice, then a prospective code should be much easier for the rat to maintain than a retrospective code. Finally, consider what occurs after four choices have been made: both types of codes become difficult to remember, but neither predicts an easier strategy. So, performance on this type of delayed radial-arm choice task should be worst if delays are inserted early in the task if a prospective code is used, worst if delays are inserted late in the task if a retrospective code is used, and of intermediate difficulty if delays are inserted into the middle of the procedure.

But, rather than using either prospective or retrospective coding, animals might strategically use prospective or retrospective coding at different points within the same task depending on the adaptive advantage of either coding strategy. Zentall et al. (1990) provide strong evidence for this kind of dual-coding strategy in pigeons.

In their experiment, five keylights were lit across the screen (in a sort of mock radial arm maze); the bird had to peck each (in any sequence) only once per trial; choosing a key that had already been chosen resulted in a timeout, whereas successfully completing the sequence lead to the delivery of grain. The experimental manipulation came in the form of delays that were inserted after pecks in the sequence of responses. A delay after the first choice produced a smaller decrement in performance than a delay after the second or third choice, suggesting that pigeons were retrospectively coding spatial locations at the beginning of the list sequence; but, a delay at the end of the sequence again produced a smaller decrement in performance than a delay in the middle of the sequence, suggesting that animals were prospectively coding spatial locations at the end of the list. So, because of the contributions of both prospective and

retrospective coding, the task proved to be most difficult in the middle of the sequence.

Related experiments have also examined the ability of prospective mediation for other aspects of the upcoming trial. Two similar studies (Wasserman, Grosch, & Nevin, 1982; Honig & Dodd, 1986) are particularly relevant. Wasserman et al. (1982) gave pigeons a conditional discrimination involving key color; pigeons had to respond when the sample stimulus and test stimulus matched in color. Inserted between the test and the comparison stimuli was a delay of either 1-s or 5-s. But, Wasserman et al. also gave pigeons a secondary cue presented on the sample stimulus (a horizontal or vertical line) which signaled whether the delay would be 1-s or 5-s. So, the pigeons could use this cue to anticipate the length of the delay.

Tests were then conducted in which the pigeons were presented with delays that were either consistent with or inconsistent with the signaling value of the line orientation stimulus. When the signal and the delay were consistent, pigeons showed much higher accuracy on the shorter delay than on the longer delay. But, when the delays were inconsistent, pigeons were more accurate on the long delay than on the short delay trials! One possible explanation for these results is that the pigeons were again controlled by a differential outcome contingency, in which they were more motivated to remember when cued to expect a short delay than when cued to expect a long delay.

The Neural Basis of Anticipation. The component processes that underlie anticipation seem to require specific neural circuitry over which to operate; considerable study has been devoted to understanding the neural mediation of this complex system. In humans, this line of research has tended to focus on the performance of planning complex behaviors across long delays (Cohen & O'Reilly, 1996) rather than the neural mediation of the relatively

simple tasks that we have discussed with animals. For example, reviews of focal lesion studies (e.g., Burgess, Veitch, de Lacy Costello, & Shallice, 2000) have concluded that patients with frontal damage lack the ability to plan for future events. Other studies which have used PET imaging (e.g., Burgess, Quayle & Frith, 2001; Okuda et al. 1998) have identified both frontal and parietal regions as critical in holding spatial responses in memory.

Animal studies have also identified key regions of interest. In particular, for both short-term prospective and retrospective coding, the prefrontal cortex codes for both “the recent past” and “the anticipated future” (Fuster, 2001). This region has been hypothesized to code both retrospectively for the sample and prospectively for the response (Quintana & Fuster, 1999).

But, just as in the behavioral literature, myriad different anticipated events have been implied in the neuroscience literature by the term “prospective coding.” For example, Watanabe (1996) reported that neurons in the prefrontal cortex are sensitive to various kinds of expected rewards. When single neurons in the prefrontal cortex were recorded during a delayed response task, in which various cues signaled various rewards, neurons were selectively activated based on the type of outcome that the animal expected. Likewise, Matsumoto, Suzuki, and Tanaka (2003) reported that prefrontal activations in macaque monkeys immediately preceded “goal-directed” movements; these activations were only found when the monkeys “anticipated” that a reward would be delivered. These data essentially provide confirmation that cells within the prefrontal cortex code for responses to particular stimuli when differential outcomes are expected—a kind of neural differential outcomes effect.

Relatedly, Rainer, Rao, and Miller (1999) reported that prefrontal cortex activations reflect the prospective component of memory during delayed response tasks. In this study, monkeys performed a go/no-go task with either a matching

discrimination or a symbolic matching discrimination. Rainer et al. reported that, although activity during the sample period was primarily sample-related, activity after offset of the sample was primarily related to the prospective object. The problem with this study is that the discriminations that were used arranged a many-to-one matching design [an experimental design in which several sample stimuli require the same response; e.g., “A” matches “1”, “B” matches “1”, “C” matches “2”, and “D” matches “2”], which may heighten the propensity of animals to represent objects in terms of a common code. Furthermore, this common code need not be *prospective*; for example, Zentall (1993) noted that birds code various samples in a many-to-one design in terms of the most discriminative available dimension. Issues in the design of Rainer et al. only serve to highlight the difficulty of separating different forms of prospective codes, such as the form of the upcoming response, the location of the upcoming response, the value of the expected reinforcer, the motivating value of the sample stimulus, the possibility of common stimulus coding unrelated to a prospective response, and the neural correlates of possible response mediation strategies.

Animal studies have also identified the parietal cortex as coding prospective response locations. In one study which examined both this region and the prefrontal cortex, Quintana and Fuster (1999) tested monkeys on a task in which they were presented with a single color (red, green, yellow, or blue) as a sample. Two of these samples (yellow and blue) were immediately followed by two white side keys; yellow predicted that the right side key would be reinforced, whereas blue predicted that the left side key would be reinforced. Similarly, the remaining two samples (red and green) could also be followed by two white side keys; red predicted that the right side key would be reinforced, whereas green predicted that the right side key would be reinforced. However, the red and green samples could also be followed by red and green side keys, in which case the

appropriate response for the monkey was to match the previously seen sample. Quintana and Fuster (1999) found that a high percentage of cells in the posterior parietal cortex coded for the spatial location of the upcoming response, but few coded for the color of the sample stimulus. However, Quintana and Fuster found that, in the prefrontal cortex, some cells coded for the spatial location of the upcoming response, whereas others coded for the color of the sample stimulus. Thus, the posterior parietal cortex may play a critical role in maintaining a spatially directed prospective memory.

A final area of neurobiological concern is the hippocampus. Early research tended to point away from the possibility that this area was involved in prospective processing (Kesner & Beers, 1988); instead, this area was typically associated with memory for the kinds of discrete events that mediate retrospective processing, such as holding a sample in memory during a matching to sample design (Squire, 1992).

However, it does appear that the hippocampus is engaged in prospective processing. In one of the best demonstrations of prospective coding in the hippocampus, Ferbinteanu and Shapiro (2003) tested rats in a plus maze; one of the lateral arms of the plus maze (e.g., “east” or “west”) was chosen as the goal arm during a given trial block, whereas the start arm was randomly chosen on every trial from the two remaining arms (e.g., “north” or “south”). The rats could therefore make one of four journeys on any given trial: north to east, north to west, south to east, or south to west; the direction of these journeys should be influenced by the start arm and the goal arm. Neural recordings indicated a high proportion of place fields that were journey-dependent, and many of these place fields were recorded while the rat was still in the start-arm, indicating that it was prospective processing about the route of the journey that occurred before the choice point.

Similar patterns of results (Lee, Griffin, Zili, Eichenbaum, & Hasselmo, 2006; Ainge, Tamosiunaite, Woergoetter, & Dudchenko, 2007) also strongly suggest that place fields in the hippocampus are dependent on the prospective destination. In Lee et al. (2006), rats were given a continuous alternation task in a modified T-maze while place fields were recorded; Lee et al. reported that the hippocampal place fields shifted toward the prospective location across trials. And, imaging studies on humans (Spiers & Macguire, 2008) have found that activation in the hippocampus may depend on the distance from a spatial goal. These results strongly imply that the hippocampus integrates information about an anticipated goal with information about the current spatial environment, an integration which implies prospective processing.

CHAPTER 2

BASIC ANTICIPATION TASK WITH PIGEONS AND RATS

Chapter Introduction

We believed that the successive discrimination procedure that was used in Experiment 2 of Wasserman et al. (1978) would prove to be a robust discrimination task to study pre-choice pecking because it could provide a sensitive index of anticipatory behavior. This procedure could already answer a simple question: How strongly would animals shift their behavior to one or the other of the two side keys in anticipation of an upcoming stimulus which immediately preceded food delivery, even in the absence of differential reinforcement to do so?

Certain aspects of the task, however, were not especially well suited to this investigation. First, we had no centrally located stimulus with which to measure pre-choice anticipatory behavior, a central focus of this investigation. Second, although the autoshaping procedure had yielded convincing results, we would inevitably have different numbers of responses on each trial precisely because the animals are not required to respond a fixed number of times in an autoshaping design. Last, we were unsure if rats would autoshape in the same way as pigeons.

So, we took three further steps to adapt this design to our experimental questions. First, we added a third stimulus which was centrally presented before the onset of CS2; this stimulus gave us the opportunity to directly measure pre-choice behavior. Second, rather than studying autoshaping, we required an FR schedule to be completed to each set of keys. Third, rather than referring to the key presentations as CS3, CS2, and CS1 (the conventional terminology for the conditioned stimuli in an autoshaping design), we referred to the stimuli in the order in which they were presented (instead of their distance from food): Link 1,

the centrally presented, initial stimulus; Link 2, the two stimuli presented on the left and right sides of the initial stimulus; and, Link 3, the stimulus presented on either the left or the right sides of the initial stimulus (responding to this stimulus immediately preceded the delivery of food).

Therefore, the current procedure (Figure 1) was adopted primarily as a direct way to capture spatial anticipation. In this basic procedure, the animal was given a simple discriminative stimulus located in the center of the screen and was required to complete an FR to that stimulus (“Link 1”); the animal was then given the opportunity to complete an additional FR on one of two laterally presented side keys (“Link 2”); finally, the animal was presented with a third stimulus which replaced one of the two side keys and was required to complete a third FR in order to receive food reinforcement (“Link 3”).

The current design allows for two measures of spatial anticipation. (a) During Link 1, the animal might spatially distribute its responses toward one or the other side of the middle key. (b) During Link 2, the animal might spatially distribute its responses to one of the two laterally presented side keys.

[A methodological note: Although choices are technically neither “correct” nor “incorrect” in the current task, because all trials end in the delivery of food, “congruent” and “incongruent” will be used to describe behavior in each of the experimental designs presented in this dissertation. In these cases, “congruent” refers to behavior in which the animal chooses the key in the same spatial location as the one to which its responses will be directed in Link 3, regardless of any other features of the trial; “incongruent” refers to behavior in which the animal does the opposite.]

Experiment 1

In Experiment 1, we trained four pigeons on this basic three-step anticipation procedure with visually matching stimuli in Link 1 and Link 2.

Method

Participants. The participants were 4 feral pigeons (*Columba livia*) kept at 85% of their free-feeding weights on a 14-h light/10-h dark schedule with free access to water and grit.

Apparatus. Four custom-built operant chambers were used for training and testing (Gibson, Wasserman, Frei, & Miller, 2004). Each operant chamber measured 36 (h) x 36 (l) x 41 (w) cm in size and was constructed of 0.635-cm black opaque Plexiglas. Centered on the front wall of each chamber was a 28.5-cm x 18.5-cm square opening. Behind the opening was a 38.1-cm glass touchscreen (Model 452981-000, EloTouch Systems, Fremont, CA). Behind each touchscreen, visual stimuli were displayed on a 38.1-cm (15-inch) LCD flat screen monitor (NEC, Melville, NY, Model 1550V). Reinforcers were 45-mg pellets (Pigeon Pellets Formula C1, Research Diets, New Brunswick, NJ) delivered by a rotary pellet feeder (Model ENV-203IR, Med Associates Inc., Georgia, VT) positioned behind the back wall of the chamber. Each chamber was controlled by an Apple eMac (Model Z083, Apple, Cupertino, CA) or iMac (Model Z0GC, Apple, Cupertino, CA) with computer programs created with Matlab (Mathworks, Natick, MA), using the Psychophysics Toolbox extension set (Brainard, 1997; Pelli, 1997).

Stimuli. Three squares, 7.44-cm x 7.44-cm, were used as stimuli. Each of these stimuli occupied 250 square pixels of space on the monitor. These keys were a red square, a green square, and a black star on a white background.

Procedure.

Shaping. The four pigeons were initially trained to peck both the 7-cm x 7-cm center and 3-cm x 3-cm corner areas of the computer screen. This training consisted of 150 trials during which one of four colors (green, yellow, red, or blue) was displayed on the screen. Initially, one peck at the color produced pellet

delivery and the screen went black. The number of pecks necessary to complete each trial was increased daily until each pigeon completed a Fixed Ratio (FR) of 20 pecks on each trial. This is standard procedure for shaping all birds in our operant conditioning lab.

Pretraining. The pigeons were then presented with one session in which a single 7.44-cm x 7.44-cm stimulus was displayed in one of the three locations to be used in Experiment 1. Five pecks to this stimulus resulted in food reinforcement. The stimuli that appeared in this location were either a red square, a green square, or a black star on a white background. After the pigeons reliably responded to each of the stimuli, training commenced.

Training. Each training trial began with a centrally located stimulus (hereafter, Link 1). Following 5 pecks to this stimulus, two laterally presented side keys were presented (hereafter, Link 2). Following 5 total pecks to these two keys, a third stimulus was presented on one side of the screen (hereafter, Link 3). Following 5 pecks to this Link 3 stimulus, food reinforcement was delivered. The Link 1 and Link 2 stimuli were always one of the two colored squares; the Link 3 stimulus was always the black star on a white background.

There were two types of trials, which are shown in Figure 1. In Link 1 and Link 2 of one trial type, the red square was presented; in Link 1 and Link 2 of the second trial type, the green square was presented. Each of these trial types uniquely signaled the location of the upcoming Link 3 stimulus; e.g., Red might signal “left,” whereas Green might signal “right.” These color-location assignments were counterbalanced across pigeons. Importantly, food reinforcement in this task was not contingent on discriminative responding in Link 2; choice of either key resulted in the presentation of the Link 3 stimulus, which was always followed by food. Training lasted for 12 sessions of 110 trials each (55 Red trials and 55 Green trials).

Results and Analysis

Analysis Plan. The main statistic used to analyze the spatial response distributions in Link 1 was Herrnstein's Rho; the main statistic used to analyze the spatial response distribution in Link 2 was Discrimination Ratio.

Rho is a nonparametric measure of the difference between response distributions, which has been primarily used to analyze disparities in peck rates in go/no-go experiments (e.g., Herrnstein, Loveland, & Cable, 1976). Rho is formally equivalent to the area under the ROC curve in signal detection theory (Bamber, 1975); it is computed by first calculating the Mann-Whitney U statistic for the two distributions and then dividing U by the maximum possible value for this statistic, $N1*N2$. Ties (i.e., multiple choices of the same spatial location) were solved by using a Fractional Rankings algorithm. The minimum value for Rho, with completely overlapping distributions, is 0.5; the maximum value for Rho, with completely non-overlapping distributions, is 1.0.

Discrimination ratio was computed as the total responses to the congruent side over the total number of responses for each trial type.

Results and Discussion

Figure 2 plots the behavioral measures of anticipation in both Link 1 (Rho) and Link 2 (Discrimination Ratio). Despite the absence of differential reinforcement contingencies during Link 2 as to which of the two keys must be pecked in order to advance to Link 3, all four pigeons quickly began to peck the congruent key in Link 2 (signaled by the color of the Link 1 and Link 2 stimuli), which was the key that would next be illuminated in Link 3 (Figure 2). One pigeon (60Y) exceeded a DR of .80 in the first session, one pigeon (16W) took 2 sessions to do so, one pigeon (87Y) took 3 sessions to do so, and the slowest pigeon (85Y) took 5 sessions to do so. Each of the pigeons maintained a high

level of accuracy following that first .80 session, with mean scores hovering around .90.

As can also be seen in Figure 2, anticipatory responses to the Link 1 stimuli emerged in concert with anticipatory responses to the Link 2 stimuli; over training, the correlation between these response measures was high, $R = .849$. The Link 1 anticipatory responses were slower to develop and overall less robust than the Link 2 anticipatory responses, with scores averaging between .70 and .80; this result is not difficult to understand given that Link 2 responses can be distributed to two different report areas, whereas Link 1 responses can only be distributed to one report area (the Link 1 response region being only half as large as the Link 2 response area).

To convey the general meaning of these Rho scores, we have also plotted the probability of making a pecking response in 25-pixel bins across the Link 1 stimulus over the last four sessions. These data, split by left-signaled and right-signaled trials, are shown in Figure 3. The pigeons were much more likely to peck the left side of the key when the Link 3 stimulus would be located on the left than when the Link 3 stimulus would be located on the right; similarly, the pigeons were much more likely to peck the right side of the key when the Link 3 stimulus would be located on the right than when the Link 3 stimulus would be located on the left.

Additionally, we also did an analysis of interresponse times (IRTs) over the last four sessions. IRTs are a classic way of reporting latency data in behavioral experiments (e.g., Blough, 1963). They are computed by subtracting the timestamp associated with each peck from the timestamp associated with each previous peck; thus, they are a measure of response rate. Lower IRTs indicate higher response rates; higher IRTs indicate lower response rates. Additionally, we filtered the IRTs so that IRTs above 5 seconds were excluded from the analysis;

this corrects for birds inexplicably waiting around in the operant box rather than pecking at the keys.

Three general patterns were evident. The first was a systematic decrease in IRT (i.e., an increase in response rate) over the course of the three successive links (see Figure 4). This result replicates previous data concerning behavior in three-link VI (variable interval) schedules in which response rates to initial link stimuli are generally slower than middle link or terminal link stimuli (e.g., Williams Ploog, & Bell, 1995) as well as data from serial conditioning which found that response rates were higher on stimuli more temporally proximal to primary reinforcement (e.g., Wasserman et al., 1978). So, even with a three-link paradigm using FR schedules instead of autoshaping or VI schedules, we can replicate basic phenomena concerning response rate from these past projects.

Second, each link was characterized by an initial “spike” in IRT; these spikes were undoubtedly caused by the bird having to shift to the general location of each stimulus before responding to it. Each of these spikes in IRT contain valuable information. At the beginning of Link 1, the spike in IRT is reflective of when the bird will ultimately initiate each trial. Even with IRTs greater than 5-s trimmed from the dataset, the birds tended to wait 3-s on average before responding to the Link 1 stimulus. At the beginning of Link 2, the spike in IRT is reflective of the shift that the bird must make from responding on the Link 1 key to responding on a Link 2 key. This spike is useful because it provides a good baseline for how long it takes the birds to make a single spatial shift between the central key and one of the side keys; even with perfectly predictive information, this shift takes about 1.5-s on average. Lastly, at the beginning of Link 3, the substantially smaller spike in IRT is reflective of the fact that on most trials by this point in training, the bird is already located at the location where it will next respond (i.e., it is already standing at the Link 3 stimulus). This spike is useful

because it provides a good baseline for what latency between the Link 2 and Link 3 responses can be expected at the end of training; this latency was around .5 s.

Third, following this initial spike in IRT were four shorter IRTs that corresponded to the four additional required pecks to each stimulus; there appeared to be a systematic trend for IRTs to fall (i.e., response rates to rise) within individual links, even after the first peck is discounted (see Figure 4 – bottom panel). To analyze whether the IRT did fall even past the initial peck and statistically evaluate the trends reported above, the IRT data for pecks 2-5 of each Link were entered into a repeated measures ANOVA (Peck Number x Link x Bird as a random factor). This analysis revealed a significant main effect of Peck Number, $F(3,9) = 17.44, p < .001$, a significant main effect of Link, $F(2,6) = 21.57, p < .001$, and a significant interaction between these variables, $F(6,18) = 3.74, p < .05$. To unpack that interaction, tests were done individually for each Link; these revealed significant effects of Peck Number in Link 1, $F(3,18) = 15.47, p < .001$, and in Link 2, $F(3,18) = 6.04, p < .005$, but not in Link 3. Therefore, IRT generally fell across the first two Links of the three link procedure, but response rate had stabilized by the third Link.

Experiment 2

In Experiment 2, we replicated the procedure used in Experiment 1 with eight rats. But, because using color stimuli with these functionally colorblind animals is impossible, half (Orientation Group) received training with stimuli that varied in orientation (horizontal vs. vertical); the other half (Brightness Group) received training with stimuli that varied in brightness (dark vs. light dot density displays).

Method

Participants. The participants were 8 Long-Evans rats kept at 85% of their free-feeding weights on a 12-h light/12-h dark schedule with free access to water.

The four Orientation rats had some training on various touchscreen tasks. They also had a small amount of pre-exposure to this procedure during which 5 responses were required during each Link, but no learning was observed under these contingencies. Although the first response on these trials tended to be directed toward the stimuli, subsequent responses tended to be directed at random places on the screen, perhaps due to the rats' previous training in which only one response was required per trial. This observation led us to switch to an FR1 schedule; all learning data from this group of animals is reported from the start of that FR1 schedule. The four Brightness rats had never participated in experimental testing and started on the FR1 schedule.

Apparatus. Two custom-built operant chambers were used for training and testing (Gibson, et al. 2004); these were similar to those used in Experiment 1, with minor changes to suit the rats. In these and all of the following experiments with rats, aluminum boxes were used rather than Plexiglas to prevent gnawing or biting into the chamber walls. Also, the square opening was shifted downward by 5-cm, so that the rats could respond to the screen without rearing. Last, an infrared touchscreen (EloTouch Systems, Fremont, CA) was used in place of a touch-resistive screen due to the lesser force with which the rats would reliably respond.

Stimuli. Three keys, 7.44-cm x 7.44-cm, were used as stimuli for each group. Each of these stimuli occupied 250 square pixels of space on the monitor. For the Orientation group, these keys were a square with horizontal lines, a square with vertical lines, and a black star on a white background. The width of the stripes on these pictures was 10-px. For the Brightness group, these keys were a square with light dot-density (80% white pixels), a square with dark dot-density (20% white pixels), and a black star on a white background. The rats were re-

shaped to these stimuli immediately before training regardless of prior experimental history.

Procedure.

Shaping. The rats were presented with one session in which a single 7.44-cm x 7.44-cm stimulus was displayed in one of the three locations to be used in Experiment 2. One response to this stimulus resulted in food reinforcement. The stimuli that appeared in this location were one of the three stimuli that were used in each group (either Brightness or Orientation). After the rats reliably responded to each of the stimuli, training commenced.

Training. Training was identical to that given in Experiment 1, with the exception that an FR1 schedule was used. Figure 5 shows a schematic representation of the experimental design used in both groups.

Training lasted for 10 sessions of 120 trials each (60 of each stimulus type).

Data Analysis. Data analysis was identical to Experiment 1, but no IRT analysis could be conducted as the rats only made a single FR response in each Link.

Results and Discussion

Figure 6 illustrates that the rats showed a strong preference to shift responding toward the congruent side within the first few sessions. This shift in responding occurred in both Link 1 and Link 2, and for both types of discrimination (orientation and brightness). Link 1 and Link 2 behavior appeared to rise in concert, although Link 2 behavior approached ultimately higher asymptotic levels. After 10 sessions of training, rats in both tasks had Link 2 discrimination ratios above 85% and Link 1 Rho scores above 70%.

Both Link 1 and Link 2 scores were again highly correlated. For the Orientation group, the correlation between average Link 1 and Link 2 scores

across the 10 days of training was $R = .94$; for the Brightness group, the correlation between these scores was $R = .97$. Thus, there was a clearly predictive relationship between scores in Link 1 and Link 2.

To once again convey the meaning of these Rho scores, we plotted the mean response probability across the Link 1 response key in 25-pixel bins for the two groups of rats over the last four sessions. These data, split by left-signaled and right-signaled trials, are shown in Figure 7. The rats were much more likely to peck the left side of the key when the Link 3 stimulus would next be located on the left than when the Link 3 stimulus would next be located on the right; similarly, the rats were much more likely to peck the right side of the key when the Link 3 stimulus would next be located on the right than when the Link 3 stimulus would next be located on the left. These data closely mirror the data from the pigeon experiments.

IRT analyses could not be conducted for this set of animals because of the FR1 response requirement, which produced no within-link IRT data.

Experiment 3

Experiment 3 aimed to discover if these anticipatory spatial responses emerge when the stimuli used in Link 1 differ from those used in Link 2. To accomplish this goal, two different stimuli were used in Link 1 than were used in Link 2. In Link 1, horizontal and vertical lines signaled the location of the Link 3 stimulus; in Link 2, green or red keys (as in Experiment 1) signaled the location of the Link 3 stimulus.

Method

Participants. The participants were 4 feral pigeons. Deprivation and housing conditions were the same as in Experiment 1. One bird had participated in an earlier study with similar response requirements but different stimuli.

Apparatus. The apparatus was the same as in Experiment 1.

Stimuli. Five 7.44- x 7.44-cm visual textures were used as stimuli. Each of these stimuli occupied 250 square pixels of space on the monitor. These stimuli were a red square, a green square, black-and-white horizontal lines, black-and-white vertical lines, and a black star on a white background.

Procedure

Shaping and Pretraining. Shaping and pretraining was as in Experiment 1.

Training. The basic experimental procedure was conducted as in Experiment 1, with minor changes. In Experiment 3, the Link 1 stimuli were always one of two line orientations and the Link 2 stimuli were always one of two colored squares; the Link 3 stimulus was always the black star on a white background.

In Link 1, horizontal and vertical lines signaled the location of the Link 3 stimulus (and the color of the Link 2 keys); in Link 2, green or red keys (as in Experiment 1) signaled the location of the Link 3 stimulus. As is depicted in Figure 8, any given pigeon had two different types of trials. In Link 1, one of two line tilts was presented on the center key. Each of these line tilts uniquely signaled the location of the upcoming Link 3 stimulus; e.g., Horizontal might signal “left,” whereas Vertical might signal “right.” In Link 2, one of two different sets of colored squares was presented on the side keys; e.g., Red might signal “left,” whereas Green might signal “right.”

Results and Discussion

The results of Experiment 3 were somewhat less clear than those of Experiment 1. The average discrimination ratios (during Link 2) and Rho values (during Link 1) are plotted in Figure 9. Whereas all of the birds strongly discriminated the colors (in Link 2) and they appropriately directed their responses to those colors (with mean discrimination ratios approaching 1.00),

discriminative responses to the line tilt stimuli in Link 1 were much less consistent (with mean Rho values never exceeding .65).

Similar to the birds in Experiment 1, Bird 39R showed a strong tendency to shift its responses in the direction of the Link 3 location during Link 1. Birds 85R and 45W showed an initial tendency to shift their responses toward the Link 3 location in Link 1, with peak Link 1 Rho values in the 4th and 5th sessions respectively; but, this preference declined over the remaining sessions. Bird 13Y showed a weak preference to anticipate, but appeared strongly controlled by a side bias in Link 1.

As was done for Experiments 1 and 2, we again plotted the mean response probability across the Link 1 response key in 25-pixel bins over the last four sessions. These data, split by left-signaled and right-signaled trials, are shown in Figure 10. Overall, this figure shows a much weaker tendency to respond on the congruent side of the Link 1 response key; maximal response probabilities approached 60% here, where in Experiments 1 and 2 they approached 80-90%.

IRT analysis was also completed for this study. These IRTs revealed similar trends to those observed in Experiment 1. Once again, we observed significant spikes at the first peck of each link and a progressive decrease in IRTs across successive links.

Statistical analysis was again carried out on to analyze whether the IRT fell past the initial peck. The IRT data for pecks 2-5 of each Link were entered into a repeated measures ANOVA (Peck Number x Link x Bird as a random factor). This analysis revealed a significant main effect of Peck Number, $F(3,9) = 4.57, p < .05$, a significant main effect of Link, $F(2,6) = 7.62, p < .05$, and a significant interaction between these two variables, $F(6,18) = 3.63, p < .05$. To unpack that interaction, tests were done individually for each Link; these revealed a significant effect of Peck Number in Link 1, $F(3,18) = 11.18, p < .001$, but not

in Link 2 or Link 3. Therefore, IRT generally fell across the first Link of the three Link procedure, but had stabilized at maximal responding by the second and third Link.

Chapter Discussion

Experiments 1 and 2 describe investigations with four pigeons and eight rats on a three-step schedule using identical stimuli in Link 1 and Link 2. In these experiments, the subject was required to complete an FR schedule during each Link in order to progress to the next link. During Link 1, the subject could respond anywhere on the central key; during Link 2, the subject could respond to either of the two side keys. These Link 1 and Link 2 stimuli signaled the location of the Link 3 stimulus, which immediately preceded food delivery. Although it was not required, the subject could express its anticipation of the location of that Link 3 stimulus by making differential responses during Link 1 and Link 2: responding to one or the other side of the Link 1 key or responding preferentially to one of the two Link 2 keys. Both pigeons and rats displayed a strong tendency to shift their responses toward the congruent side, effectively anticipating the location of the Link 3 stimulus.

These two experiments were modeled after the designs of Wasserman et al. (1978). In those experiments, pigeons showed a strong tendency to respond to spatially contiguous stimuli in an autoshaping design. Here, we chose to utilize FR schedules rather than the response-independent methodology of autoshaping; our procedure ensured equivalent numbers of responses on all trials, whereas the Wasserman et al. (1978) procedure engendered relatively weak responding to stimuli the farther they were temporally and sequentially removed from food reinforcement. Despite the use of these FR schedules instead of autoshaping, we replicated the main features of that previous report: namely, that pigeons would shift their response location toward the location of an upcoming stimulus.

However, Wasserman et al. (1978) measured this spatial contiguity phenomenon only in locations that overlapped with the CS1. To extend these results, we also measured responding during the presentation of a central stimulus which did not overlap in location with either the Link 2 or Link 3 response locations. To accomplish this task, we utilized a touchscreen which could precisely measure the location of each response to the stimulus. Using this touchscreen method, the tendency of the animals to make spatially contiguous “anticipatory” responses could be measured earlier in time, but these behaviors were directed at a stimulus that did not overlap with the location of either the Link 2 or Link 3 stimuli. These Link 1 reports provide an additional indication that animals shift responding in the direction of an upcoming stimulus when a cue signals its location.

Additionally, with the pigeons, we were able to recreate a second feature from these previous experiments and a well-established fact in the conditioned reinforcement literature that concerns rate of response. Both Wasserman et al. (1978) and Rescorla and Cunningham (1979), as well as other data on chain schedules (i.e., Royalty, Williams & Fantino, 1987), report a general increase in response rate for stimuli (or Links in the chain) nearer to the delivery of primary reinforcement. This increase in response rate has been interpreted in two primary ways: (1) that each member of a multiple-link schedule is independently linked to primary reinforcement and that the gradient of response rate that develops is due to each stimulus’ temporal relationship to primary reinforcement modeled over some form of exponential decay (e.g., Staddon & Cerutti, 2003; Killeen, 1994) or (2) that each member of a multiple-link schedule is linked to primary reinforcement through conditioned reinforcement by the subsequent link, and that the progressive increase in conditioned reinforcement across the links serves to increase response rate (e.g., Williams, 1994). Although the data presented in this

chapter are insufficient to support one or the other of these hypotheses, data presented in Chapter 3 will speak more directly to this issue.

In Experiment 3, we tested pigeons with a modified procedure in which they were shown stimuli in Link 1 that did not match those they were shown in Link 2. The pigeons did reveal some modest tendency to anticipate the location of the Link 3 response; 60% of the responses to the left half of the Link 1 key were on trials in which the next response would be left, whereas 60% of the responses on the right half of the Link 1 key were on trials in which the next response would be right. But, the pigeons appeared substantially impaired during Link 1 in this discrimination, at least when compared to Experiment 1. Whereas Experiment 1 and Experiment 2 both showed a progressive rise in Rho over the course of the experiment that nicely correlated with the rise in Discrimination Ratio, in Experiment 3 we saw virtually no rise in Rho. What could account for these disparities between experiments? One possibility is the use of less discriminable stimuli in Link 1 than in Link 2; orientation may be more difficult for the pigeons to process (Urcuioli & Zentall, 1986). In fact, we tried to run a set of pigeons using a similar procedure in which the Link 1 and Link 2 stimuli were switched, but only two pigeons acquired a congruent Link 2 response. So, it might be that orientation is a generally harder cue for pigeons to learn in the current task. It may also be that a hypothesized prospective signal is weaker when the two stimuli differ; whereas similar stimuli in Link 1 and Link 2 may promote a strong prospective signal to make a spatial response, this may not be the case with highly dissimilar stimuli. This last interpretation will be more fully discussed in the General Discussion (see the section “Returning to Dynamics”).

In most animal testing procedures, the subject is taught to respond in one way or another using differential reward or punishment. For example, an experimental subject might be taught to categorize different objects by pecking

different response keys (e.g., Bhatt, Wasserman, Reynolds, & Knauss, 1988). On correct trials, the subject is given food; on incorrect trials, the subject is given a brief timeout and must often repeat a long FR sequence. These tasks can be called *supervised* learning tasks, because they involve direct experimenter supervision in the form of reward, which is used to shape behavior toward some ideal state. And, if the animal can adjust its behavior based on reward prediction, then it will successively approach that ideal state.

In the present task, however, there is no such differential reward: the subject receives food for any response it makes in any Link. Therefore, in contrast to the supervised design, this kind of task is nondifferentially reinforced, or *unsupervised*. Unsupervised tasks provide a potentially effective means to evaluate the kinds of psychological processes which govern spatial learning, allowing us to effectively measure the way an organism might process environmental stimuli without the intrusion of direct tutelage. The potential usage of this paradigm as a test for unsupervised vs. supervised learning will be more fully discussed in the General Discussion (see section on Nondifferential vs. Differential reinforcement).

Finally, that the anticipatory behavior observed in Links 1 and 2 can be so easily replicated using an unsupervised task in animals as evolutionarily and neurologically divergent as pigeons and rats attests to the generality of the phenomenon (see Chapter 5 for additional evidence regarding the generality of this phenomenon in other tasks). However, although we documented such similar behavior in these two species, critical features of this task are still unspecified. The remainder of this project will be an investigation into the necessary and sufficient conditions to observe this kind of anticipatory responding in pigeons and rats in an attempt to uncover the underlying mechanism(s).

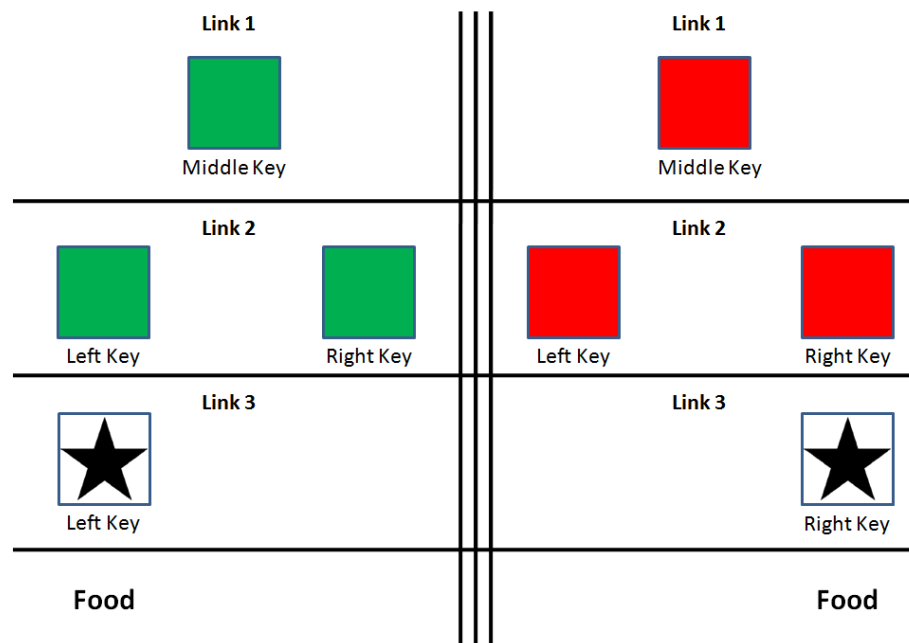


Figure 1 - Trial types in Experiment 1. The two types of trials in Experiment 1, shown in the left and right panels of the figure. On each trial, the pigeon was presented with three stimuli (represented by the vertical panels from top to bottom) followed by food.

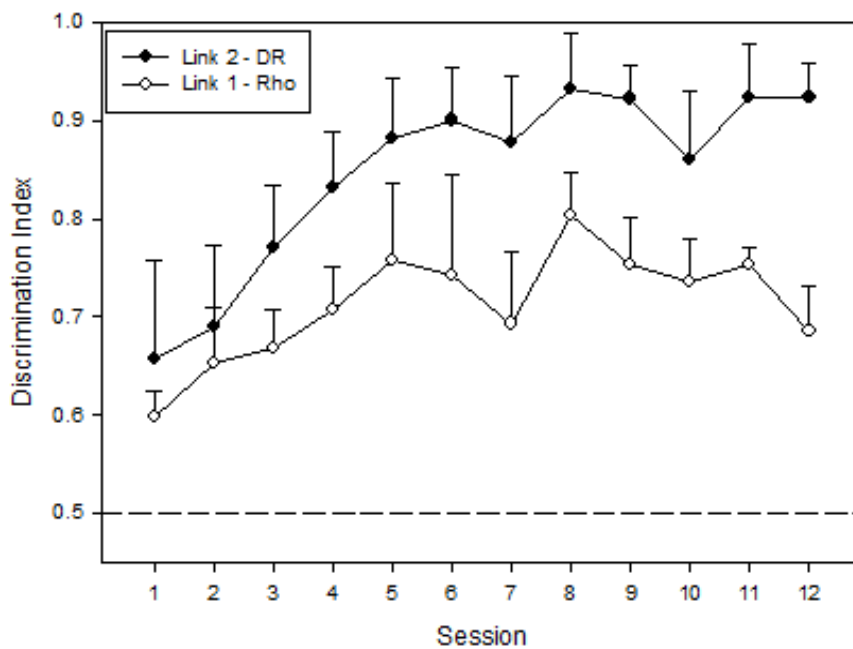


Figure 2 - Discrimination Ratio and Rho during Experiment 1. Herrnstein's Rho for Link 1 and Discrimination Ratio for Link 2 behavior in Experiment 1.

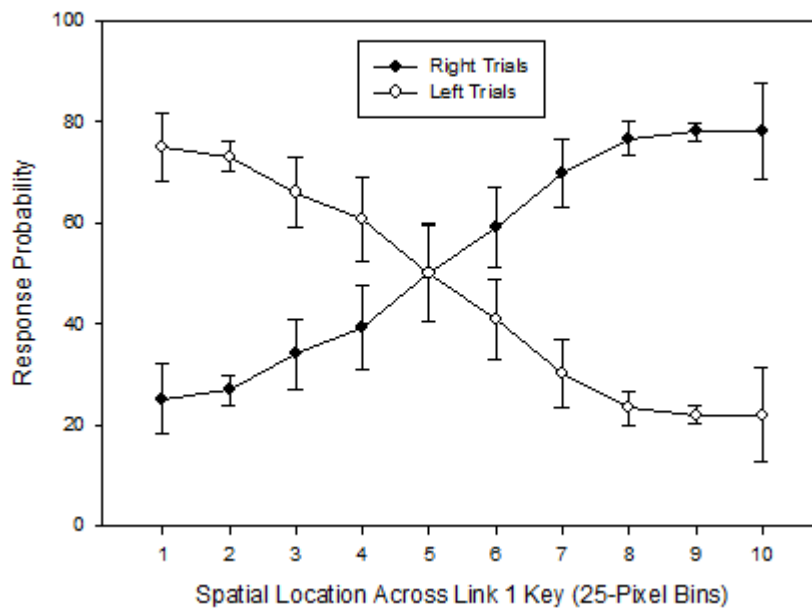


Figure 3 - Response probability across Link 1 key in Experiment 1. Average response probability of the four pigeons in Experiment 1 for each spatial location in Link 1.

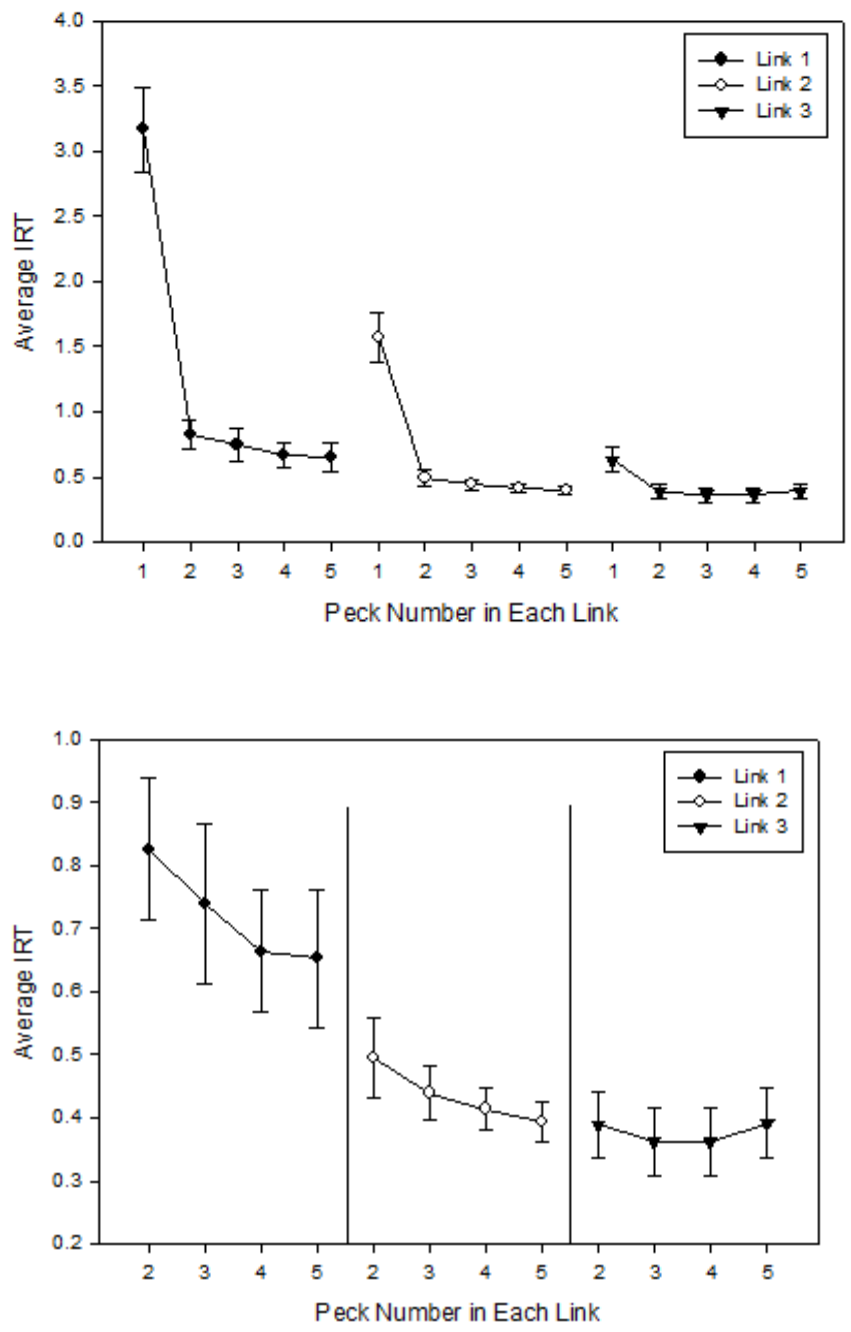


Figure 4 – IRT analysis for Experiment 1. Average IRT for each peck in each Link in Experiment 1. The top panel includes the “spikes” in IRT characteristic of the first peck in each link; the bottom panel omits these spikes to highlight the within-link IRT changes that occur in Links 1 and 2.

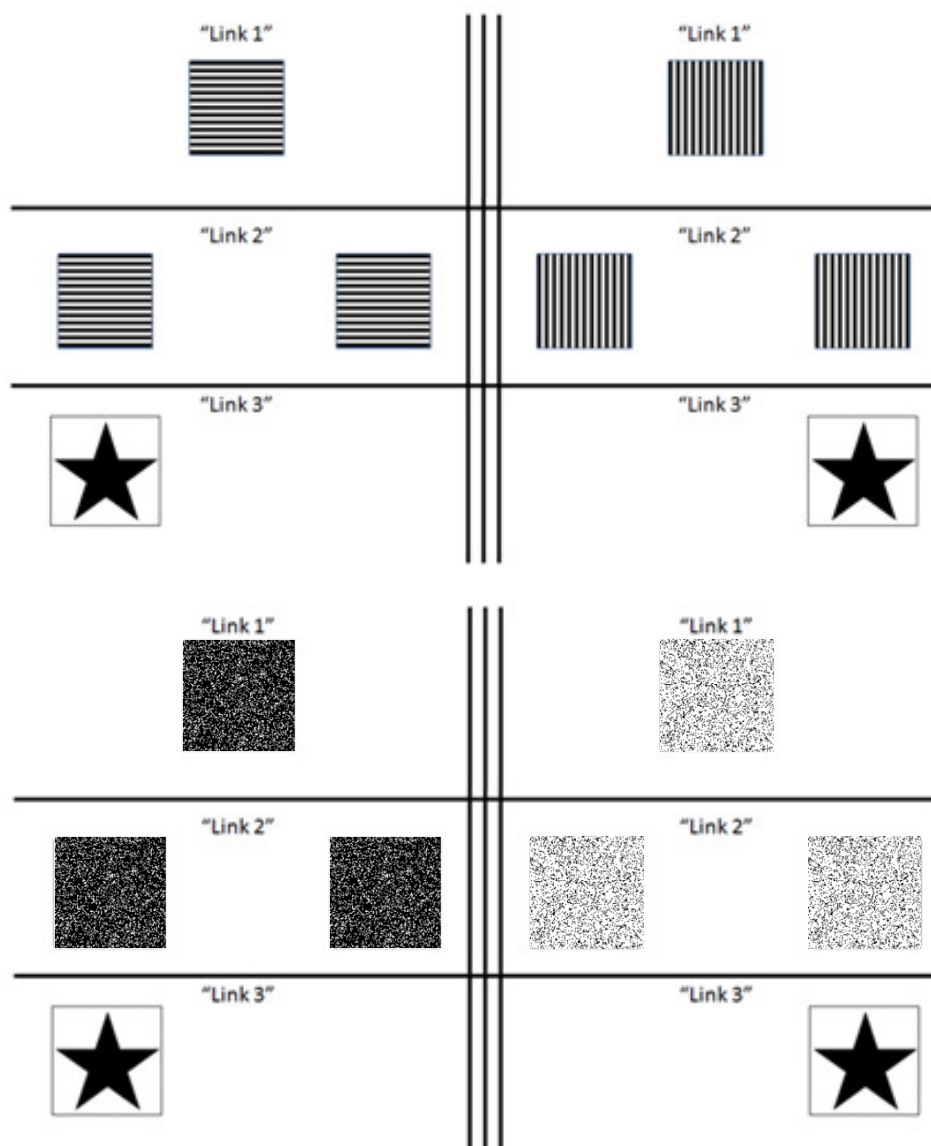


Figure 5 - Trial types in Experiment 2. The two types of trials for each group of animals in Experiment 2, shown in the left and right panels of the figure. On each trial, the rat was presented with three stimuli (represented by the vertical panels from top to bottom) followed by food.

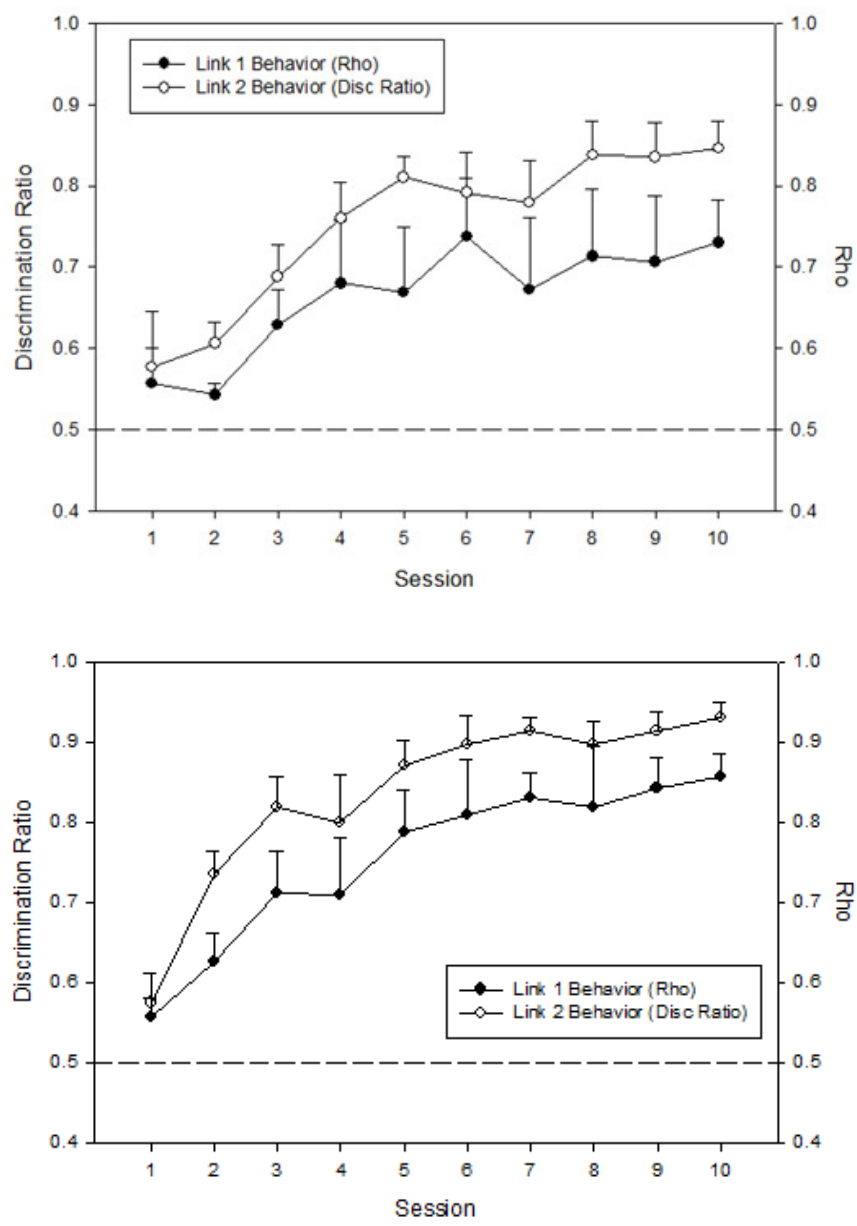


Figure 6 - Discrimination Ratio and Rho during Experiment 2. Herrnstein's Rho for Link 1 and Discrimination Ratio for Link 2 behavior in Experiment 2. Top Panel: Orientation. Bottom Panel: Brightness.

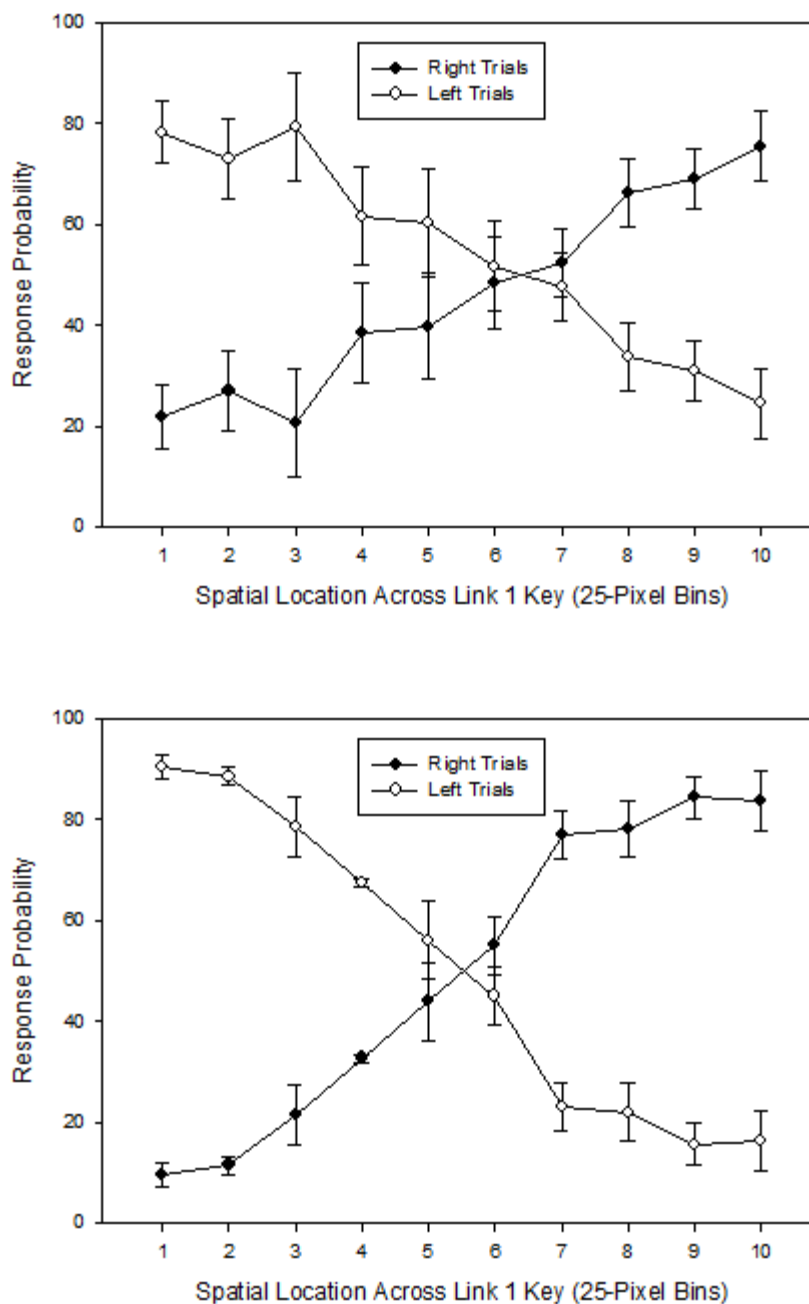


Figure 7 - Response probability across Link 1 key in Experiment 2. Average response probability of the rats in Experiment 2 for each spatial location in Link 1. *Top panel:* Orientation Group. *Bottom Panel:* Brightness Group.

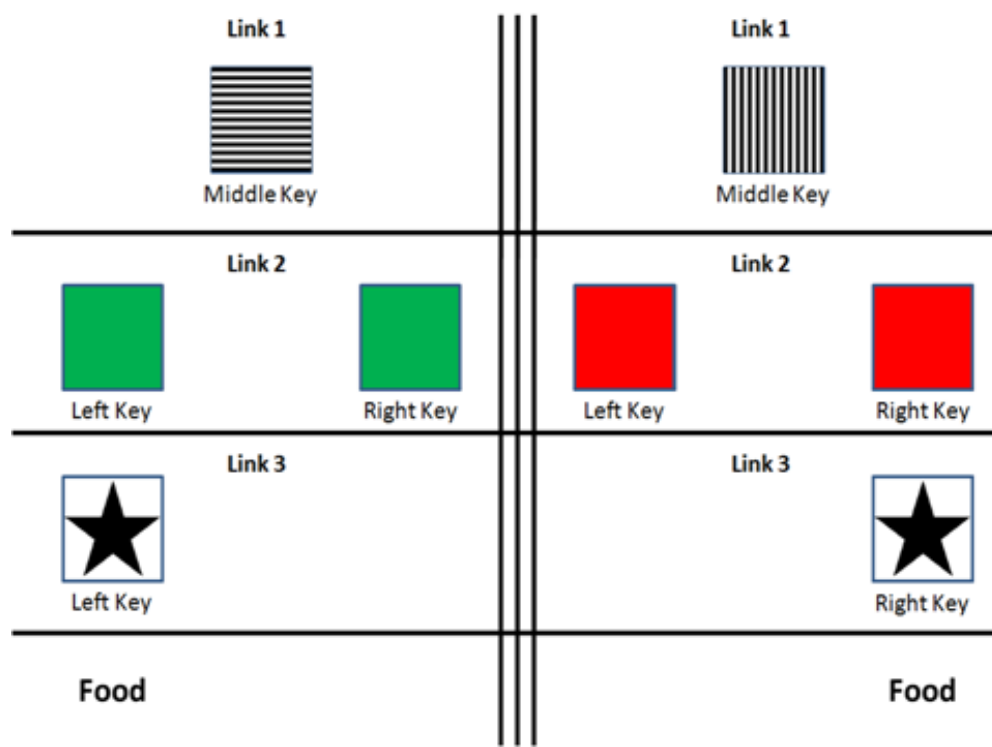


Figure 8 - Trial types in Experiment 3. The two types of trials in Experiment 3, shown in the left and right panels of the figure. On each trial, the pigeon was presented with three stimuli (represented by the vertical panels from top to bottom) followed by food.

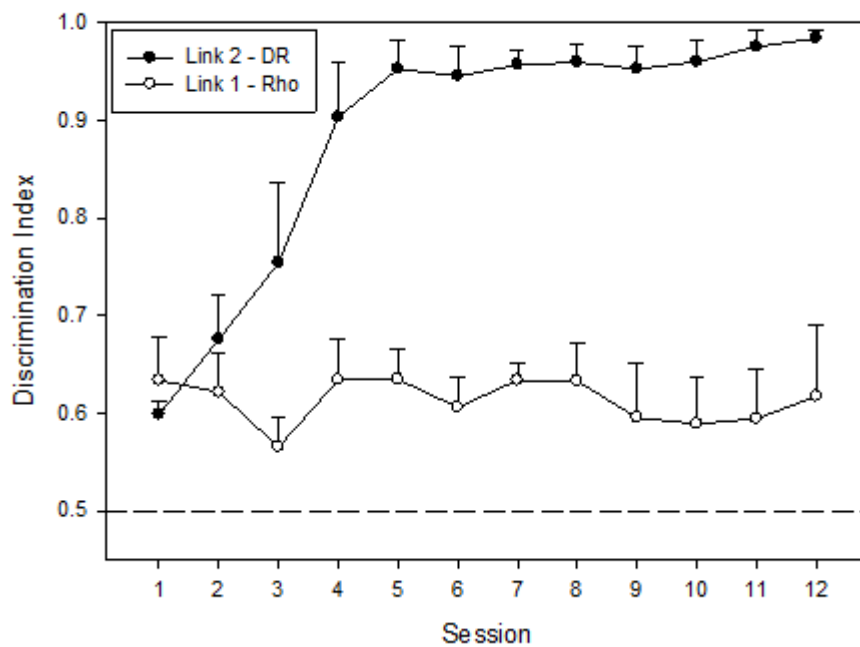


Figure 9 - Discrimination Ratio and Rho during Experiment 3. Herrnstein's Rho for Link 1 and Discrimination Ratio for Link 2 behavior in Experiment 3.

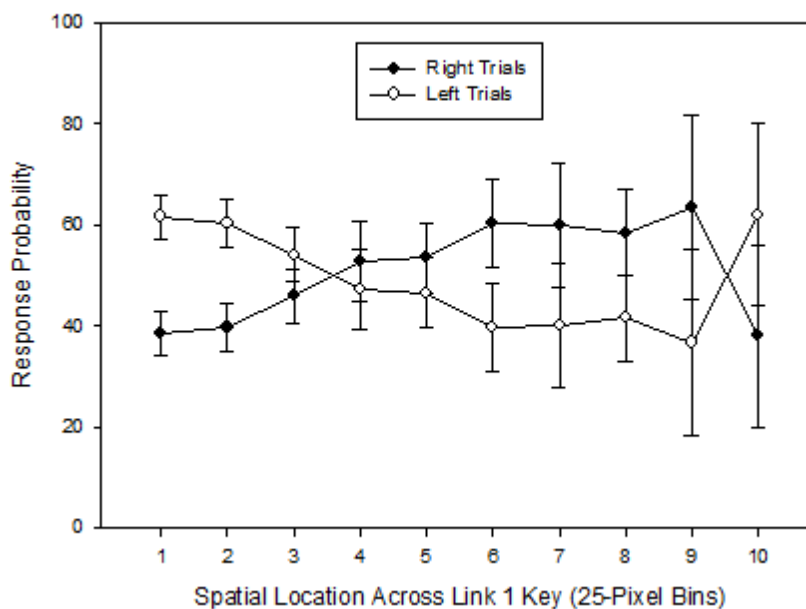


Figure 10 - Response probability across Link 1 key in Experiment 3. Average response probability of the 4 pigeons in Experiment 2 for each spatial location in Link 1.

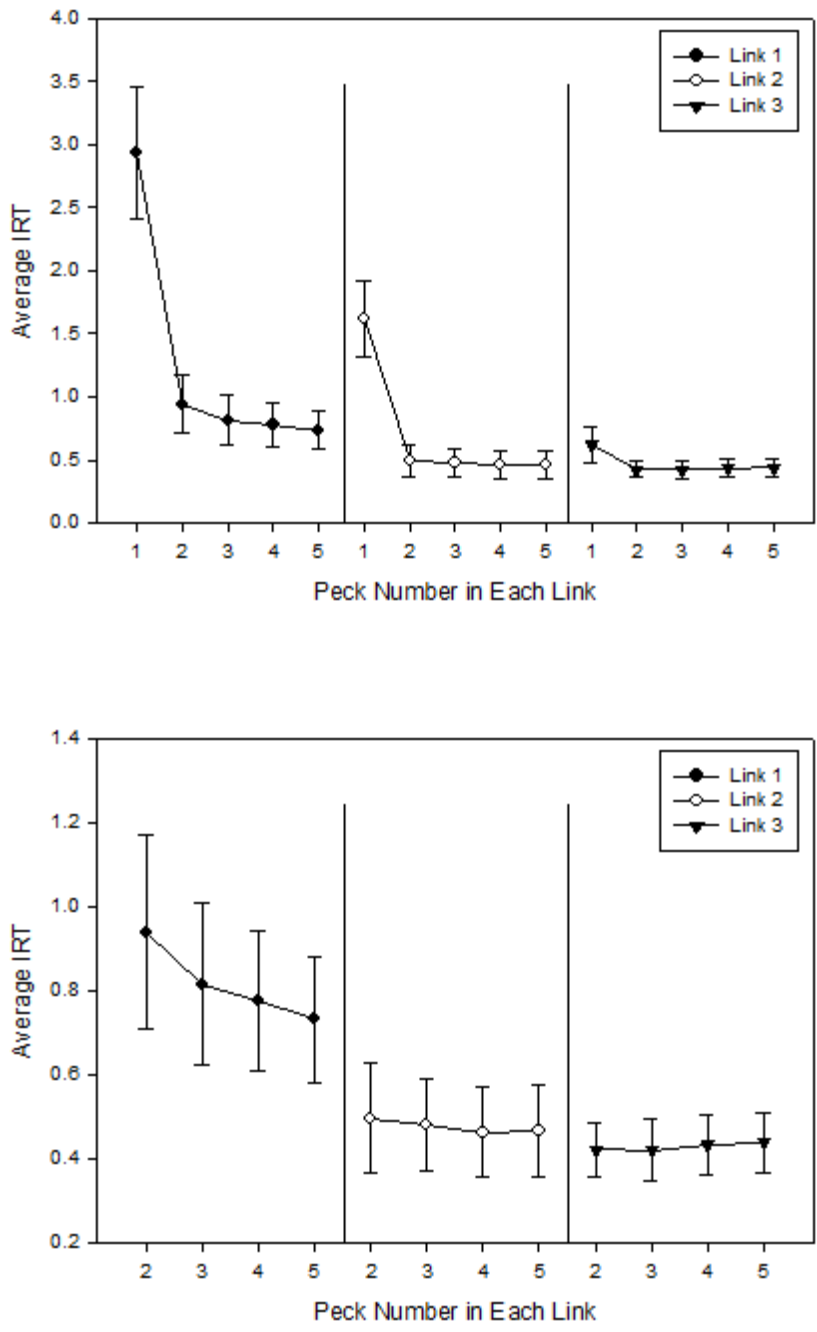


Figure 11- IRT analysis for Experiment 3. Average IRT for each peck in each Link in Experiment 3. The top panel includes the “spikes” in IRT characteristic of the first peck in each link; the bottom panel omits these spikes to highlight the within-link IRT changes that occur in Links 1 and 2.

CHAPTER 3

DELAY TO REINFORCEMENT

Chapter Introduction

One simple explanation for the congruent responses observed in Experiments 1, 2, and 3 is that they are motivated by a shorter delay to reinforcement after a congruent response than after an incongruent response. After an incongruent response, the animal has to ‘switch sides’ to continue responding to the sequence of stimuli, so that a longer delay to reinforcement occurs. However, such a long delay would not be present following congruent responses. If congruent responses yielded food faster than incongruent responses, perhaps this quicker route to reinforcement increased the likelihood of making congruent responses in the future. As such, this account focuses on the relationship between a response to specific stimuli and primary reinforcement.

An alternative account is the one suggested by the earlier autoshaping studies of Wasserman et al. (1978). This account holds that the spatial contiguity between stimuli facilitates the formation of associations between them, and that these associations promote congruent responding. This account views the third link stimulus as a conditioned reinforcer, and views the primary association that drives congruent responding as one between Link 2 and Link 3.

The main focus of this chapter will be on the merits of these two possible accounts. To start, we will begin with an overview of literature concerning associations, paying close attention to contiguity and conditioned reinforcement, as these concepts may be more foreign to the reader than traditional contingency accounts of learning (i.e., Rescorla & Wagner, 1972). We will then present three experiments that systematically address these concepts.

Contingency, Contiguity, and Conditioned Reinforcement

In learning theory, associations between events have been broadly described in terms of two basic features: contingency and contiguity (see Schwartz, Wasserman, & Robbins, 2002).

Contingency reflects the probabilistic relationships between events occurring. For example, if there is a high probability of shock following tone (and a low probability of shock at any other time), then we might say that the shock is contingent on the tone. And, we might expect that an animal exposed to a number of tone-shock pairings will learn something about the probabilistic relationship between the tone and the shock occurring (Rescorla & LoLordo, 1965; Chatlosh, Neunaber, & Wasserman, 1985; see Papini & Bitterman, 1990 for a review). Contiguity, on the other hand, reflects the temporal or spatial co-occurrence of stimuli in the environment (Williams, 1976). If the tone and shock both occur close together in time, we might say that they are contiguous; due to this contiguity, an association might be formed between these stimuli regardless of the occurrence of the shock at any other time.

Temporal Contiguity

Inserting a delay between a response and an outcome disrupts the temporal contiguity between these events. Early experiments, such as those described by Tolman (1932), involved placing a rat inside a box for a fixed amount of time (with delays ranging from 1 to 6 minutes) dependant on the rat's previous runway choice. Here, Tolman found that rats would choose paths that resulted in a quicker route to reinforcement. In a later study, Chung and Herrnstein (1967) gave pigeons a concurrent operant task in which two simultaneously available keys produced food on VI-60 schedules. Chung and Herrnstein then instituted a fixed delay to reinforcement (DTR) of 8-s after schedule completion on the left key and varied DTR on the right key from 1-s to 30-s in different trial blocks. Chung and

Herrnstein found that the proportion of responses to the fixed delay key varied as an inverse function of the delay on the alternative key. When it was less advantageous to peck the variable delay key because its DTR was greater than 8-s, pigeons directed the majority of their pecks to the fixed delay key; when it was more advantageous to peck the variable delay key because its DTR was shorter than 8-s, pigeons directed the majority of their pecks to the variable delay key. Similar results have confirmed the preference of both pigeons and rats for short delays over long delays (Ainslie, 1974; Green & Snyderman, 1980; Logan, 1965).

Thomas (1981) noted that two factors might lead to short-delay choices in these delay to reinforcement experiments: either the shorter delay to reinforcement on any individual trial or the higher rate of reinforcement over a long period of time. For example, in the previously described concurrent schedule design, pigeons that persistently chose to make the response associated with the short delay would be fed at a higher rate over the course of the experimental session than those animals that chose to make the response associated with the long delay. And, on individual trials, those pigeons would be reinforced more proximally to their keypeck on short-delay trials than on long-delay trials. Such is the distinction between molar and molecular analyses of behavior. Molar analyses (e.g., Baum, 1973; Baum 2002) are concerned with variables on a session-wide or long-term timescale and include such constructs as reinforcement rate; molecular analyses (e.g., Thomas, 1981, Dinsmoor, 1977) focus on event-by-event variables such as associative strength which is continuously updated.

To equate for molar variables such as reinforcement rate while varying the molecular variable of temporal contiguity, Thomas (1981) designed an experiment in which a pellet was scheduled to be delivered to a rat every 20-s regardless of the rat's behavior. During each trial, the rat could press a lever to move the delivery of this pellet closer in time, but doing so would not yield *extra*

pellets that the rat would not otherwise have received. In fact, over the course of the experimental session, a rat that bar-pressed on every trial in Thomas' design would have achieved the net effect of moving a single reinforcer forward in time and then receiving constant reinforcement on the same time schedule that it would have otherwise received. Therefore, in Thomas' experiment, the behavior of the rat can influence the molecular relationship between response and reinforcer on any individual trial without influencing the molar variable of reinforcement rate. Despite this clever control, rats quickly learned to bar-press for contiguous food delivery. In an additional experiment, Thomas (1983) showed that rats will bar-press for food *now* even at the cost of an overall reduction in the rate of reinforcement.

The preceding experiments used appetitive schedules in which responses were reinforced; a similar question about the effect of delay on punishment can also be asked: would an increase in delay-to-shock be favored over contiguous shock? An experiment similar to Thomas (1981) had been conducted by Hineline (1970). In that procedure, shock could be delayed (but not averted) by lever pressing, but the rate of shock remained constant regardless of the rat's behavior. In that task, trials were broken into 20-s cycles; at the start of each cycle, a lever was inserted into the chamber and a shock was scheduled to occur in the 8th second of the cycle. If the rat did not press the lever during these first 8 seconds, the rat was shocked and the lever was withdrawn until 20 total seconds had elapsed, upon which the cycle would restart. If the rat did press the lever during these first 8 seconds, the lever was withdrawn and the shock was rescheduled for the 18th second. Thus, lever presses delayed shocks by 10-s, but the total number of shocks during each session was equivalent and thus lever pressing did not affect the frequency or rate of shock. Despite the lack of such a contingency,

responding to the lever quickly developed and was sustained over a number of experimental sessions.

As demonstrated by Wasserman and Neunaber (1986), humans are also sensitive to such temporal factors. In Wasserman and Neunaber, a schedule similar to that arranged by Thomas (1981) and Himeline (1970) was arranged for college undergraduates. Participants were instructed that they could earn points by activating a white light that could be lit using a telegraph key. Similar to Thomas (1981) and Himeline (1970), the light would be lit regardless of the participants' actions at the end of a preprogrammed time window, thus equating for the rate of total light activations. Participants were given one of three schedules. On the Contiguity (C) schedule, participants could advance the scheduled light activation forward in time by pressing the telegraph key, immediately earning the points scheduled for that time window upon executing the key-press. On the Contiguity-(C-) schedule, participants could advance forward in time the scheduled light activation just as in the (C) schedule, but key-presses in the current interval canceled light presentation in the next interval. And, on the Response Independent (I) schedule, key pressing had no effect on light presentation. Wasserman and Neunaber found high rates of responding and causality ratings for the C schedules, lower but still above-chance responding and lower causality ratings for the C- schedules, and very low rates of responding and low causality ratings for I schedules. Essentially, humans were controlled by the same temporal contiguity as the rats in Thomas (1981) or Himeline (1970).

Spatial Contiguity

Beyond temporal contiguity, a second possible concurrence between stimuli is spatial contiguity, or the collocation of two stimuli in space. For a trivial example, a light switch that activates a nearby lamp might be said to be more spatially contiguous than one that activates a distant lamp. In operant settings,

spatial contiguity is often correlated with temporal contiguity. For example, if the grain hopper is located close to the response panel, we might say that the two are spatially contiguous, but the production of the response and the receipt of the reinforcer might also be temporally contiguous due to the shorter delay between the response and reinforcement compared to a situation in which the grain hopper is located farther from the response panel and the animal must travel some distance to retrieve it.

But, spatial contiguity can be manipulated independently of temporal contiguity. As an example, this manipulation has been achieved in autoshaping. In the autoshaping study from which the current procedure was devised (Wasserman et al., 1978), all trials ended with food reinforcement after a fixed time interval regardless of the pigeon's response. Therefore, there could be no temporal contiguity between responses to one or the other key and the delivery of food, because responses were unrelated to food delivery (in fact, such responses might be slightly negatively correlated if the bird was spending time at the response panel instead of near the food hopper). So, the only possible feature of that task that might have facilitated responding to one or the other of the CS2 keys was the spatial contiguity between CS2 and CS1.

Rescorla and Cunningham (1979) also investigated the role of spatial contiguity between stimuli using an autoshaping design. In that experiment, which was similar to Wasserman et al. (1978), the response rate of two groups of pigeons was measured to two keylight stimuli that preceded food delivery, CS1 (more proximal to food) and CS2 (more distal from food). Pigeons were first autoshaped to peck CS1 when it appeared on the left key on some trials and on the right key on other trials. Pigeons were then given CS2-CS1 pairings in the absence of food. For those pigeons in Group Same, CS2 stimuli appeared on the same key as CS1 stimuli; for those pigeons in Group Different, CS2 stimuli

appeared on the key opposite to CS1. Although both groups eventually responded to CS2, the pigeons in Group Same learned faster and responded at higher rates than the pigeons in Group Different. A second experiment replicated this effect using conditioned suppression; mean suppression ratios were much lower for pigeons in Group Same than in Group Different. Again, there could be no possible temporal contiguity between CS2 and primary reinforcement that could motivate behavior. In fact, because CS2 and CS1 were paired only on trials without food delivery, the only possible feature that would promote greater responding in Group Same than in Group Different was the spatial contiguity of the two lights. This same spatial contiguity effect in second-order autoshaping was also reported by Marshall, Gokey, Green, and Rashotte (1979).

In a recent study, Cabrera, Sanabria, Shelley, and Killeen (2009) demonstrated that pigeons pecked more vigorously at stimuli closer to a food source (the food hopper) than farther from it. In that same study, pigeons also tracked stimuli that were moving in the direction of or away from the same food hopper; more pecks were recorded when the stimulus was moving toward the food hopper than away from the food hopper despite what might otherwise be a weaker cue for reinforcement. This result may further demonstrate the important role of spatial contiguity in conditioning.

Beyond pigeons, other animals are also sensitive to spatial contiguity. In rats, much of the study of spatial contiguity has dealt with the associability of various arbitrary stimuli with gustatory stimuli. Testa (1975) conducted a set of studies using location and temporal intensity patterns that reemphasized the role of space in determining stimulus similarity, which he felt had been a neglected source of similarity. Later, Testa and Ternes (1977) proposed that discriminative cues that occurred closer in time and space to food that preceded the onset of an illness would be more readily associable with this illness. Supporting this

hypothesis, Galef and Dalrymple (1981) demonstrated that the spatial proximity of discriminative visual cues to sickness causing food influences the formation of a learned aversion to these visual cues. In that experiment, the visual cue was either the color of a food capsule, the color of the food bin from which the rats received food capsules, or the color of the conditioning chamber in which the rats received food. The visual cues more proximal to the food itself (i.e., the food capsule condition) were more readily associable with sickness.

Relatedly, Ellins, Cramer, and Whitmore (1985) reported that rats could learn to associate arbitrary auditory events with sickness caused by a new food, but only if these arbitrary events were contiguously paired with that novel taste. In that experiment, rats were tested with the auditory signal emanating from a speaker far from, near to, or inside of the novel food stimulus. Ellins et al. (1985) found that rats would only demonstrate conditioning to the auditory stimuli when these sounds emanated from the food-well. This result may suggest the heightened importance for spatial contiguity when the stimuli differ in modality.

A similar spatial contiguity effect in auditory conditioning is noted by Wright (2007); there, monkeys would not respond appropriately in a serial memory task unless the monkey's response location and the source of stimulus presentation were spatially contiguous. This fact is similar to those results reported by Harrison, Iverson, and Pratt (1977), which showed that monkeys learned a simple auditory discrimination much faster when the sound and response emanated from the same key than when they were spatially displaced.

Conditioned Reinforcement

In experiments such as those designed by Thomas (1981), contiguity is assumed to be a temporal or spatial relationship between a response (or stimulus) and *primary* reinforcement (i.e., food). But, there is also a second possibility for spatial or temporal contiguity: the contiguity between a response and *conditioned*

reinforcement. Conditioned reinforcers (or second-order reinforcers) are stimuli that have acquired reinforcing properties after being paired with primary reinforcers (see Schwartz, Wasserman, & Robbins, 2002). For example, a chimpanzee might produce responses in a behavioral task for tokens that can later be exchanged for bananas. Or, humans might produce responses in a behavioral task for money, which has no intrinsically reinforcing property itself.

In an early demonstration of conditioned reinforcement, Schuster (1969) arranged a concurrent-chains procedure in which responding to one of two keys during the initial link was reinforced on a VI 1-min schedule. One of these alternatives led to a new schedule that resulted in both primary and conditioned reinforcers, the other alternative led to a new schedule that resulted in only primary reinforcement. After choosing the alternative that resulted in conditioned reinforcement, responding was reinforced on a VI-30s schedule concurrent with the brief presentation of a light stimulus that also occurred during food delivery on an FR11 schedule; therefore, the animals received periodic conditioned reinforcers (light stimulation) while completing the second VI-30s schedule. After choosing the alternative that did not result in conditioned reinforcement, the animals received only food on a VI-30s schedule. All of the animals in this study showed a distinct preference to choose the second schedule that resulted in the presentation of the extra light stimuli despite equivalent primary reinforcement from responding on the two schedules.

Conditioned reinforcement is most useful for explaining responses to a chain of stimuli and has been the prevailing view since at least Keller and Shoenfeld (1950). In a chain of stimuli, each stimulus in the chain acquires conditioned reinforcing properties (Williams, 1994). For example, the terminal link in a chain acquires conditioned reinforcement from its contiguous presentation with primary reinforcement and function as a discriminative cue for

the delivery of primary reinforcement. Middle links in the chain also acquire conditioned reinforcement; this conditioned reinforcement then drives responding to the initial link. At first glance, this theoretical addition is useful (or, perhaps, even necessary) to account for human behavior because so few stimuli result in what we might think of as primary reinforcement. For example, money might be linked to the ability to engage in pleasurable activities or eat tasty food, chaired professorships might be linked to money, and supervising successful Ph.D. theses might be linked to chaired professorships, thus offering some external explanation for a time-consuming, patience-draining, and otherwise profitless activity. Thus, the capacity of stimuli to function as conditioned reinforcers greatly increases the scope and reach of associationist theories to explain behavior.

An alternative account has been offered by Staddon and Cerutti (2003). In that account, each stimulus in the chain might drive responding through its own link to primary reinforcement. So, in this account, the animal's response to each stimulus is a function of temporal delay to reinforcement. There is good evidence that this too might explain behavior in chain schedules; for example, as mentioned in Chapter 1, response rates and time to initiate responses to the first links of chains tend to be much lower than responses to subsequent links. This result might be taken as evidence that differences in response rates between these links are the result of the temporal disparity between each link and primary reinforcement. Relatedly, chains in which a fixed order of six stimuli are presented show this falling-off effect during initial links, but pigeons respond to chains in which the six stimuli are presented in a mixed order (scrambled-stimuli chains) with high response rates throughout the chain, presumably because each stimulus is presented contiguous to food reinforcement on some proportion of the trials (Staddon & Cerutti, 2003).

One study designed to address these alternatives was conducted by Royalty, Williams, and Fantino (1987). In that study, 3-s delays were inserted after the initial, middle, or terminal link of a three-link chain schedule and the magnitude of the response rate decrement was measured for each link following the delay insertion. When delays were inserted after the terminal link, there was a small effect on terminal link responding but there was no effect on middle or initial link responding; when delays were inserted after the middle link, there was a large effect on middle link responding but no effect on terminal or initial link responding; when delays were inserted after the initial link, there were large effects on initial link responding but no effect on middle or terminal link responding. Not only was the relative magnitude of the effect on responding actually smallest when the delay was inserted after the terminal link, but it had no carryover effect on middle-responding. Similar to the present study, the nominal delay to reinforcement in each experimental condition was equivalent; the only change was where the delay was inserted.

Present Experiments

In the present set of studies, we sought to investigate if the congruent responses were caused by the contiguity between the Link 2 response and food (as advanced by the DTR hypothesis) or between the contiguity of Link 2 and Link 3 (as in Wasserman et al., 1978, and Rescorla et al., 1979). We settled on two ways to test this general idea. The first was to manipulate the amount of work that the pigeons would be required to perform once they reached Link 3, effectively delaying reinforcement for making certain choices. The other was to insert nominally equivalent delays at different points in the sequence and measure Link 2 responding, similar to Royalty et al. (1987). If the temporal delay to primary reinforcement hypothesis is correct, then inserting the same delay at different points in the schedule should have the same effect on behavior. But, if the prime

mechanism for congruent Link 2 responding was the contiguity between Link 2 and Link 3, then inserting the same delay at different points in the schedule might have very different effects on behavior. In the latter case, a delay inserted between Link 2 and Link 3 might cause large shifts in congruent responding, whereas a delay inserted between Link 3 and primary reinforcement might have very little effect on congruent responding.

So, in these upcoming experiments, we explored the relationship between making a spatially contiguous response (i.e., making a response in Link 2 in the same location as in Link 3) vs. making a response that reduces overall delay to reinforcement. In each of these tasks, we used a generally similar design. Three pairs of stimuli were used: one Advantage, one Disadvantage, and one Control. Each experiment called for some relatively positive outcome to occur for making congruent Link 2 responses during Advantage trials, such as a shorter delay to reinforcement, and some negative outcome to occur for making incongruent Link 2 responses on these same trials, such as a longer delay to reinforcement. For the Disadvantage pair of stimuli, these contingencies were reversed; congruent Link 2 responses produced negative outcomes and incongruent Link 2 responses produced positive outcomes. In the Control pair of stimuli, the outcomes were always random regardless of the bird's Link 2 response, but each outcome was programmed to occur equally often throughout the course of each session.

In Experiment 4, we manipulated the amount of work that the pigeons would be required to perform during Link 3 after either a congruent or incongruent Link 2 response in each of these three pairs of stimuli. To briefly foreshadow the results, we found that relatively high FR differences were required in order to cause the birds to shift their response location away from the congruent response in Link 2 toward the incongruent spatial response that will lead to less work.

In Experiments 5 and 6, we explicitly manipulated the delay to reinforcement by inserting a delay during the procedure on some types of trials. In Experiment 5, we inserted a delay between Link 2 and 3 and found that when the contiguity between the Link 2 and Link 3 stimuli was disrupted, the insertion of this delay exerted strong control over the pigeon's choice response. But, in Experiment 6, we inserted a delay between the completion of the Link 3 FR and the actual receipt of food; in that case, we found that the same nominal delay to reinforcement had a very weak effect on the pigeon's behavior.

Experiment 4

In Experiment 4, we added a differential response component to the task to measure the effect of doing so on anticipatory spatial behavior. To add this differential component, we changed the amount of work that was required of the pigeon to receive reinforcement when it reached Link 3. The amount of work was manipulated by varying the FR schedule that the animal had to complete to the Link 3 stimulus in order to receive food pellets.

Three pairs of stimuli were used; each pair had one stimulus which signaled that the Link 3 location would be on the left and one stimulus which signaled that the Link 3 location would be on the right. The first pair of stimuli, the Control pair, randomly entailed high or low work requirements during Link 3 regardless of which stimulus the animal chose in Link 2 or how it directed its behavior in Link 1. The second pair of stimuli, the Advantage pair, had work requirements in which congruently directing pecks (in Link 2) toward the location of the Link 3 stimulus was *rewarded* with a low work requirement in Link 3, but incongruently directing pecks away from the location of the Link 3 stimulus was punished with a high work requirement in Link 3. The final pair, the Disadvantage pair, had work requirements in which congruently directing pecks toward the location of the Link 3 stimulus was *punished* with a high work

requirement in Link 3, but incongruently directing pecks away from the location of the Link 3 stimulus was rewarded with a low work requirement in Link 3.

We initially trained the pigeons with values of 5 and 10 pecks for the low and high work requirements, respectively. As these values did not ultimately produce a strong shift in responding, we held the low work requirement constant at 5 pecks and progressively increased the high work requirement by 5 pecks every 5 sessions. By conducting the experiment in this stepwise fashion, we could measure any shift in responding as we increased the work required of the pigeons in Link 3; in other words, we could pit differential work in Link 3 against the spatial contiguity of an anticipatory response in Link 2.

Method

Participants. The participants were 4 feral pigeons. Deprivation and housing conditions were the same as in Experiment 1 and 3.

Apparatus. The apparatus was the same as in Experiment 1 and 3.

Stimuli. Seven 7.44- x 7.44-cm visual textures were used as stimuli. Each of these stimuli occupied 250 square pixels of space on the monitor. These stimuli were colored textured surfaces with no large figures that might themselves direct pecking. The textures were “black and white camouflage,” a “field of flowers,” a “graffiti covered wall,” “abstract ink art,” a “chain link fence,” “linoleum tiles,” and “swimming pool surface.” These seven stimuli can be seen in Figure 12.

Procedure.

Shaping and Pretraining. Shaping and pretraining were as in Experiment 1 and 3.

Training. The basic experimental procedure was as in Experiment 1. The texture presented on the center key in Link 1 was presented on the side keys in Link 2. The Link 3 stimulus was always the “swimming pool surface” texture. Each of the six remaining stimuli was used in one of three pairs: Advantage,

Disadvantage, or Control. Each stimulus signaled the location (left or right) of the upcoming Link 3 stimulus. Figure 13 contains a visual representation of the design.

On Advantage trials, responses during Link 2 to the congruent side resulted in a low Link 3 FR, whereas responses during Link 2 to the incongruent side resulted in a high Link 3 FR. Initially, these values were set at 5 pecks for the low Link 3 FR and 10 pecks for the high Link 3 FR.

On Disadvantage trials, responses during Link 2 to the congruent side resulted in a high Link 3 FR, whereas responses during Link 2 to the incongruent side resulted in a low Link 3 FR. Initially, these values were set at 5 pecks for the low Link 3 FR and 10 pecks for the high Link 3 FR.

On Control trials, responses during Link 2 to the congruent side resulted in an unpredictable high or low Link 3 FR. Responses to the incongruent side also led to an unpredictable high or low Link 3 FR. Initially, these values were set at 5 pecks for the low Link 3 FR and 10 pecks for the high Link 3 FR.

FR Increase Phase. The value of the high Link 3 FR was systematically increased by 5 pecks every 5 days, whereas the low Link 3 FR remained at 5. One bird was removed during this phase because its weight fluctuated erratically and it had difficulty finishing sessions during the FR Increase Phase.

Results and Discussion

Training. The first and most striking result of this three-pair arrangement was the fact that the birds robustly pecked toward the location of the upcoming Link 3 stimulus, regardless of trial type, given the initial values of 5 and 10 pecks (see Figure 14). Whereas this behavior was ultimately advantageous for the Advantage stimuli because it led to fewer responses in Link 3, and it was neutral for the Control stimuli, this location tracking behavior was maladaptive in the case of the Disadvantage stimuli because it led to more responses in Link 3. That

the birds persisted in spatially anticipating the location of the Link 3 stimulus even during the initial Disadvantage trials suggests that the birds were more strongly controlled by the location of the Link 3 stimulus than by the amount of work that the birds would be required to perform during the Link 3 stimulus.

As in Experiment 1, the pecking distributions for Link 1 and Link 2 were analyzed. As can be seen in the top panel of Figure 14, despite the fact that they were more strongly controlled by the Link 3 location than by the Link 3 work requirement, the birds appeared to show some sensitivity to the work requirement during baseline training. Numerically, the Advantage stimuli appeared to reach asymptote at a higher level than did the Control stimuli, which in turn appeared to reach asymptote at a higher level than did the Disadvantage stimuli.

To analyze these apparent trends, we conducted an ANOVA on Link 2 Discrimination Ratio scores (Stimulus Type x Session x Bird as a random factor). But, this analysis revealed only a significant main effect of Session, $F(9,27) = 27.08, p < .001$, with no main effect of Stimulus Type or interaction between Session and Stimulus Type. This result suggests that although the birds increased their congruent Link 2 reports across days, there was little difference among the different stimulus conditions, suggestive of a systematic lack of effect of the differential response requirements.

We also conducted an analysis on Link 1 data. Here, we used a repeated measures ANOVA (Space x Trial Type x Link 3 Location x Bird as a random factor) rather than Rho. This was done because the birds might have directed their pecks in different spatial locations on Advantage and Disadvantage trials, and Rho is only sensitive to the disparity between these distributions. The data from this analysis are shown in the bottom panel of Figure 14. One bird (28B) was excluded from this analysis because visual observation showed a “scythe-like” pecking motion that produced inaccurate touchscreen recordings as the bird

dragged its beak across the screen. This analysis revealed a marginally significant interaction between Link 3 Location and Space, $F(9,18) = 2.18$, $p = .07$, indicative of the congruent Link 1 anticipatory response dependent on Link 3 response location. No other main effects of interactions approached significance.

Increasing FR. The proportion of congruent choices that were made during Link 2 in this phase is plotted in Figure 15. The first pattern that was evident in these data was that as the work increased for making congruent choices to the Disadvantage pair, the birds gradually began to shift their pecking behavior away from the congruent response. After each 5 peck increment in FR, responding to the congruent side fell for the Disadvantage pair.

Another pattern that was evident in these data was the lack of difference between the Control and Advantage trials. If the pigeons were only controlled by variables such as the delay to reinforcement, then we might expect that Control stimuli should not exert control by location, because the delay to reinforcement or the work that was required to obtain reinforcement was randomly high or low. Relatedly, due to the strong differential contingency, we might expect that the Advantage contingency should promote even stronger anticipation than the Control trials. However, the pigeons showed no change in their behavior on either Advantage or Control trials as a function of the FR Increases.

An ANOVA was conducted on these Link 2 data to analyze these effects. This ANOVA (FR x Stimulus Type x Bird as a random factor) revealed highly significant effects of FR, $F(4,12) = 17.25$, $p < .001$, and Stimulus Type, $F(2,6) = 29.41$, $p < .001$. There was also a highly significant interaction between these variables, $F(8,24) = 24.70$, $p < .001$. This interaction indicated that accuracy in at least one of the pairs of stimuli changed significantly as a function of the FR. To isolate which of the conditions changed, separate ANOVAs were conducted for each Stimulus Type; whereas the Advantage and Control types each had $F_s < 1$,

indicating no effect of the FR, an ANOVA on the Disadvantage trial type revealed significant effects of the FR, $F(4,24) = 63.89, p < .0001$. Thus, the changes in Link 2 responding that occurred during the FR Increase phase were solely attributable to changes in behavior during the Disadvantage trials.

Although the average scores nicely described the overall pattern of results and each of the birds followed this trend, each of the birds nevertheless showed an idiosyncratic tradeoff between spatial anticipation and the amount of Link 3 work to which they were sensitive. These data are plotted in Figure 16. For example, even from the outset, Bird 28B showed little control by spatial contiguity in the Disadvantage condition, even with only the small work requirement disparity of 5 pecks; this bird most quickly switched from anticipating the Link 3 location to pecking in the location that would result in a lower work requirement in Link 3. Bird 28B responded at near 50% to the spatially congruent side after only one 5 peck FR increase and clearly responded below chance after later FR increases (to 5 pecks vs. 20 pecks).

Conversely, the other two birds did not show pecking distributions in Link 2 which indicated much control by the differential work requirements until they reached 15 or 20 pecks; indeed, these birds only behaved in accordance with a strong preference for the smaller work requirement when the required pecks were 5 vs. 30.

One possibly interesting side-note here is the lack of preference for the pigeons for the FR-30 stimulus over the FR-5 stimulus; this somewhat odd preference might have been counter intuitively expected based on the results of Friedrich and Zentall (2004), which found that in some conditions, pigeons actually prefer stimuli that cause them additional work (like a “cognitive dissonance effect” in pigeons). But, this result was not found in the present study.

Instead, as the FR progressively increased for making congruent responses on Disadvantage trials, congruent responses decreased.

Experiment 5

Similar to Experiment 4, this experiment was an attempt to understand what kinds of conditions contribute to the anticipatory spatial responses in Link 1 and Link 2. As previously reviewed, one consequence of making a response directed toward the congruent location is that it may hasten the delivery of reinforcement by eliminating a costly switch to the other side of the box. For example, despite the fact that the pigeons had no explicit differential contingency for the receipt of reward in Experiment 1, birds which responded on the congruent side of the screen during Link 2 might be able to respond to the Link 3 stimulus more quickly, thereby more quickly receiving food.

However, recalling the omission procedure from autoshaping in which food is withheld on trials following a keypeck, pigeons will often engage in potentially maladaptive behaviors under certain experimental conditions which would be peculiar and unlikely in their natural environment. If we were to break the linkage between the cost of making a switch and correctly anticipating the Link 3 location by inserting a delay, then might pigeons maladaptively anticipate and delay reinforcement? Or, would pigeons adaptively shift their behavior away from the upcoming Link 3 location in order to hasten the delivery of reinforcement? In Experiment 4, despite the ability of pigeons to readily discriminate between differential work requirements, a rather large work requirement was required before all of the pigeons shifted from the maladaptive anticipation response for the Disadvantage stimuli to the adaptive anticipation response; this shift meant responding away from the upcoming location of the Link 3, but it also required fewer Link 3 responses.

Before starting Experiment 5, however, we needed to answer an important question: how costly is the switch to go from one side of the box to the other? Without including a purely random condition, it is difficult to know. Measuring the actual time to receive reinforcement on congruent and incongruent choices is difficult, because pigeons routinely achieve very high accuracies in this task after only 2 to 3 sessions; so, these incongruent trials become less and less frequent. Also, RT generally fell over the course of the experiments (as pigeons learned to peck the sequence of three keys); so, choosing values from the first sessions is likely to overestimate the actual delay encountered by the birds on an incongruent trial after even 2 or 3 sessions of training. Nevertheless, because these first sessions were the only ones in which there was a substantial likelihood that the birds would make incongruent responses in Link 2, the data from these first sessions were used to find baseline delay values.

In the first 2 sessions of Experiment 1, pigeons received reinforcement in an average of 0.5 s when they made the correct choice in Link 2 and after an average of 3.5 s when they made the incorrect choice in Link 2. Additional corroborating evidence about the relative temporal cost of a single shift can be inferred from the IRT data presented in Experiment 1, where 1.5-s was the average cost of a shift in one spatial location (between Link 1 and Link 2); here, we are interested in estimating the cost of two spatial locations, which works out to around 3 s. Taken together, we can assume a relatively short, 3-s disparity between one choice and the other; but, to a hungry pigeon, this 3-s disparity may be vitally important. In fact, Williams (1976) found that a 3-s delay was enough to substantially lower response rates in a free-operant procedure to near that of yoked control animals. So, whereas 3-s of delay might sound small, it seemed to be enough to support changes in behavior.

To see whether this 3-s disparity might indeed control pigeons' behavior, we designed Experiment 5 to be similar to Experiment 4. Three pairs of stimuli were again used: one set of Control, one set of Advantage, and one set of Disadvantage stimuli. The Control pair had random 0.5-s or 3.5-s delays inserted between the final peck to the Link 2 stimulus and the onset of the Link 3 stimulus. The Advantage pair had a 0.5-s delay when the animal made the congruent response in Link 2, but a 3.5-s delay when the animal made the incongruent response in Link 2. And, the Disadvantage pair had a 3.5-s delay when the animal made the congruent response in Link 2, but a 0.5-s delay when the animal made the incongruent response.

Method

Participants. The participants were 4 feral pigeons. Deprivation and housing conditions were the same as in Experiments 1, 3, and 4.

Apparatus. The apparatus was the same as in Experiments 1, 3, and 4.

Stimuli. The same seven textures used in Experiment 4 were also used in this experiment. These textures can be found in Figure 12.

Procedure.

Shaping and Pretraining. Shaping and pretraining were the same as in Experiments 1 and 3.

Training. The basic experimental procedure was as in Experiment 4. Six stimuli were divided into three pairs: Advantage, Disadvantage, and Control. Each pair had one stimulus which signaled that the Link 3 location would be on the left and one stimulus which signaled that the Link 3 location would be on the right. Figure 17 contains a visual representation of the experimental design.

During Advantage trials, responses during Link 2 to the congruent side resulted in a short delay before the onset of Link 3, whereas responses during Link 2 to the incongruent side resulted in a long delay before the onset of Link 3.

These values were set at 0.5-s for the short Link 3 delay and 3.5-s for the long Link 3 delay.

During Disadvantage trials, responses during Link 2 to the congruent side resulted in a long delay before the onset of Link 3, whereas responses during Link 2 to the incongruent side resulted in a short delay before the onset of Link 3.

These values were set at 0.5-s for the short Link 3 delay and 3.5-s for the long Link 3 delay.

During Control trials, responses during Link 2 to the congruent side resulted in an unpredictable short or long delay before the onset of Link 3. Responses to the incongruent side also led to an unpredictable short or long Link 3 delay. These values were set at 0.5-s for the short Link 3 delay and 3.5-s for the long Link 3 delay.

Results and Discussion

Data from Link 2 responses can be found in Figure 18 (top panel). An ANOVA (Stimulus Type X Session X Bird as a random factor) conducted on these data revealed a significant effect of Session, $F(14,42) = 3.62, p < .001$, a significant effect of Stimulus Type, $F(2,6) = 96.32, p < .0001$, and a significant interaction between these variables, $F(28,84) = 6.97, p < .0001$. Therefore, increasing the delay to the Link 3 proved to be an important factor for encouraging the birds to switch sides and to respond to the key that would hasten the presentation of the Link 3 stimulus, even if that meant responding on the opposite side of the box.

As well as promoting obvious differences in behavior during Disadvantage trials, a planned contrast revealed a significant difference between the Control and Advantage conditions across days, $F(1,84) = 57.42, p < .001$. This result stands in contrast to the lack of a disparity between these conditions in

Experiment 2, in which no difference between the Control and Advantage trials was apparent during the FR Increase phase.

Separate analyses were also carried out on the Link 1 data. However, as in Experiment 4, rather than using Rho to analyze these response distributions, we found it more useful to analyze the physical location of the pecks to the Link 1 stimulus, because these could be targeted either in the direction of the Link 3 stimulus or in the direction of the Link 2 report (which might differ during Disadvantage trials). The relative frequency of response location to the Link 1 stimulus is plotted in the bottom panel of Figure 18; only Advantage and Disadvantage trials are shown because they provide the clearest picture of responding during Link 1 during this experiment.

Pecks to Link 1 during Advantage trials showed clear anticipation in the congruent direction; reports to the set of stimuli in which the Link 3 stimulus appeared on the left (Advantage Left) were distributed to the left side of the key, whereas reports to the set of stimuli in which the Link 3 stimulus appeared on the right (Advantage Right) were distributed on the right side of the key. Conversely, pecks to Link 1 during Disadvantage trials showed clear anticipation in the incongruent direction; reports to the set of stimuli in which the Link 3 stimulus appeared on the left (Disadvantage Left) were distributed to the right, whereas reports to the set of stimuli in which the Link 3 stimulus appeared on the right (Disadvantage Right) were distributed on the right side of the key. This result indicates that the anticipatory responses distributed in Link 1 were primarily shifted in the direction of the next response.

To statistically analyze these trends, we used a repeated measures ANOVA (Space x Trial Type x Link 3 Location x Bird as a random factor). Here, the significant result of interest was the three-way interaction between Space, Trial Type, and Link 3 Location, $F(9,27) = 10.93, p < .001$. This three-way

interaction is indicative of the fact that the response distributions do not overlap on the basis of Link 3 Location, which is represented by the non significant Space by Link 3 Location interaction, $F(9,27) = 1.14, p > .05$, but rather by the combination of both Link 3 Location and Trial Type. Additionally, individual interactions independently conducted with each trial type indicated a significant ($p \leq .05$) Space x Link 3 Location interaction, confirming anticipatory pecks on both Advantage and Disadvantage trials. Therefore, this three-way interaction confirms the trend observed in the peck location data.

As in Experiments 1 and 3, we also analyzed the IRT distributions for each peck, but included the additional factor of trial type (Advantage, Control or Disadvantage). These distributions are plotted in Figure 19. The top panel of Figure 19 again contains the IRT data with the first-peck “spike” included. One first result of note is that the animals did not start all of the trial types equally fast, $F(2,6) = 14.5, p < .005$; planned contrasts revealed that Advantage trials were faster than both Control trials, $F(1,6) = 17.83, p < .01$, and Disadvantage trials, $F(1,6) = 25.07, p < .005$, but that Control trials and Disadvantage trials were started at equivalent rates, $F(1,6) < 1$. Additionally, the entry peck into the third link was larger for the Control trials than the other two trial types; this result was caused by the forced delays that occurred on half of the Control trials. Beyond the first peck, we also saw significantly smaller IRTs to Advantage Trials across the first two successive links (see Figure 19, bottom panel). Additionally, we again replicated the shorter IRTs for Links 2 and 3 than for Link 1, but this was mainly disclosed in the Link by Trial Type interaction, $F(4,12) = 6.26, p < .05$. For each of the trial types, there was a significant main effect of Link, indicating the increase in response rate from Link 1 to Links 2 and 3.

Experiment 6

One possibility is that the disparity in the effectiveness of differential work vs. differential delays observed between Experiments 3 and 4 was due to the placement of the delay/work requirement at different points in the three-link sequence. This possibility is predicated on the idea that congruent anticipation would be maintained if the temporal contiguity between Link 2 and Link 3 remained intact. In Experiment 4, the FR requirement was increased during Link 3, but the contiguity between the Link 2 and Link 3 stimuli was preserved. In Experiment 5, the delay was inserted between Link 2 and Link 3, which both delayed primary reinforcement and disrupted the contiguity between Link 2 and Link 3. Therefore, one major difference between the experiments was the contiguous presentation of the Link 3 stimulus given the completion of the Link 2 response requirement.

A second reason this difference may be critical is because the presentation of a conditioned reinforcer can help ameliorate the deleterious effects of delays between a response and the delivery of primary reinforcement on discrimination performance (Williams & Dunn, 1991). In other words, the presentation of the Link 3 stimulus in Experiment 4 may serve as a conditioned reinforcer that promotes congruent anticipation in the Disadvantage condition, even though a higher FR schedule (and therefore, a longer delay to primary reinforcement) will ultimately result from congruent Link 2 responses. On the other hand, because the delay in Experiment 5 occurred before the presentation of Link 3, there was no similarly immediate presentation of conditioned reinforcement that might promote congruent anticipation in Link 2 during Disadvantage trials.

Therefore, in Experiment 6, we inserted a delay after the presentation of the Link 3 stimulus rather than before the presentation of the Link 3 stimulus. This change helped us to identify whether the shift in anticipatory responses

observed in Experiment 5 was tied to both the delay of the primary reinforcer and to the disruption of spatial contiguity or to the delay of the primary reinforcer alone.

Method

Participants. The participants were 4 feral pigeons. Deprivation and housing conditions were the same as in Experiments 1, 3, 4, and 5.

Apparatus. The apparatus was the same as in Experiments 1, 3, 4, and 5.

Stimuli. The same seven textures used in Experiment 4 and 5 were also used in this experiment. These textures can be found in Figure 12.

Procedure.

Shaping and Pretraining. Shaping and pretraining were the same as in Experiments 1, 3, 4, and 5.

Training. The basic experimental procedure was as in Experiments 3 and 4. Six stimuli were divided into three pairs; Advantage, Disadvantage, and Control. Each pair had one stimulus which signaled that the Link 3 location would be on the left and one stimulus which signaled that the Link 3 location would be on the right. Figure 20 contains a visual representation of the experimental design.

During Advantage trials, responses during Link 2 to the congruent side resulted in a short delay after the completion of the Link 3 FR but before the delivery of reinforcement, whereas responses during Link 2 to the incongruent side resulted in a long delay after the completion of the Link 3 FR but before the delivery of reinforcement. These values were set at a 0.5-s delay for the short reinforcement delay and a 3.5-s delay for the long reinforcement delay.

During Disadvantage trials, responses during Link 2 to the congruent side resulted in a long delay after the completion of the Link 3 FR but before the delivery of reinforcement, whereas responses during Link 2 to the incongruent side resulted in a short delay after the completion of the Link 3 FR but before the

delivery of reinforcement. These values were set at a 0.5-s delay for the short reinforcement delay and a 3.5-s delay for the long reinforcement delay.

During Control trials, responses during Link 2 to the congruent side resulted in an unpredictable short or long delay after the completion of the Link 3 FR but before the delivery of reinforcement. Responses to the incongruent side also will lead to an unpredictable short or long delay. These values were set at a 0.5-s delay for the short reinforcement delay and a 3.5-s delay for the long reinforcement delay.

Data Analysis

One bird (13Y) demonstrated a protracted length of time (7 days) at chance performance, after which the acquisition function for this pigeon resembled ordinary learning data. Rather than include these 7 initial chance sessions (the reasons for which were unclear, technical issues with the operant chamber may have caused the delay in learning), we chose to run the bird an additional 7 days to gain a fair window of comparable data. The data analyzed in this Experiment reflect that comparable window of time, from the seventh session onward.

Results and Discussion

The choice data in this Experiment (Figure 21 – top panel) show a striking contrast to those in the previous experiment. Both the Advantage and Control pairs of stimuli in this experiment showed strong evidence of congruent responding; and, the Disadvantage pair of stimuli did not show the same “switching” behavior observed in the previous experiment. Instead, the pigeons were just as likely to produce congruent responses during Disadvantage trials, responding during Link 2 in the location of the Link 3 stimulus even with an ultimate cost in terms of absolute time to obtain reinforcement.

Link 2 data from this experiment were entered into a repeated measures ANOVA (Stimulus Type X Session X Bird as a random factor) for analysis. As expected, there was a highly significant effect of session, $F(14,42) = 32.19, p < .001$, indicating learning over the 15 testing sessions. However, despite the apparent trend in Figure 21, there was no effect of Stimulus Type, $F(2,6) < 1$, suggesting no consistently higher congruency effect for the Advantage over the Disadvantage trials or Control trials. There was also no reliable interaction between Stimulus Type and Session, $F(28,84) < 1$.

On a bird by bird basis, there was only sparse evidence that the Disadvantage pair of stimuli elicited weaker congruent responding than the Advantage or Control pairs of stimuli. For example, one bird showed a slightly weaker congruency effect with the Disadvantage delay pair; 13Y routinely scored between 65-85% congruent responding for the Disadvantage condition while scoring 95-100% congruent responding for the Advantage and Control conditions. But, the other three birds tested showed absolutely no effect of delay to primary reinforcement, scoring between 95-100% congruent responses for all trial types. Direct observation of these birds revealed that they would turn to the hopper and “wait” for the delivery of their reward on Disadvantage trials. Thus, although there was some evidence that delay to primary reinforcement might affect responses for one bird, this effect was clearly weaker than the insertion of delays between Link 2 and Link 3.

The bottom panel of Figure 21 demonstrates this lack of a difference between the Advantage and Disadvantage pair of stimuli in the Link 1 data. Here, as in Experiment 5 (see Figure 18), the birds responded in Link 1 in the direction in which they would next direct their Link 2 response choice. But, unlike in Experiment 5, both the Advantage and Disadvantage trials that resulted in a leftward Link 3 presentation were superimposed, and the Advantage and

Disadvantage trials that resulted in a rightward Link 3 presentation were superimposed.

To statistically analyze these trends, we again used a repeated measures ANOVA (Space x Trial Type x Link 3 Location x Bird as a random factor) similar to the one conducted in Experiment 5. Here, the significant result of interest was the interaction between Space and Link 3 Location, $F(9,27) = 8.51$, $p < .001$. The three-way interaction observed in Experiment 5 between Space, Trial Type, and Link 3 Location was not significant in this analysis, $F(9, 27) < 1$. The lack of this three-way interaction coupled with the significant Space by Link 3 Location interaction is indicative of the fact that the response distributions overlap on the basis of the Link 3 Location regardless of the trial type, confirming the trends discussed above.

We again conducted IRT analyses for this experiment (see Figure 22). However, contrary to the results of Experiment 5, we found no significant differences among the trial types. As seen in the top panel of Figure 22, which contains the initial “spikes” caused by the first peck at each link and specifically the peck that began each trial, the birds were no more “eager” to begin Advantage trials than they were to begin the other two trial types (compare to Figure 22, from the previous experiment). Additionally, it did not appear that there was any difference between entry pecks into the other links.

As before, the bottom panel of Figure 22 shows the IRT data with these initial pecks removed. And, as before, we were able to replicate the general effect of IRT declining from Link 1 to Links 2 and 3. But, unlike in Experiment 5, we found no increased speed in the case of the Advantage trials; here, we found no differences in trial type. In short, using IRT analysis, we were able to replicate the same basic effects as those replicated in Experiment 1, with no differences between any of the trial types. This provides complementary evidence about the

lack of any differences among the trial types to that evidence presented from the spatial discrimination that occurred during Link 1 and Link 2.

Chapter Discussion

Taken together, these three experiments reveal a set of important features about the nature of anticipatory responding. The main issue addressed in this chapter is a suggested interpretation which states that congruent choices are favored over incongruent choices because delay to food reinforcement will be shorter following congruent choices. But, in Experiment 4, the pigeons routinely performed time-consuming additional work after making congruent choices in the Disadvantage condition despite the opportunity to forgo this additional work by making incongruent choices; nevertheless, they persisted in making congruent choices. Only after the work requirements between the conditions were substantial were the birds ultimately driven to make incongruent responses on Disadvantage trials (see Figure 16).

More incisively, equivalent delays inserted either between Link 2 and Link 3 or between Link 3 and primary reinforcement produced vastly different results in terms of behavior, despite being nominally equivalent in terms of delay to food reinforcement. Whereas a delay inserted between Link 3 and the delivery of primary reinforcement (in Experiment 6) may have produced some marginal decrement on Disadvantage trials (see Figure 21), a delay inserted between Link 2 and Link 3 (in Experiment 5) produced both a large incongruency bias on Disadvantage trials and an even stronger congruency bias on Advantage trials (see Figure 18). Clearly, the placement of this delay at different points in the sequence made all the difference.

Why is the placement of the delay within the sequence so vitally important in terms of its effect on behavior? If the prime cause for the congruency effect is not the delay to food reinforcement, but is instead dependent on the preservation

of both temporal and spatial contiguity between the Link 2 and Link 3 stimuli, then manipulations that affect the temporal and spatial contiguity between the Link 2 and Link 3 response should have the largest effect on behavior.

Serial conditioning, or the idea that associations might form between the stimuli that precede primary reinforcement, has, as described by Wasserman and Miller (1997), been “reasonable enough” as a concept, but the evidence for such a theory “has been slow in coming” (p.583). One reason for this dearth of evidence is that most experiments of this sort rely solely on response *rate*, which is lacking in interpretative value. As previously observed, the experiment offered by Royalty et al. (1987) provided good evidence for the formation of associations between contiguous stimuli, but the added component of response location provides a much more obvious and direct measure of this phenomenon. Because our method allows for the confirmation of these early findings with response rate coupled with our new observations about response location, it seems clear that stimulus contiguity and not delay to food reinforcement is the most parsimonious explanation for the results.

Furthermore, when evaluating this explanation, it is important to remember that the mere contiguity of the CS2 and CS1 stimuli in the experiments by Wasserman et al. (1978) were enough to drive congruent anticipatory pecks; in those experiments, which utilized an autoshaping design, no key-contact responses were ever reinforced or required, but a strong congruency preference was still established. Therefore, it appears that the spatial contiguity of the Link 2 and Link 3 stimuli was primarily important for driving these anticipatory Link 2 pecks, and that the prime mechanism for promoting responding is the tendency to shift in the direction of the contiguous Link 3 stimulus.

An important component of this explanation is that the contiguity between the Link 2 stimulus and Link 3 stimulus matters because the Link 3 stimulus

functions as a conditioned reinforcer. That these congruency effects are strongly driven by a spatial tendency to move toward this conditioned reinforcer may be related to the phenomenon of sign-tracking (Hearst & Jenkins, 1974) or approaching appetitive stimuli. Because reinforcers naturally result in approach (Hinde, 1973), the opposite kind of behavior is difficult to teach. For example, in a clever experiment, Hershberger (1985) taught chicks to approach a food cup for reward. He then arranged the situation so that the food cup moved in the same direction as the chicks, but twice as fast. In this setting, it is impossible to “chase” the cup; instead, the chicks must learn the odd behavior of running away from the food cup in order to have it eventually “catch up” with them. He describes the near impossibility in teaching this “backwards” behavior, in which an animal can receive food by making spatially non-contiguous responses. The results of Hershberger are similar to the results obtained in Experiment 6; rather than make responses that will move them closer temporally to food, the pigeons routinely made responses that were closer spatially to a conditioned reinforcer despite instrumental punishment for doing so. These experiments also recall omission training in autoshaping, in which once an appetitive reaction toward a keylight has been trained, even the negative contingency between keylight pecking and food delivery is insufficient to stamp it out (Schwartz, 1973; Williams & Williams, 1969). In other words, approaching and responding toward a strong signal for food delivery is a powerful force in controlling behavior and one that is not easily eliminated.

Similarly, Cabrera et al. (2009) report what they term the “lunching” effect in pigeons; pigeons will make more vigorous responses to stimuli that are located close to the grain hopper. These results are similar to those of Hershberger (1985); the pigeons are more inclined to respond when these responses appear directly linked to the delivery of food, and only weakly respond

when the key appears to move away from the grain hopper. It would be interesting in future studies to know if pigeons show similar response biases when making responses toward stimuli moving in the direction of strongly conditioned reinforcers; the present experiments suggest that this may indeed be the case.

In our view, the sum total of the evidence against delay-to-reinforcement provided by these studies significantly weakens delay-to-reinforcement as a possible explanation for these data. We should note that one serious omission in our dataset (uncollectable with our current operant boxes) concerns the actual time-to-obtain-reinforcement (see Staddon & Cerutti, 2003). It may be that inserting the same nominal delay at different points in the schedule produces different actual times to receive reinforcement, and that these differences in reinforcement time would explain the data.

But, even if this hypothesis offered by Staddon and Cerutti (2003) were true and the collection of time to primary reinforcement is a critical omission from the dataset, this type of hypothesis has a very difficult time accounting for responding during the original autoshaping report task, Wasserman et al (1978). This difficulty is caused by the fact that, as in all autoshaping designs, responses were never required nor explicitly paired with food. One could conceivably construct a strained scenario in which congruent responses during CS2 heightened the likelihood of obtaining primary reinforcement due to some attentional mechanism operating on those trials; for example, perhaps responses during CS2 were facilitated by the immediately following CS1 stimulus, but the primary linkage that promoted responding to CS2 was between CS2 and primary reinforcement. However, the study by Rescorla and Cunningham (1979) in which CS2-CS1 presentations are never followed by food completely eliminates this possibility, as CS2 can only serve as a signal for CS1 and not for CS2.

Additionally, further evidence against the delay to reinforcement hypothesis is presented in Experiment 11 (see next Chapter).

Thus, it appears as though the most parsimonious account for the data presented in this chapter and that accounts for previous results concerns each response's contiguity with the presentation of a conditioned reinforcing stimulus. If this contiguity is sufficient to form a memory for a prospective goal location, this spatial memory might affect responding in both Link 1 and Link 2. The utility of such a spatial memory formed by the contiguity between stimuli and conditioned reinforcement for explaining the observed data will be tested later in a dynamic field model presented in the General Discussion.

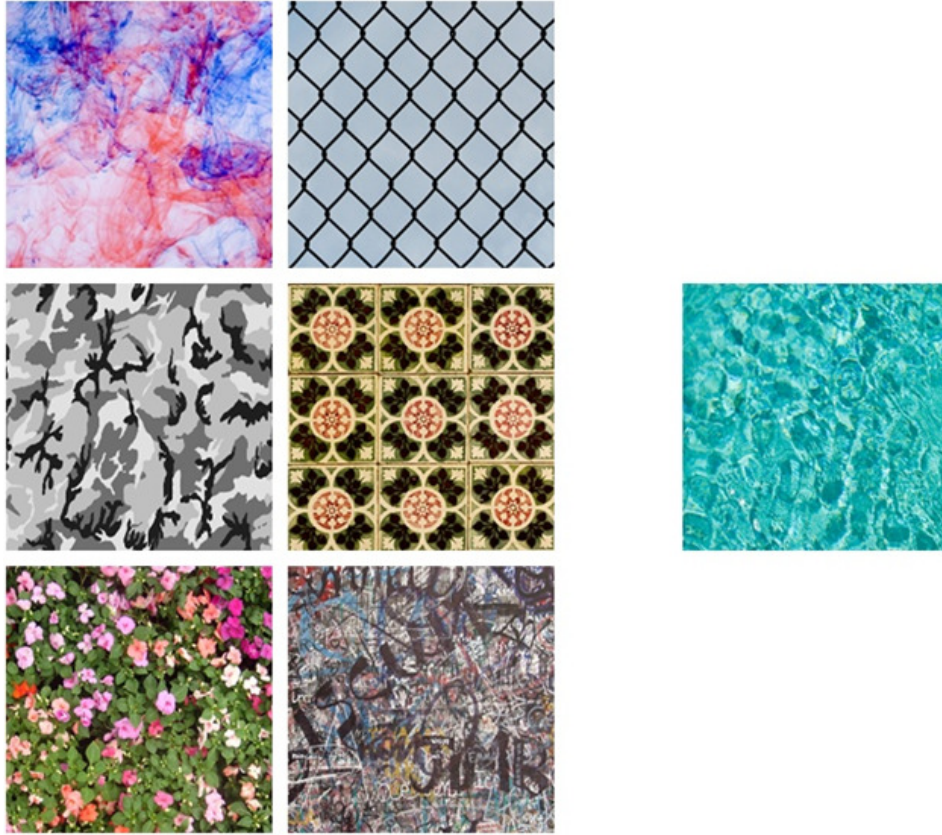


Figure 12 - Textures used in multiple experiments. Textures on the left served as counterbalanced stimuli; the texture on the right was always the Link 3 stimulus.

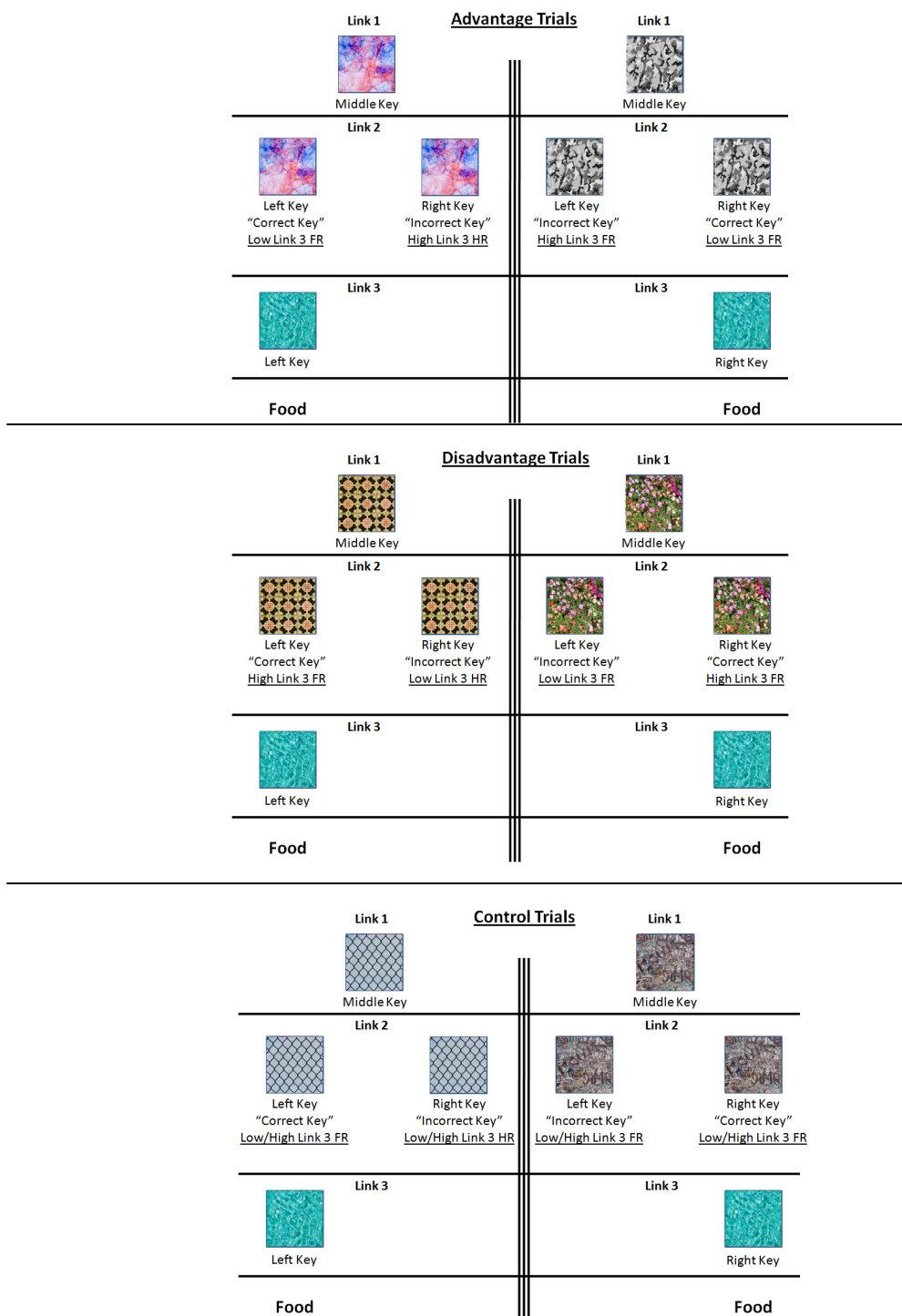


Figure 13 – Experimental Design in Experiment 4. See text for details.

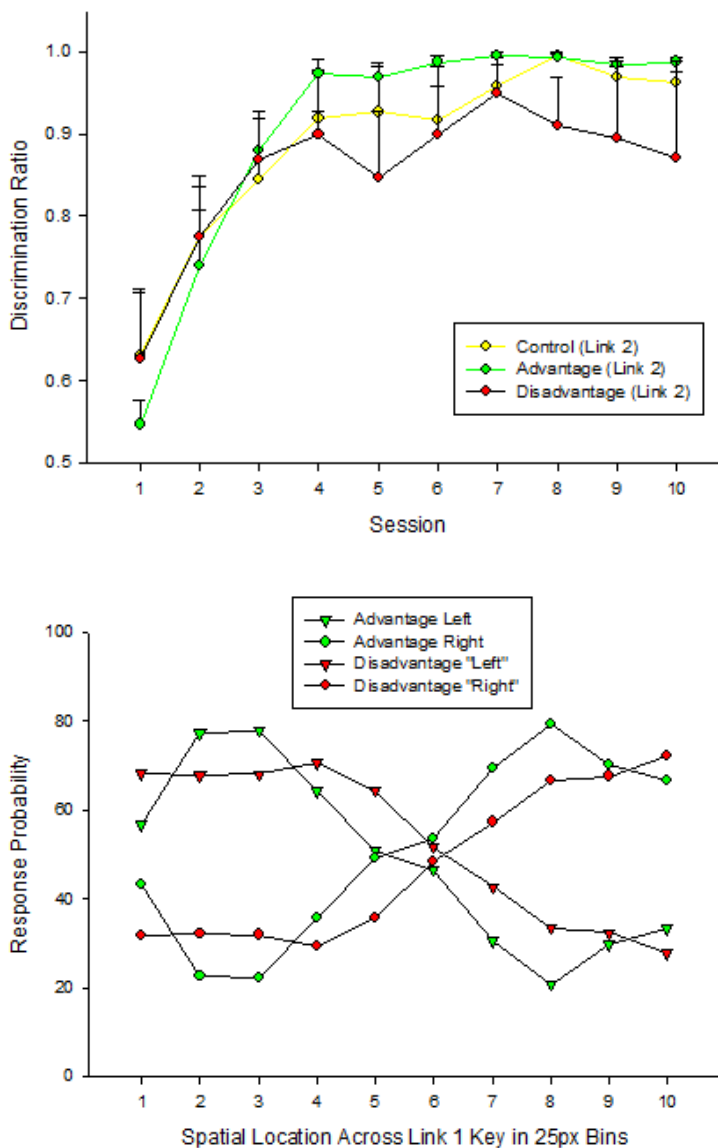


Figure 14 – Discrimination Ratio in Link 2 and response probability across Link 1 key in Experiment 4. *Top panel:* Discrimination ratio (both in Experiment 4 over the first 10 sessions of training. *Bottom Panel:* Link 1 discrimination in Experiment 4. The green symbols indicate Advantage trials; the red symbols indicate Disadvantage trials. Triangles indicate trials in which the Link 3 stimulus will appear on the left, Circles indicate trials in which the Link 3 stimulus will appear on the right.

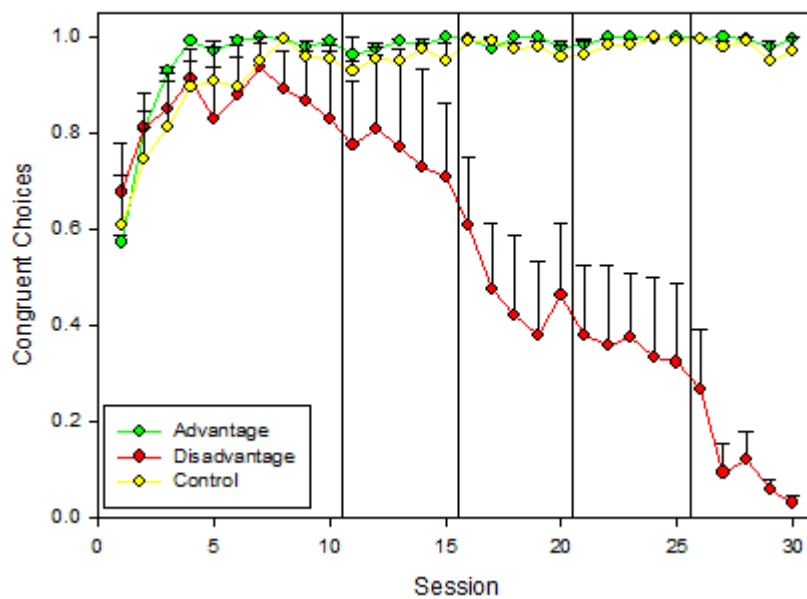


Figure 15 - Discrimination in Experiment 4 during FR Increase Phase by Trial Type. Lines denote sessions in which the FR was increased (see text for details).

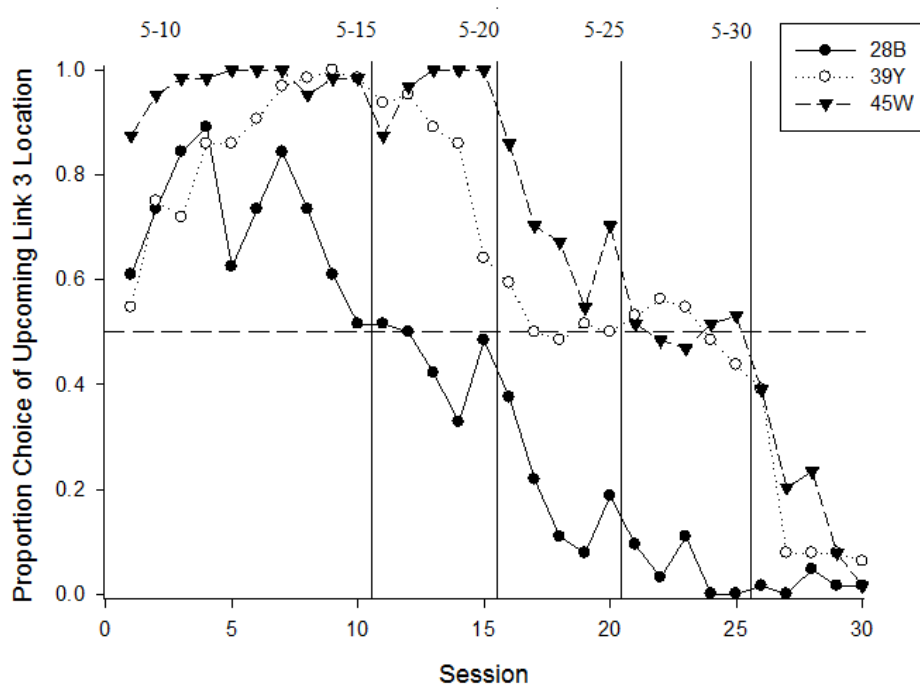


Figure 16 - Discrimination in Experiment 4 for each Disadvantage Pair, separated by bird.

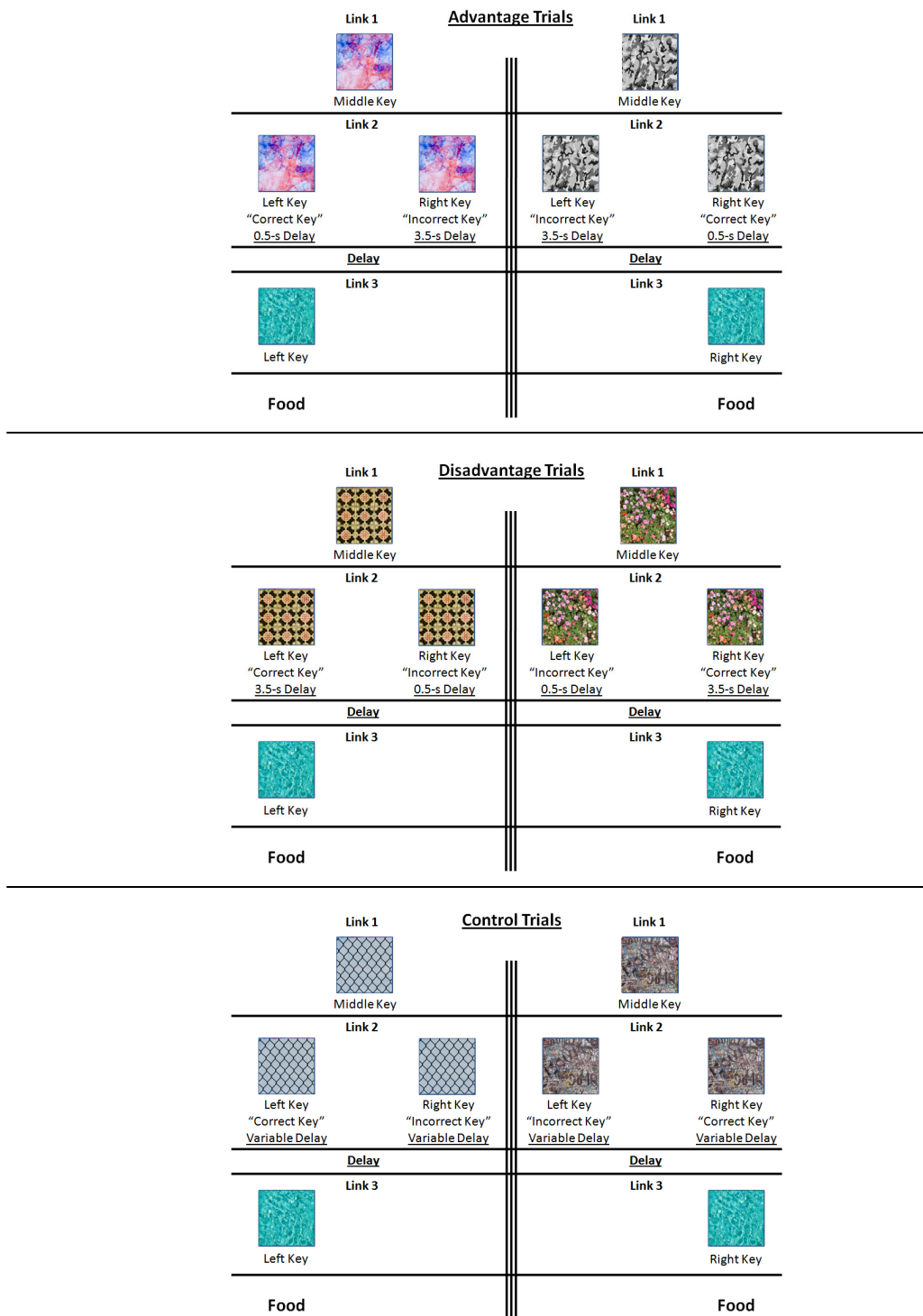


Figure 17 - Experimental Design in Experiment 5. See text for details.

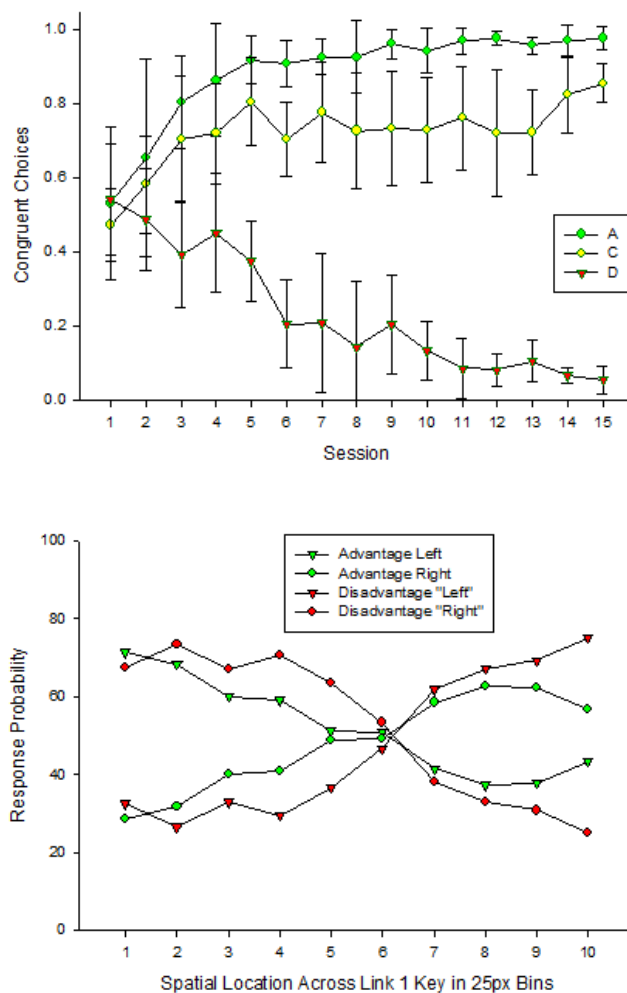


Figure 18 – Discrimination Ratio in Link 2 and response probability across Link 1 key in Experiment 5. *Top Panel:* Link 2 Discrimination in Experiment 5. *Bottom Panel:* Link 1 discrimination in Experiment 5. The green symbols indicate Advantage trials; the red symbols indicate Disadvantage trials. Triangles indicate trials in which the Link 3 stimulus will appear on the left, Circles indicate trials in which the Link 3 stimulus will appear on the right. Note that the shape symbols do not overlap; evidence for “reverse” anticipation on disadvantage trials.

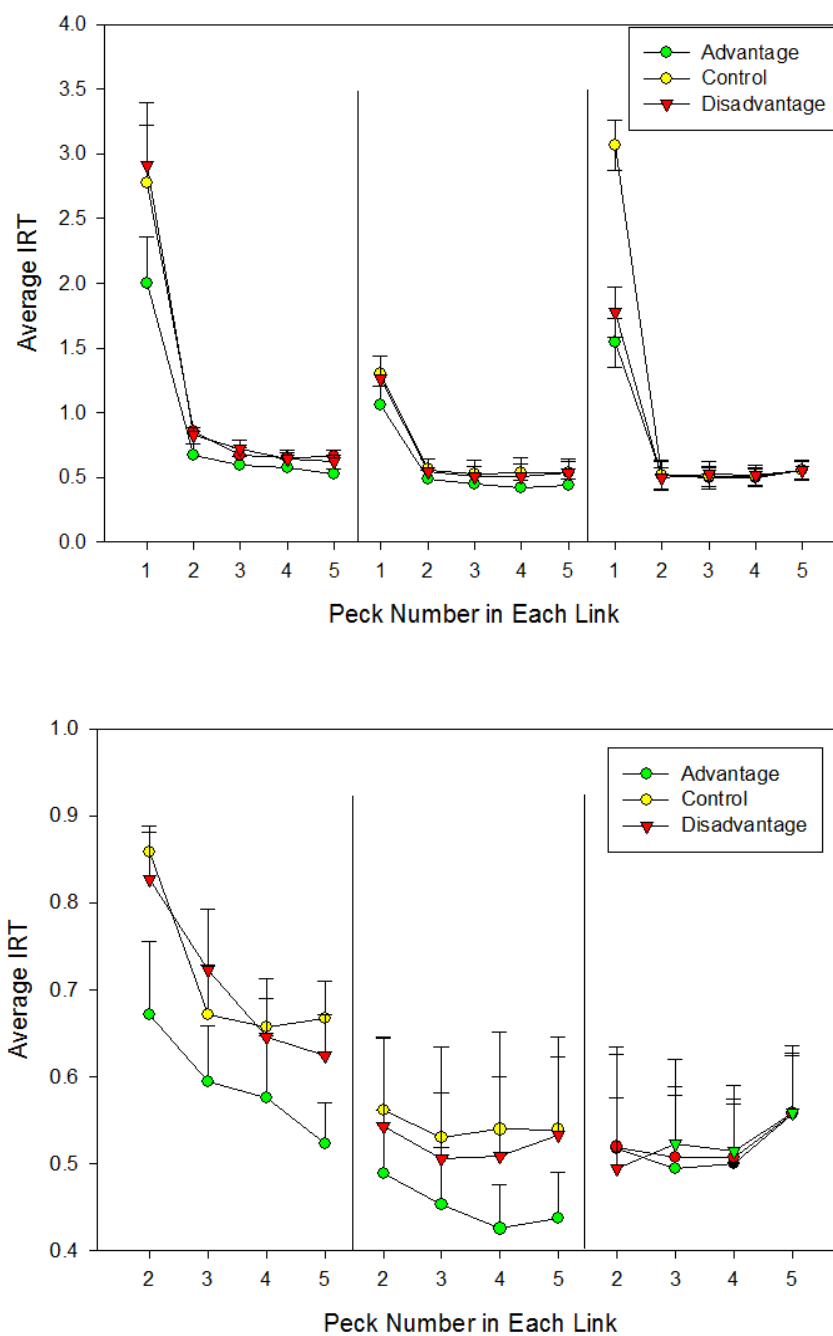


Figure 19 - IRT analysis for Experiment 5. The top panel includes the “spikes” in IRT characteristic of the first peck in each link; the bottom panel omits these spikes to highlight the within-link IRT changes that occur in Links 1 and 2.

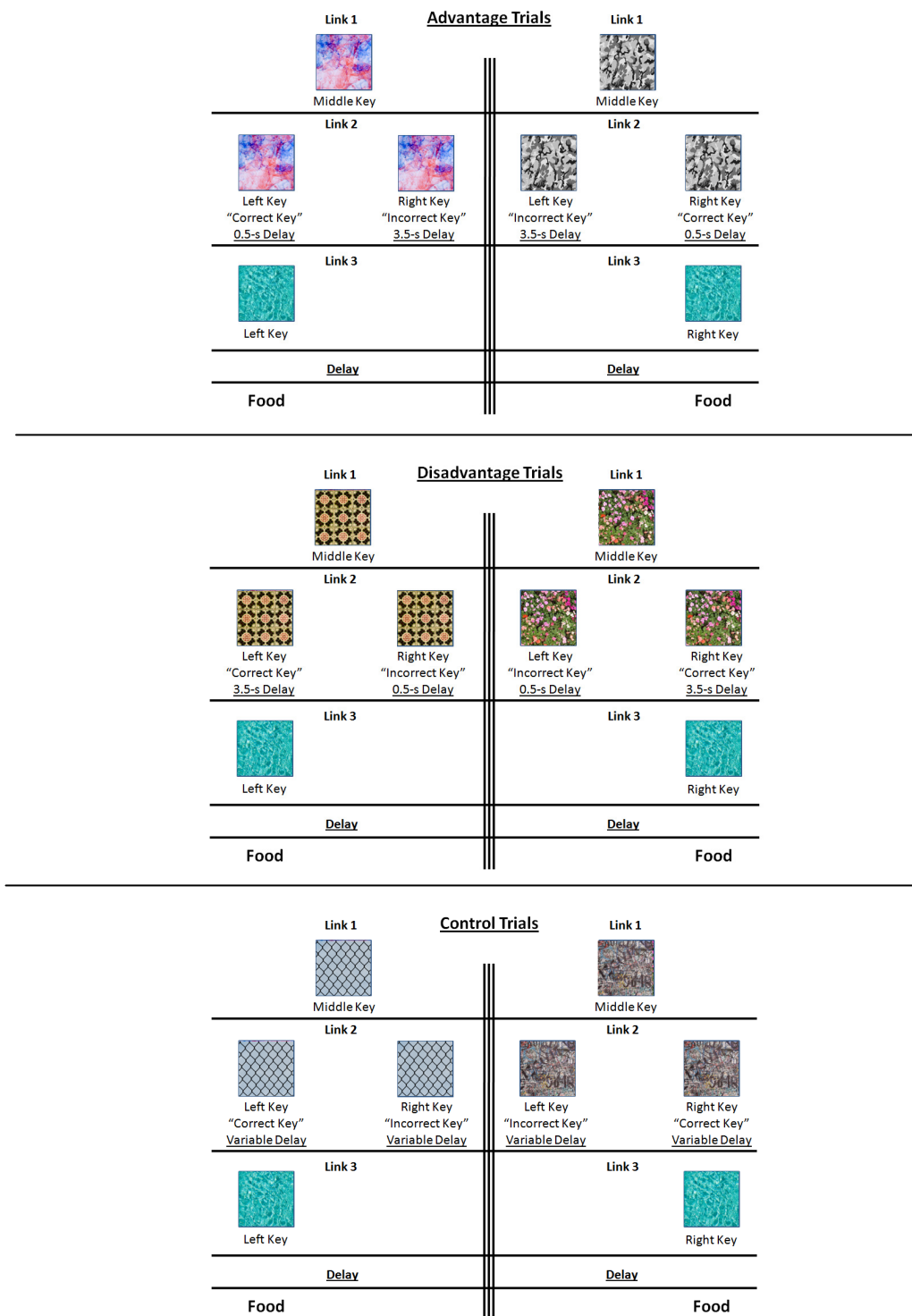


Figure 20 - Experimental Design in Experiment 6. See text for details.

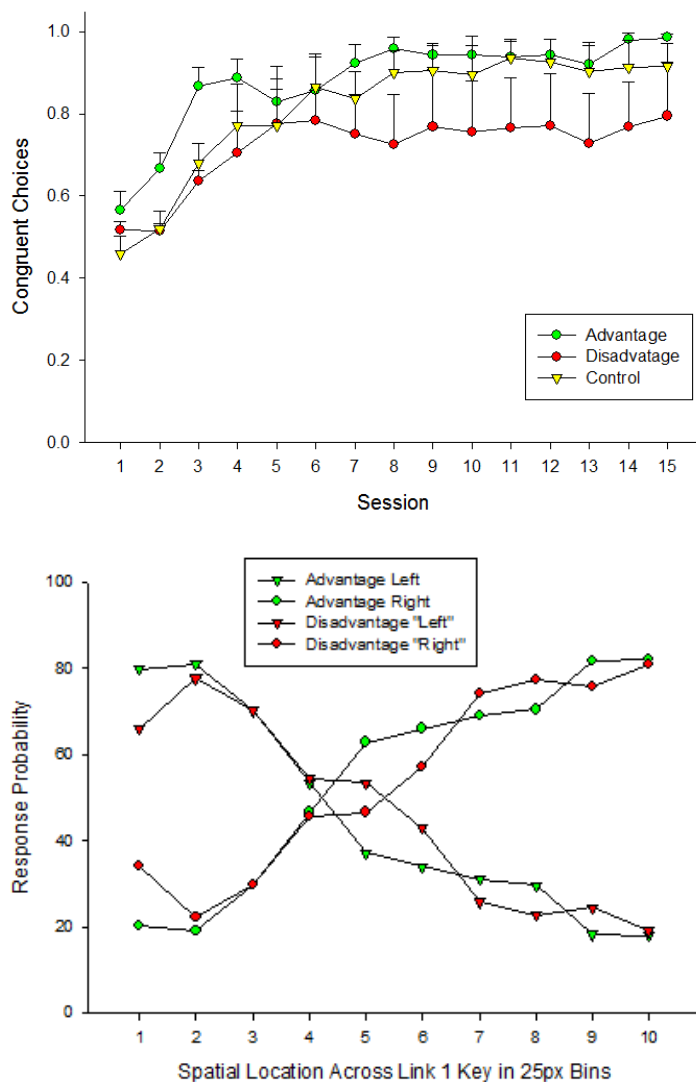


Figure 21 - Discrimination Ratio in Link 2 and response probability across Link 1 key in Experiment 6. *Top Panel:* Link 2 Discrimination in Experiment 6. *Bottom Panel:* Link 1 discrimination in Experiment 6. The green symbols indicate Advantage trials; the red symbols indicate Disadvantage trials. Triangles indicate trials in which the Link 3 stimulus will appear on the left, Circles indicate trials in which the Link 3 stimulus will appear on the right. Note that the shape symbols overlap; evidence for congruent anticipation on both advantage and disadvantage trials.

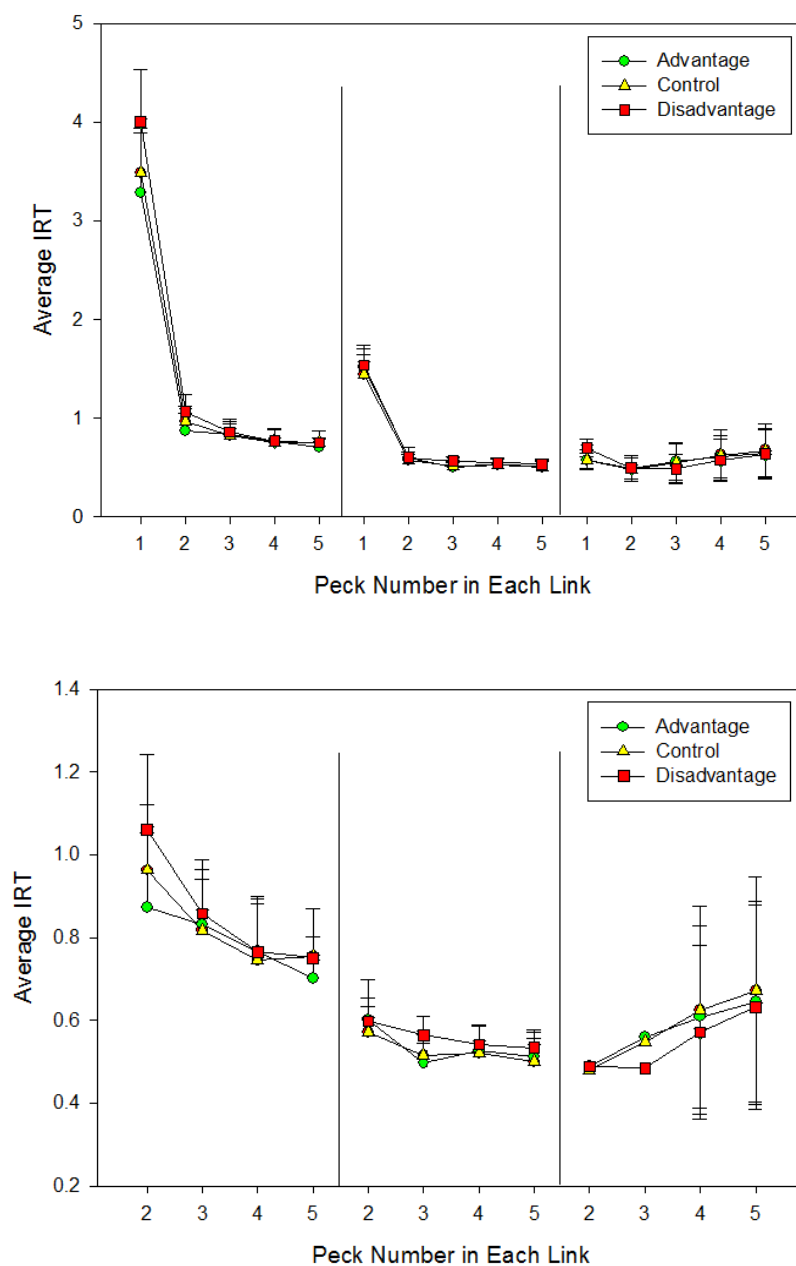


Figure 22 - IRT analysis in Experiment 6. The top panel includes the “spikes” in IRT characteristic of the first peck in each link; the bottom panel omits these spikes to highlight the within-link IRT changes that occur in Links 1 and 2.

CHAPTER 4

SPATIAL ORGANIZATION

Chapter Introduction

Although both the pigeons and rats quickly shifted both their Link 1 and Link 2 reports in Experiments 1 and 2, the actual arrangement of the display panel was somewhat arbitrary. Whereas the sizes and distances of the keys had been chosen systematically in that they were non-overlapping and symmetrical, this positioning was chosen without prior experimentation. Whereas our choices were clearly effective in promoting anticipatory behavior, we had little idea about how effective these choices were relative to other possible display organizations. Whereas the experiments presented in Chapter 4 are necessarily more exploratory in nature than those presented in Chapter 3, we hoped that a parametric investigation of distance and spatial organization would aid our understanding of the psychological processes that underlie the observed anticipation.

So, we were curious to know how the layout of the display that we presented on each trial would affect this prospective phenomenon. Would animals be more inclined to shift their responses in Link 1 or choose the congruent key in Link 2 if the Link 2 keys were located close to or far from the central Link? Would it be possible to observe anticipatory responses in both the horizontal and vertical orientations, as opposed to only the horizontal orientation? What if the pigeons were given the option to keep responding to the center key during Link 2?

To answer these questions, this chapter contains five additional experiments related to the spatial organization of the display panel. The first two experiments were completed with rats. In Experiment 7, we investigated how the distance (near or far) between the terminal link stimuli would influence the production of anticipatory responses. In Experiment 8, we leveraged the

experimental design used in Experiment 7 to investigate generalization to intermediate stimulus values in brightness and orientation.

The next three experiments were completed with pigeons. In Experiment 9, we presented the pigeons with a task in which four Link 2 response keys (and Link 3 terminal locations) were used instead of the two used in previous experiments. This experiment was designed to allow us to measure anticipatory responses in both the horizontal and vertical axis. When this experiment failed, we conducted an additional experiment, Experiment 10, which separated the four-key task into two two-key tasks. Using this tactic, we could measure the impact of separating the horizontal and vertical discriminations, attempting to replicate the basic anticipatory effect with the horizontal keys while simultaneously training the vertical keys on separate trials.

The final experiment in this chapter probed how the general display panel organization might have promoted anticipatory behavior. In Experiment 11, we presented three keys (left, middle, and right) in Link 2, instead of two keys (left and right) in Link 2. This design effectively allowed the birds to switch in the direction of the terminal link either after the completion of Link 1 or the completion of Link 2.

Experiment 7

In Experiment 7, we investigated the spatial placement of the choice keys in Links 2 and 3. Specifically, we were interested in how the distance between the keys in Link 2, and the placement of the terminal response in Link 3, would influence the production of anticipatory responses.

One might conceive of more distantly located Link 3 stimuli as a more powerful psychological “lure”, consistent with sign-tracking (Hearst & Jenkins, 1974). But, in fact, animals in truly Pavlovian autoshaping tasks engage in two types of directed behaviors: sign-tracking (i.e., CS directed behaviors such as

pecking the autoshaped keylight) and goal-tracking (i.e., US directed behaviors such as approach and contact with the food hopper). Few experiments have parametrically tested the location of the CS relative to the US in Pavlovian autoshaping designs. As noted in the introduction, Hearst (1980) found that pigeons would traverse great distances (and cost themselves valuable reinforcers) to sign track, but as noted by Silva, Silva, and Pear (1992) and Holland (1980), the quantitative measures in this demonstration were not adequate to distinguish between sign-tracking and goal-tracking nor was a parametric manipulation of distance conducted. Silva et al. (1992) found that pigeons tended to engage in sign-tracking behaviors to close CSs and goal-tracking behaviors to far CSs; this is reminiscent of the previously discussed results of Cabrera et al. (2009) in which peck rates to stimuli located at various distances to the hopper were measured. The most relevant data to the current project may be those collected by Holland (1980), who conducted an experiment with rats in which the distance of keylight CSs to the US was parametrically manipulated; he found diminished sign-tracking in the case of more distant CSs, with animals engaging in increased goal-tracking on those trials.

But interpreting these previous experiments in the context of our current task is not so straightforward. For one, despite having strong undertones of Pavlovian associations between stimuli, our task is fundamentally instrumental. Our sequential presentation task presents the animal with a very different route to reinforcement than is present in the typical Pavlovian autoshaping design, as our task *requires* that the animals generate a response before the delivery of the reinforcer. This response requirement may attenuate or eliminate otherwise strong goal-tracking behaviors or promote increased sign-tracking to conditioned reinforcers. Indeed, given Holland's (1980) finding that goal-tracking increases when sign-tracking results in nonreinforcement, the opposite may well be true;

our rats may initially engage in hopper-directed activity that is later suppressed when this goal-tracking activity prior to responding to the presented stimuli is found to be fruitless, due to operant contingencies.

If the sign-tracking of the Link 3 conditioned reinforcer in our study is indeed stronger as a result of these instrumental contingencies, then we might observe more robust learning in the case that the stimuli are far than in the case that they are near. Two additional lines of research would suggest that this result might occur. First are previous reports of the effects of spatial distance manipulations on choice behavior during instrumental maze-running tasks by rats, such as those conducted by Brown and Huggins (1993). Brown and Huggins suggested that rats may use a different choice criterion when choosing among shorter radial arms because the cost for choosing these arms is less severe when compared to the cost of choosing longer arms. Therefore, one possible reason for observing a possible effect of display panel arrangement might be the relative cost of making an incongruent report in Link 2 when the keys are near to the central location as compared to when they are far from the central location. Following this logic, when the keys are near to the center link they will also be close together, which might lead to a small cost for choosing the incongruent key and having to shift response location in Link 3. On the other hand, when the keys are far apart, there is a relatively larger distance to travel in Link 3 if an incongruent response has been made in Link 2, perhaps leading to increased Link 2 discrimination. In other words, the increased spatial or temporal discontinuity when making an incongruent choice during far key trials may help bias animals to learn to make congruent choices in that condition more quickly.

There has also been prior research conducted by Eckerman (1970), which suggested that a second possible explanation for increased discrimination in the case that the keys are farther apart might be that more distant Link 3 locations are

more discriminable than near Link 3 locations. For example, when Eckerman (1970) required that animals make differential sample behaviors to keys that were close together or keys that were far apart, he found better discrimination on the latter task. So, it might be that arranging the display panel so that the keys are more distant from one another will produce better discrimination because the far choices are more discriminable than the near choices.

To investigate this distance effect in the current task, we trained a group of 8 rats on two concurrent two-key tasks, an example of which is shown in Figure 23. One of these two tasks had keys located near to the central Link 1 stimulus (e.g., Figure 23, top panel), and the other of the tasks had keys located far from the Link 1 stimulus (e.g., Figure 23, bottom panel). Because we had previous success training the orthogonal dimensions of brightness and orientation independently in Experiment 2, we again used these dimensions in Experiment 7; one dimension was used for one set of keys, the other dimension was used for the other set of keys, counterbalanced across animals.

Method

Participants. The participants were 8 Long Evans rats kept at 90% of their free-feeding weights on a 12-h light/12-h dark schedule with free access to water and grit.

Apparatus. The same apparatus was used as in Experiment 2.

Stimuli. Five keys were used as stimuli for each group. These keys were a square with horizontal lines, a square with vertical lines, a square with light dot-density, a square with dark dot-density, and a concentric circle. Because these stimuli were used on both the central (large) key and the adjacent side (smaller) keys, care was taken to ensure that the stimuli presented on the side keys were equivalent to those presented on the large key in terms of image resolution, bar width, pixel size, and periodicity. To accomplish this equivalence, the central

keys were 2 x 2 tiled repetitions of the side key stimuli. So that display symmetry could be maintained, central keys were 240 pixels wide and side keys were 120 pixels wide.

Procedure

Shaping. The rats were presented with one session in which a single stimulus was displayed in one of the five locations to be used in Experiment 7. One response to this stimulus resulted in food reinforcement. After the rats reliably responded to each of the stimuli, training commenced.

Training. As in Experiment 2, each training trial began with a centrally located stimulus. Following one response to this stimulus, two laterally presented side keys were presented on either the near or far keys. Following one response to these two keys, a third stimulus was presented on one side of the screen. Following one response to this Link 3 stimulus, food reinforcement was delivered. The Link 1 and Link 2 stimuli were always one of the two brightness or orientation stimuli; the Link 3 stimulus was always the concentric circle. Training lasted for 30 sessions of 120 randomly ordered trials (30 of each stimulus type).

Data Analysis. Data analysis was as in Experiment 2.

Results and Discussion

The 30 sessions of acquisition are plotted in Figure 24, split by data from Link 1 (Rho) in the top panel and data from Link 2 (Discrimination Ratio) in the bottom panel. Overall, as in Experiment 2, there was a strong tendency to shift responses during both Link 1 and Link 2 in a direction congruent with the upcoming Link 3 location. Additionally, the rats learned to shift responses toward the congruent side more quickly when the subsequent key would be far from the center than when it would be near to the center.

To statistically analyze this trend, we conducted a repeated measures ANOVA (3-Session Blocks x Key Distance x Rat as a random factor) on both

Link 1 and Link 2 scores. Analysis of the Link 1 data (Figure 24, top panel) revealed a significant main effect of session, $F(9,63) = 18.84$, $p < .0001$, indicating a stronger spatial preference as training progressed. Additionally, an interaction between session and distance was found, $F(9,63) = 2.08$, $p < .05$. This interaction confirms that, over training, a stronger shift in Link 1 response location emerged for far keys than for near keys. However, no main effect of key distance was found.

Link 2 analysis (Figure 24, bottom panel) confirmed a similar pattern of results. That ANOVA revealed a significant main effect of session, $F(9,63) = 29.36$, $p < .0001$, again demonstrating the development of a congruence preference following training. There was also an interaction between session and distance, $F(9,63) = 3.25$, $p < .01$. This interaction confirms that, over training, a stronger shift in Link 2 congruent responses emerged for far keys than for near keys. Again, however, no main effect of key distance was found.

There was some evidence that there may have been an effect of stimulus dimension during training despite the fact this was not the prime focus of the experiment. Specifically, two rats (R3466 and R3467) showed faster learning with the near keys than the far keys early in training; these rats both had brightness stimuli as near keys and orientation stimuli as far keys. But, one of these rats (R3466) showed greater Link 1 Rho values for the far keys despite the stimuli being orientation rather than brightness. Additionally, one of the rats that showed the largest distance effect (R3469) had brightness stimuli as the close stimuli and orientation stimuli as the far stimuli. In short, it is difficult to reconcile these possible effects of stimulus dimension; both dimension and key distance may affect learning. To analyze these effects, we conducted separate analyses using dimension rather than distance as the factors. This analysis revealed no significant

effect of dimension, $F(1,7) = 4.11$, $p > .05$, and no interaction between dimension and session, $F(9,63) < 1$.

Experiment 8

The main goal of Experiment 8 was to leverage the fact that we had trained two concurrent discriminations to examine generalization on these two dimensions in both Link 1 and Link 2. Therefore, to demonstrate control by both dimensions of the stimuli, we conducted transfer tests using intermediate values of brightness and line orientation. Here, we presented intermediate values of brightness and orientation on randomly interspersed testing trials.

Method

Participants. The participants were the 8 rats that had participated in Experiment 7.

Apparatus. The same apparatus was used as in Experiment 2 and 7.

Stimuli. During training trials, five keys were used as stimuli for each group. These keys were a square with horizontal lines, a square with vertical lines, a square with light dot-density, a square with dark dot-density, and a concentric circle. During testing trials, five intermediate values of brightness and orientation were shown. Generalization brightness stimuli were dot-density displays with 30%, 40%, 50%, 60%, or 70% percent white pixels; generalization orientation stimuli were striped lines with 15, 30, 45, 60, or 75 degrees of line tilt.

Procedure

Testing. The rats had already been shaped and well trained in the basic task. On testing trials, the Link 3 stimulus appeared in whichever location the rat had chosen during Link 2. This approximates the conditions of nondifferential reinforcement given during most generalization testing trials; in short, it prevents us from unintentionally teaching the animal to make one response or another in the presence of the generalization stimuli.

A total of 160 trials were given each session. 120 trials were training trials (60 brightness, 60 orientation). 40 trials were testing trials (20 brightness, 20 orientation). Therefore, each of the five generalization stimuli was tested four times each session.

Data Analysis. Data analysis was as in Experiment 2 and 7.

Results and Discussion

The top panel of Figure 25 shows the 20 sessions of transfer data split by stimulus dimension. As can be seen in that figure, the rats did indeed exhibit strong control by both dimensions of the stimuli, progressively shifting from one response alternative to the other as the stimuli took on intermediate values.

As we had previously examined in Brooks and Wasserman (2010), we also analyzed Link 1 responses during the generalization test. In that previous report, we found a progressively shifted distribution of responses as the value of the stimulus shifted along a dimension. For this descriptive analysis, we chose to use mean response location rather than Rho because there were more than two distributions to compare. These data are plotted in the bottom panel of Figure 25. Shown in this figure is the average response location relative to the size of the Link 1 report key as a function of which type of transfer stimulus was shown. As can be seen in this figure, response distributions progressively shifted as a function of the stimulus dimension, for both brightness and orientation. Thus, strong control by both dimensions can be found in both the Link 1 and Link 2 reports.

To further investigate the relationship between Link 1 and Link 2 scores, we also ran a correlational analysis on these transfer data. First, we normalized the Link 1 peck location and Link 2 discrimination scores so that the endpoints of each dimension were coded as 0 and 1 and the intermediate values were scaled appropriately. Then, we correlated these normalized scores, leaving out the

endpoints of the dimension so as not to inflate the correlation (see Young & Wasserman, 2001, for the logic behind this tactic). Figure 26 plots this correlation for both brightness (top panel) and orientation (bottom panel). There was a clear predictive relationship between these two variables; the correlation between the brightness Link 1 and Link 2 scores was $R=.87$; for orientation, the correlation between Link 1 and Link 2 scores was $R=.93$.

Experiment 9

Experiment 9 was an attempt, with pigeons, to teach the anticipation task with four keys rather than two. But, rather than manipulating distance from the center key with these four response keys (as in Experiments 7 and 8), the spatial organization used in Experiment 9 was a very different type of spatial manipulation. Here, we hoped to train this task with four keys arranged in a “cross” and observe the birds simultaneously “pulled” in each of four directions in both Link 1 and Link 2. In so doing, we hoped that this spatial organization would open avenues with which to conduct experiments using the vertical and horizontal axes as orthogonal response dimensions.

We thought that the ability to use these two orthogonal dimensions might be particularly important for revealing aspects of prospective processes under differential conditions, such as differential outcomes (cf. Trapold, 1970). But, before conducting these more ambitious experiments, we aimed to start by using a “basic” four-key task, similar to our basic three-link task (e.g., Experiment 1).

In this task, shown in Figure 27, the pigeons were presented with a single texture in Link 1 (as in previous experiments), but were then presented with an array of four possible response locations in Link 2. As before, the same texture in Link 1 was presented on each of the four keys in Link 2. This texture uniquely cued one of the four Link 2 keys as the location of the upcoming Link 3 stimulus. As before, the pigeon had to make five pecks to any of these Link 2 keys to

produce the Link 3 stimulus; also as before, five pecks to the Link 3 stimulus would produce food. Thus, the major changes were the addition of the four possible response locations in Link 2 and the slight recalibration of the size and positioning of the stimuli to accommodate these four response locations on the monitor.

Method

Participants. The participants were 4 feral pigeons with housing conditions identical to those in Experiments 1, 3, 4, 5, and 6.

Apparatus. The same apparatus was used as in Experiments 1, 3, 4, 5, and 6.

Stimuli. Five textures were used as stimuli for each pigeon. These textures were randomly chosen from the seven textures used in Experiments 4, 5, and 6. These textures can be seen in Figure 12. So that the four keys could fit on the display panel, we changed the size of the keys to 4.76-cm x 4.76-cm. Each of these stimuli occupied 160 square pixels of space on the monitor.

Procedure.

Shaping. The pigeons were presented with one session in which a random texture appeared in one of the five key locations used in Experiment 9 to acclimate the birds to pecking at each location.

Training. Each training trial began with a centrally located stimulus. Following 5 pecks to this stimulus, four adjacent side keys were presented. Following 5 total pecks to any of these four keys, a third stimulus was presented in one of these four locations. Following 5 pecks to this Link 3 stimulus, food reinforcement was delivered. The Link 1 and Link 2 stimuli were always one of the four arbitrary textures; the Link 3 stimulus was always the “swimming pool surface” texture.

As in previous experiments, individual textures signaled response locations. These texture-location assignments were counterbalanced across pigeons. Training lasted for 16 sessions of 192 trials each (48 top trials, 48 bottom trials, 48 left trials, and 48 right trials).

Results and Discussion

As can be seen in Figure 28 (top panel), the four pigeons trained in this task had an overwhelming bias to choose the bottom key (see Figure 28, filled diamonds). Beyond that finding, two pigeons had a smaller side-bias to choose the left key, one had a smaller side bias to choose the right key, and one chose the bottom key virtually every trial. When averaged across each pair of responses (Figure 28, bottom panel), this average unsurprisingly revealed extremely poor discrimination ratios for both the top/bottom and left/right pairs of keys.

To statistically confirm this trend, these data were entered into a repeated measures ANOVA (Session x Key x Bird as a random factor). This ANOVA revealed a significant effect of session, $F(15, 45) = 2.22, p < .05$, which reflected the marginal rise above chance responding in this task. This ANOVA also revealed a significant effect of key, $F(3,9) = 10.01, p < .01$. Post-hoc tests in the form of paired t-tests revealed a significant difference between the bottom key and every other key, indicative of the fact that the bottom key attracted the most responding. There was no observed interaction between session and key.

We also analyzed the data grouped by the top/bottom and left/right pairs of keys in a separate ANOVA (Session x Key Pair x Bird as a random factor). Here, as before, we again observed an effect of session indicative of marginally better discrimination over time, but we observed no significant difference between the top/bottom and left/right pairs of keys or any interaction with session, indicative of the relatively little difference between these different key pairs either

on average or across days. Again, these relatively poor results are likely the result of the intrusion of the strong bottom-key bias.

It is difficult to speculate on exactly what caused the pigeons to have such strong key preferences in this study. Perhaps there is a sort of increased “naturalness” of making downward-directed pecking motions in these typically ground-feeding animals (e.g., Bodily, Katz, & Wright, 2008), or perhaps an association had formed between the bottom key and the food hopper location (located on the bottom of the back wall). More troubling than failure with the top/bottom keys was failure with the left/right keys. We had trained dozens of animals on this task without an entire group of pigeons failing to express anticipatory responding, and suddenly that failed as well.

It is almost certain that on left/right trials, the bottom-key bias was so strong that it attracted much of the responding that would otherwise be directed at the left or right keys. The expression of this bias was likely exacerbated by the physical location of the keys in this experiment. Due to the physical dimensions of the response panel, we were forced to both shrink the keys and locate the keys much closer in space to the central key. Given what we discovered in Experiment 7, using a smaller response panel most likely made it even more difficult for the birds to learn to generate any anticipatory responses.

It should be noted that this bottom-key bias is not endemic to our current task. Other published data on errors made by pigeons in MTS tasks (Cook, Chechile, & Brooks, 2005) showed that pigeons will often make “correctable” errors to bottom key locations. In that experiment, pigeons were presented with a single sample stimulus and a large ring of comparison stimuli; if the pigeons made an error on their first choice, they were allowed to continue to make a second choice. Pigeons often made immediate, “rushed” responses toward the bottom key location, despite the fact that second-choice behavior was far above

chance. This pattern of behavior suggests that the original error was not due to misinformation, but the intrusion of some other bias. A second study conducted in that same lab (Koban & Cook, 2009) found similarly strong bottom-key biases that made the interpretation of other experimental data difficult in some cases, similar to what we found here.

Of course, it is possible to attempt to train this bias out of pigeons; many experiments use four-key designs in which both bottom and top locations are used (or, more commonly bottom-left, bottom-right, top-left, top-right key arrangements). But, virtually every experimental design uses differential reinforcement to train the pigeons out of this strong location bias; although, even with extensive training, it may never altogether extinguish (see discussion of Cook, et al. 2005, above). So, it may be that the strong bottom-key bias that we observed in this experiment was simply unable to be counteracted by the unsupervised procedures we have applied in these experiments and was exacerbated by the close spatial proximity of the Link 3 terminal locations.

Rather than simply abandon this line of experiments, we wondered if the birds would express correct anticipation if we deconstructed the four-key task into two two-key tasks in which the pigeons could make left/right and top/bottom choices on separate trials.

Experiment 10

Experiment 9 uncovered a significant bias to peck the bottom key, even when it was not the congruent response. To discover the extent to which this bias interfered with learning, we next attempted to measure spatial anticipation using both the top/bottom and left/right pairs of keys on separate trials. A schematic representation of the design of this experiment can be found in Figure 29.

The rationale for this experiment was simple: if the bottom key bias interfered with learning even the left/right discrimination in Experiment 9, then

we should see quick signs of learning this discrimination in Experiment 10, or even direct transfer of what the birds had previously learned in Experiment 9. This direct transfer might occur if the birds had indeed learned about the predictive relationships between the texture stimuli and the upcoming Link 3 location, but were for some reason unlikely to express that learning due to the bottom key bias. Similarly, the bottom key bias should continue to exert influence during top/bottom trials, continuing to hamper performance on this discrimination.

The pigeons tested in these experiments were the same pigeons that had been originally trained to perform the four-key task in Experiment 9. Additionally, we kept the same assignments of textures and locations, to allow for the possibility of the direct transfer of unexpressed learning in Experiment 9.

Method

Participants. The pigeons were the four pigeons that had participated in Experiment 9, with identical housing conditions.

Apparatus. The same apparatus was used as in previous experiments 1, 3, 4, 5, 6, and 9.

Stimuli. The same stimuli and stimulus-response assignments were used as in Experiment 9.

Procedure.

Training. As the birds had participated in an earlier study, no additional shaping was required. Training was as in Experiment 9, with one exception. On trials in which the Link 3 stimulus would be located on either the left or right, only the left/right keys were shown; on trials in which the Link 3 stimulus would be located on either the top or bottom, only the top/bottom keys were shown. Training lasted for 10 sessions of 192 trials each (96 top/bottom trials, 96 left/right trials).

Results and Discussion

As can be seen in Figure 30 (top panel), three of the four pigeons initially started above chance with both the left/right and top/bottom keys. This transfer for three of the four pigeons was surprising, given the complete lack of discrimination found in Experiment 9. The last pigeon failed to discriminate the left/right keys even after extended training; its data were not included in further analysis. But, while the left/right discrimination for these three other pigeons remained high and above chance, as training progressed, the top/bottom discrimination once again rapidly plummeted to chance, with all of the birds again lapsing into position preferences to peck the bottom key (see Figure 30, bottom panel). An ANOVA (Session x Key x Bird as a random factor) revealed a highly significant effect of Key, $F(3,6) = 17.62, p < .001$. Here, the result was caused by poor performance on the top key. Post-hoc tests revealed a significant difference between performance on the top key (on average, below 50%) and performance on the other three keys (each above 90%).

As before, we also analyzed the two discriminations separately. An ANOVA (Session x Key Pair x Bird as a random factor) revealed a barely significant effect of key pair, $F(1,2) = 18.23, p = .05$. Of course, this difference between the key pairs was the result of comparing discrimination in which both of the individual keys was high (as in the left/right discrimination) with discrimination in which one of the keys was high and the other was low (as in the top/bottom discrimination). We suspect that this difference would have been exacerbated had we extended training in this experiment beyond 10 sessions.

Thus, Experiment 10 was successful in that we were able to re-establish the left/right discrimination when the top/bottom key pair had been removed, but it was unsuccessful in that we were unable to find any sustained evidence of anticipatory behavior in the vertical dimension.

As a final analysis of this data, Link 1 distributions for the three birds that performed above chance during left/right trials are plotted in Figure 31. Despite the smaller key size in Link 1 and nearer key distance for the Link 2 keys, both of which we know from previous experiments (i.e., Experiments 7 and 8) lessen the likelihood of observing anticipatory pecks, there was still an overall effect to anticipate in the congruent direction during Link 1. An ANOVA (Space x Response Direction x Bird as a random factor) conducted to analyze these trends revealed a significant Space x Response Direction interaction, $F(15,30) = 4.76, p < .001$, confirming the observed anticipation during Link 1.

Experiment 11

Despite our claims about prospection and spatial behavior shifting early in time (during Link 1), the fact remains that in all of our experimental designs, we *required* the pigeon to shift its behavior to some other spatial location in Link 2, forcing the pigeon to make a spatial shift in responding it might otherwise not make if given some other opportunity to respond. What might happen if we removed this forced shift prior to the presentation of the Link 3 stimulus? To answer this question, we made a major change to the response panel in Experiment 11 by presenting three keys in Link 2 instead of two keys. While the left and right keys would continue to be available in Link 2, we also added a third centrally located key that visually matched these other two side keys (See Figure 32). This design allowed the pigeon (if it was so inclined) to continue to respond to the central link stimulus during Link 2, shifting only after Link 2 in order to peck the Link 3 stimulus and receive food.

This is an experimental way of allowing the pigeon to “decide” when it might shift response location. As an analogous example in human behavior, consider walking from Spence Labs of Psychology down the street to Iowa Book. One possible route involves heading down Iowa Avenue and only choosing to

cross the road (i.e., move laterally in space) when arriving at Clinton St; a sort of “late street crossing” behavior. Another possible route involves immediately crossing the street outside of Spence Labs, and then walking down Iowa Avenue; a sort of “early street crossing” behavior.

Experiment 11 presents the pigeon with a somewhat similar arrangement of choices, as the pigeons have two “equivalent” routes to Link 3. In the first route, the pigeon could complete the FR to the Link 1 stimulus and then complete the Link 2 FR in the same central location, shifting to the location of the Link 3 stimulus only after completing both the Link 1 and Link 2 FRs in the center of the screen. As with the navigational example presented above, we might similarly label this behavior “late shifting.” In the second route to Link 3, the pigeon might complete the FR to the Link 1 stimulus and then shift to the congruent Link 2 stimulus before completing the Link 2 FR; once the bird has completed the Link 2 FR, it is then located in the appropriate spatial location to complete the Link 3 FR. We might similarly label this behavior “early shifting.”

To make this design as simple as possible, we returned to using colors (red and green) to signal the Link 3 locations. Otherwise, the most important methodological choice in this study was that we felt that we needed some cue to signal to the birds that Link 1 had ended and Link 2 had begun, otherwise, the pigeon might continue to peck the centrally located Link 2 key only because it simply had not noticed that the other Link 2 keys were available. We entertained two possible options for this cue. The first was the use of different stimuli in Link 1 and 2, similar to the “symbolic” task studied in Experiment 3. But, we considered this was a bad choice due to the poorer anticipatory behavior observed in that experiment, the difficulty of choosing equivalently discriminable stimuli for Link 1 and Link 2, and the unnecessary complication of introducing additional discriminative stimuli. The second possible choice was to use visually matching

stimuli in Link 1 and Link 2, but to insert a 0.5-s delay between each of the successive links, creating an observable “break” between the Link 1, Link 2, and Link 3 stimuli. Although there was reason to believe that the addition of this delay would disrupt the temporal contiguity between the Links and possibly create a different set of problems, we (perhaps naively) thought that the addition of this short delay was preferable to the use of different stimuli in Link 1 and Link 2. So, we added the 0.5-s delay between each of the successive Links that served as a visual cue.

Therefore, Experiment 11 takes a new route to investigating prospective, anticipatory shifts in behavior. While both the “early shifting” and “late shifting” patterns of behavior have presumptively equivalent delays to reinforcement (see Chapter 3) and spatial distances to reinforcement (as addressed in the current chapter), “early shifting” during Link 2 provides strong evidence for the anticipation of the upcoming Link 3 location, while “late shifting” might be expected if this anticipation did not occur.

Method

Participants. The participants were 6 feral pigeons with housing conditions identical to those in Experiments 1, 3, 4, 5, 6, 9, and 10. Three of these pigeons had previously served in Experiments 9 and 10, but were naïve to the stimuli used in this experiment. The other three pigeons were completely naïve animals that had never participated in any previous conditioning experiment.

Apparatus. The same apparatus was used as in previous experiments.

Stimuli. Three squares, 7.44-cm x 7.44-cm, were used as stimuli. Each of these stimuli occupied 250 square pixels of space on the monitor. These keys were a red square, a green square, and a black star on a white background.

Procedure.

Shaping. The non-naïve pigeons were presented with one session in which a random stimulus appeared in one of the three key locations used in Experiment 11 to acclimate the birds to pecking at each location and remove any potential response biases that might have been developed while the birds served in previous experiments. The naïve birds required 5-10 sessions of additional shaping to acclimate them to responding to the touchscreen.

Training. The basic experimental procedure was conducted as in Experiment 1, with minor changes. In Experiment 11, there were three response keys presented in Link 2 instead of two response keys.

In Link 1, colored keys signaled the location of the Link 3 stimulus (and the color of the Link 2 keys); in Link 2, green or red keys (as in Experiment 1) signaled the location of the Link 3 stimulus. As is depicted in Figure 32, any given pigeon had two different types of trials. In Link 1, one of two key colors was presented on the center key. Each of these key colors uniquely signaled the location of the upcoming Link 3 stimulus; e.g., Red might signal “left,” whereas Green might signal “right.” In Link 2, one of two different sets of colored squares was presented on the three keys; e.g., Red might signal “left,” whereas Green might signal “right.”

Data analysis. Data were analyzed as in Experiment 1. For this experiment, Discrimination Ratio was calculated as the total number of pecks to the congruent side over the total number of all other pecks for that trial type; this meant that chance in the experiment was 33% rather than 50%, and had the further implication that pecks to the center key were always scored as incorrect. Last, because the fully naïve pigeons had difficulty completing sessions early in training even after extra shaping, sessions in which at least half of the 128 scheduled trials were completed were scored for analysis.

Results and Discussion

The procedure with three keys in Link 2 produced essentially one pattern of results: all of the birds adopted an “early-shifting” strategy over training, with the caveat that one bird developed a strong position preference. The acquisition functions for each bird are shown in Figure 33. Because we thought that there might be a difference between naïve and non-naïve pigeons, we first examined their data separately. Taking the non-naïve birds first (Figure 33, top panel), two birds (28Y and 72Y) acquired this discrimination similarly to birds in Experiment 1, producing mainly congruent responses by the 10th or 12th session. A third bird (8B) produced moderately better than chance discrimination, though it was strongly affected by an extreme side bias to one of the three keys; but still, this bird rarely pecked the center key during Link 2 late in acquisition. This bird’s behavior can be summarized as a very slight bias to correctly anticipate. The naïve birds (Figure 33, bottom panel) also showed a strong tendency to “shift early”. Although one bird (33W) showed a relatively protracted learning curve, the other two birds (24Y and 38R) quickly learned to “shift early” and peck the congruent key in Link 2. Therefore, to summarize: no bird persistently chose the center key in Link 2 despite the availability of making that response, and four of the six birds tested chose to respond congruently.

To confirm the effects of learning in this experiment, we ran a mixed-model repeated measures ANOVA (Session x Experience x Bird as a random factor) on the discrimination scores for each pigeon. Previous experience (naïve vs. non-naïve) had no statistically measurable effect on the discrimination. There was, however, a statistically reliable effect of Session, $F(11,44) = 6.45, p < .01$, confirming an increase in discrimination ratio over the course of the 12 testing sessions.

Given this lack of difference between the naïve and non-naïve animals, we pooled their data for the next analyses. The first of these analyses more closely

examined the response strategy that the birds used. This analysis is useful because there are two possibilities for how the “early shifting” strategy might have developed. One developmental trajectory would have been a shift from random responding to “early shifting”; the other trajectory would have been a shift from “late shifting” to “early shifting”. Figure 34 shows the average response strategy adopted by each of the six birds across the 12 sessions of acquisition. Data from the first session seem to indicate a stronger preference for making “late shifting” responses than “early shifting” responses; over time, this initial bias quickly gave way to an “early shifting” strategy. A repeated measures ANOVA (Response Strategy x Session x Bird as a random factor) conducted to analyze these data revealed an interaction between Response Strategy and Session, $F(22,110) = 5.20$, $p < .001$. To more closely examine the first session, a planned contrast was run between the early and late strategies in this session. Here, the data revealed a significant preference for late over early shifting, $F(1,110) = 5.17$, $p < .05$. A similar contrast between “late shifting” and incongruent responding was also completed, $F(1,110) = 6.89$, $p < .001$. So, interestingly, and only predominantly in the first session, the birds were initially inclined to make “late shifting” responses. Then, they quickly changed to an “early shifting” response strategy, with planned contrasts revealing a significant difference between these strategies in the opposite direction (i.e., more “early shifting” than “late shifting”) by the third session, $F(1,110) = 22.23$, $p < .001$.

We also analyzed Link 1 responding during this interval, plotted in Figure 35. Interestingly, despite good Link 2 data, Link 1 responses were completely non-diagnostic of the birds’ future response location, with mean response probabilities only barely diverging from 50%. Additionally, these poor data were not caused by averaging poorer birds with more anticipatory birds; no bird showed a consistent Link 1 trend. We can think of two main possibilities for this

trend away from showing anticipatory behavior in Link 1. One possibility is the insertion of the delay between Link 1 and Link 2, which we had never done in any of the previous experiments. This disruption of temporal contiguity may be critical for the expression of spatial anticipation to the central key. Another possibility is the availability of a Link 2 response at the Link 1 response location. It could be that the acquisition of this anticipatory behavior is slowed or disrupted if responding perseverates on the central location in Link 2, a statistically reliable bias that all of the birds showed early in training. Future experiments will be required to address this curious pattern of data.

Chapter Discussion

The experiments in this chapter revealed a set of important findings about how spatial parameters of the response panel influence anticipatory responding in this task. First, Experiment 7 disclosed that responses in Link 1 and Link 2 appear importantly controlled by the spatial distance of the Link 2 or Link 3 keys from the Link 1 key; when the rats were required to make responses to far keys, they showed higher discrimination ratios in Link 2 over the course of training (and showed correspondingly higher Rho values in Link 1) than when those rats were required to make responses to near keys (and showed correspondingly lower Rho values in Link 1).

One open question is how to reconcile this distance effect with the contiguity effects observed in the second chapter. It may seem that this distance effect might be due to stimulus representation issues (i.e., Eckerman, 1970; Brown & Huggins, 1993) rather than those directly related to spatial contiguity per se. These issues will be more fully addressed in the General Discussion (see the section on “Returning to Dynamics”).

Experiment 8 revealed that the rats were sensitive to the dimensions that underlie the stimuli; when transferred to novel values of brightness and

orientation, the rats showed highly typical graded generalization gradients. Furthermore, the rats showed highly correlated Link 1 and Link 2 behaviors during these generalization tests; rats made “intermediate” levels of Link 1 responses to those stimuli to which they also made “intermediate” levels of Link 2 responses. The preceding term intermediate is in quotes because in both cases the rats essentially make binary decisions; the rats do not really make centralized Link 1 responses to intermediate stimulus values. Rather, they tend to make different proportions of leftward and rightward directed Link 1 reports, indicating that the spatial generalization gradient of Link 1 reports is an averaging affect (much like the generalization gradient of Link 2 reports). This result is consistent with previous demonstrations that generalization data tend to be based on the probabilistic distribution of responses (Shepard, 1987) rather than the production of average responses during generalization tests (Migler, 1964). Again, these issues will be more fully addressed in the General Discussion (see the section on “Returning to Dynamics”).

Next, we learned that four key anticipation tasks using pigeons appear nearly impossible to conduct, because the bottom key so powerfully attracts responding. Despite extended training with stimuli that had previously supported discriminative responding, Experiment 9 found no evidence that the birds were able to overcome their “key preference” for the bottom location. This failure was disappointing to us, because it precluded us from using other four-key designs in which we treated the horizontal and vertical keys as orthogonal response dimensions.

But, the failure in Experiment 9 did prompt us to try something new in Experiment 10, which did reveal interesting data. When the birds were transferred from the failed four-key task in Experiment 9 to the two two-key tasks in Experiment 10, they showed almost perfect transfer to the left/right pair of keys

despite showing virtually no responding on those keys during Experiment 9. Thus, there is an interesting learning/performance distinction (see Wasserman, 1981) that occurred in Experiment 9. It appeared as though the birds may have learned something about the serial associations between stimuli in Experiment 9 (e.g., “When the flowers texture is present, the Link 3 key will appear on the right”), but were unable to express this learning due to a large bias to choose the bottom key. When this bottom-key was removed, the birds were immediately able to express what they had learned about the left/right pair of keys in their prior training.

This kind of preserved anticipatory performance even in the face of a strong bias to respond elsewhere might be considered similar to the performance of birds in autoshaping tasks that were prevented from approaching the keylight due to a physical barrier. In those experiments, Moore (1973) gave otherwise regular autoshaping trials to birds that could not actually peck the key (and were thus prevented from learning an instrumental relationship between keypecking and food delivery). But, once the barrier removed, 8 of the 9 subjects tested in that experiment began to respond to the keylight immediately.

The three-key task used in Experiment 11 presented an interesting pattern of data. Here, birds that were forced to initiate a trial at a central location in Link 1 could evidence two sensible patterns of behavior: either an anticipatory “early-shifting” bias, choosing to preemptively shift toward the location of the Link 3 response and make their Link 2 responses on that side of the chamber, or, a “late-shifting” predisposition, choosing to simply carry out their Link 2 pecks on the central key at which they were already located and then shifting to make their Link 3 response. Either would seem a perfectly good strategy for responding in a nondifferential reinforcement procedure; after all, “shifting early” vs. “shifting late” confers absolutely no advantage in terms of distance or time to

reinforcement. From the birds we have run on this task, we found evidence that most birds demonstrate anticipatory “early-shifting” behavior in these three-key tasks similar to that demonstrated in two-key tasks, despite the sufficiency and availability of the “late-shifting” strategy. Additionally, the analysis of these data indicates that despite a learned tendency to use an “early-shifting” strategy, the birds all began with a “late-shifting” strategy. This fact is important because an account which explained this behavior through adventitious or superstitious reinforcement should suggest that the preservative responding that is observed in the “late-shifting” strategy should persist (as all trials end in food). Nevertheless, the “early-shifting” strategy still develops.

Thus, it appears that there is strong evidence that “early-shifting” is the default behavior chosen by pigeons in these three-key tasks. This result offers strong support for the contiguity hypothesis advanced in Chapter 3. If time-to-reinforcement were the critical variable that controlled behavior in these tasks, one might imagine little-to-no “early-shifting” behavior, or at least no marked preference for “early-shifting” over “late-shifting” behavior. On the other hand, this “early-shifting” behavior is completely consistent with the contiguity between the Link 2 stimulus and Link 3 stimuli as the critical relationship that controls key choice behavior.

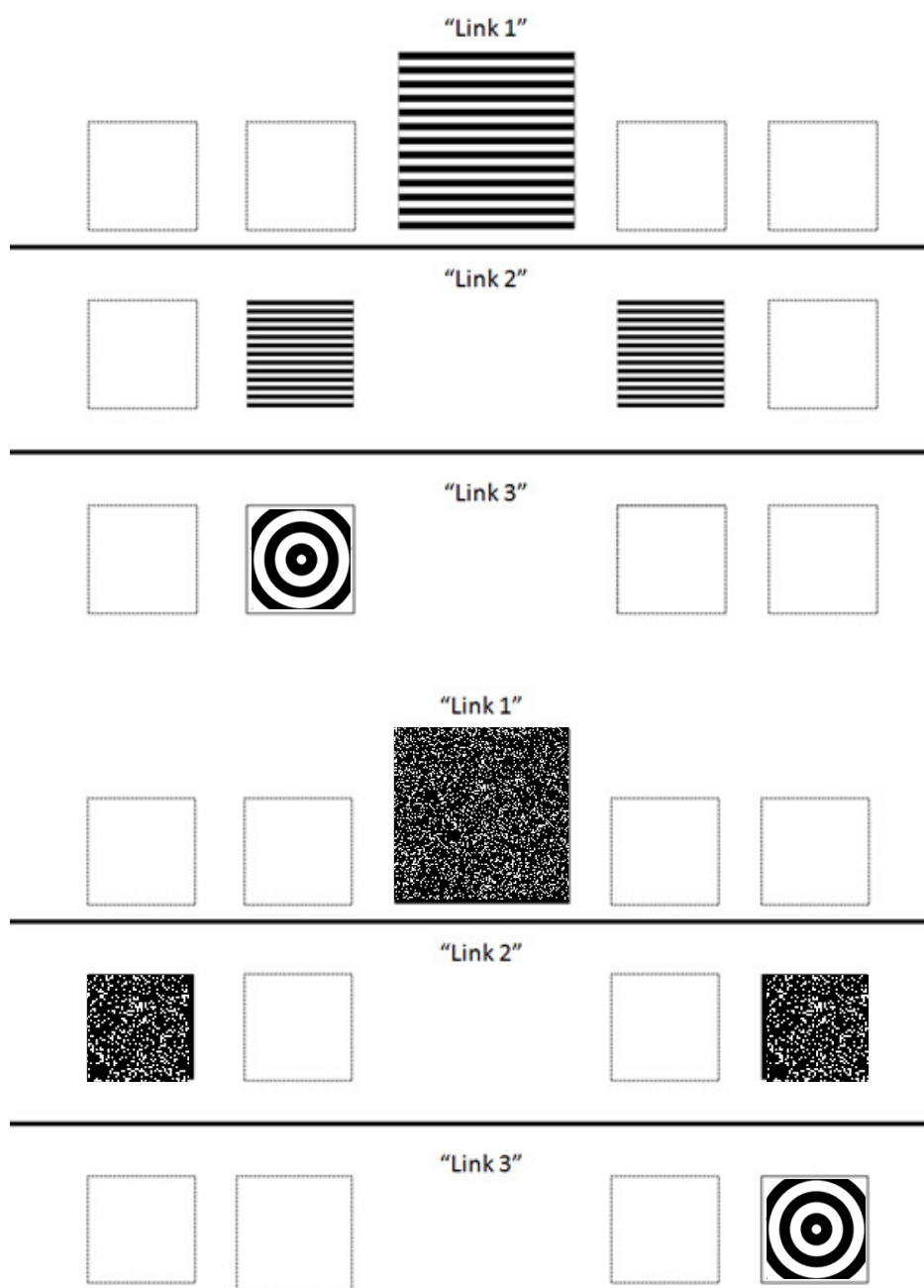


Figure 23 – A representation of the task in Experiment 7 and 8. Each trial consisted of three separate Links as in previous studies; reinforcement we delivered after the completion of all three Links. Separate dimensions cued different spatial locations; e.g., one dimension (shown here, orientation) signaled a “near” Link 2 and 3 location; the other dimension (shown here, brightness) signaled a “far” Link 2 and 3 location. The blank white squares are provided as a reference for the reader and were not actually visible to the rats during the task.

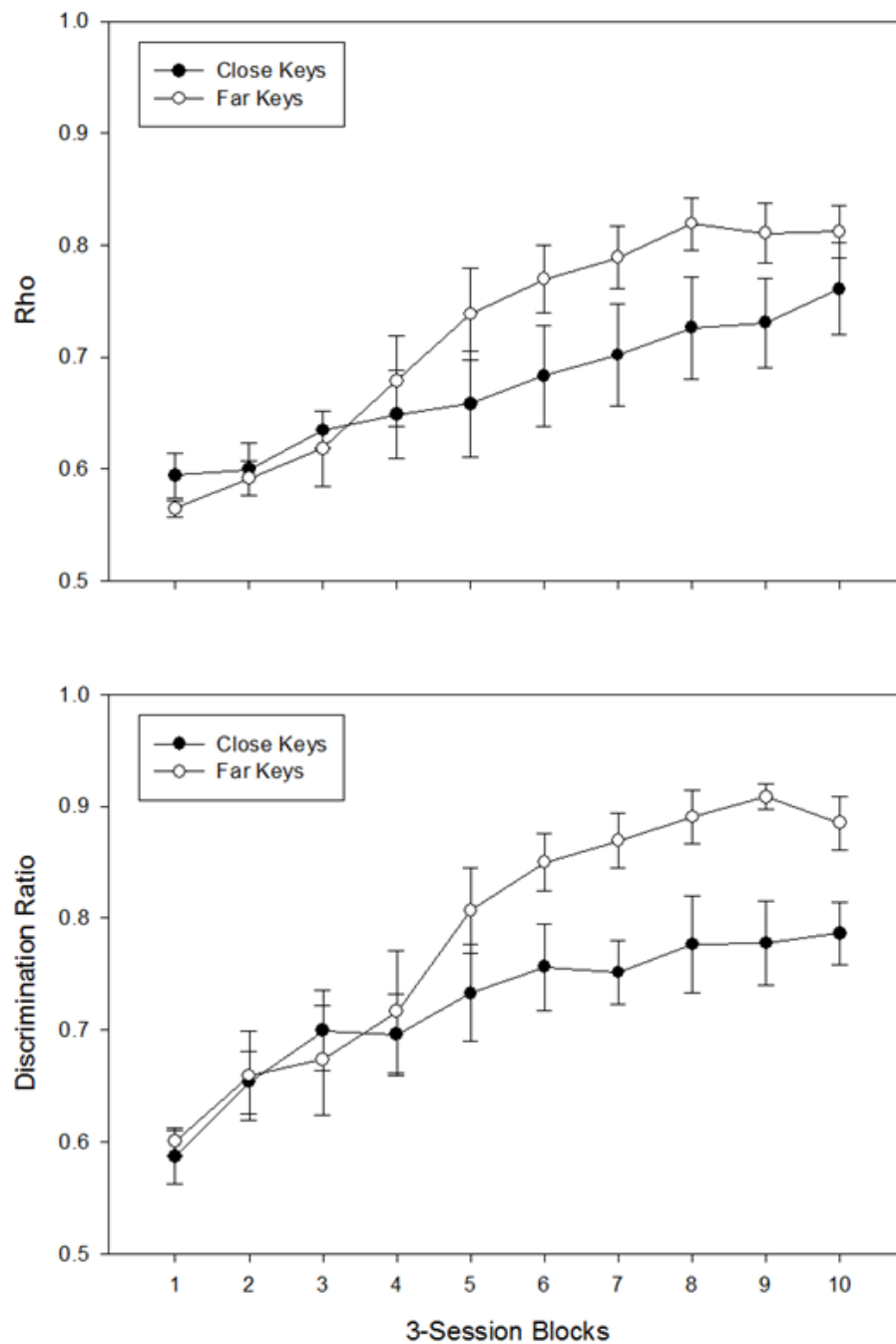


Figure 24 – Discrimination Ratio and Rho during Experiment 7. Rho (Top panel) and Discrimination Ratio (Bottom panel) from Experiment 7. In both cases, there was a significant interaction of key distance and session.

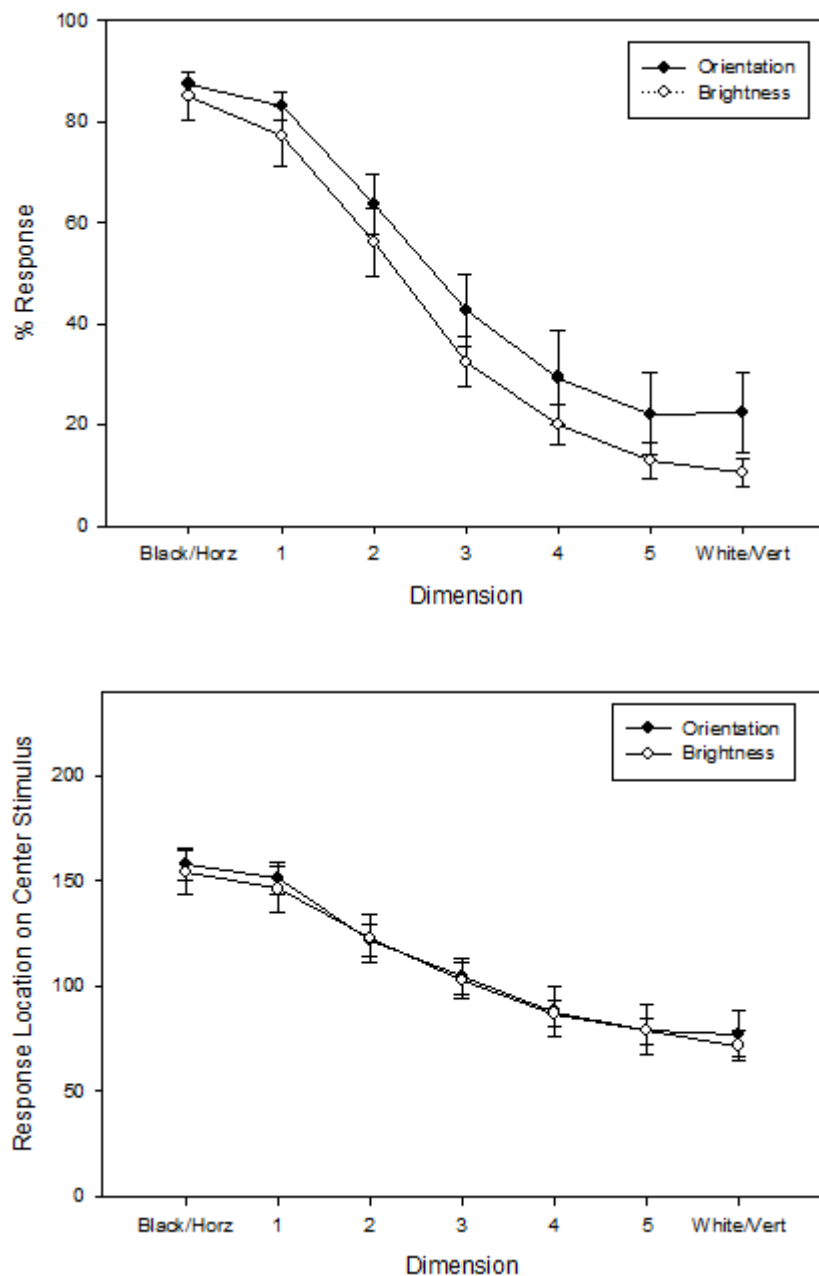


Figure 25 – Generalization data from Experiment 8. The top panel shows generalization during Link 2 as a function of choice; the bottom panel shows generalization in response location on the Link 1 key.

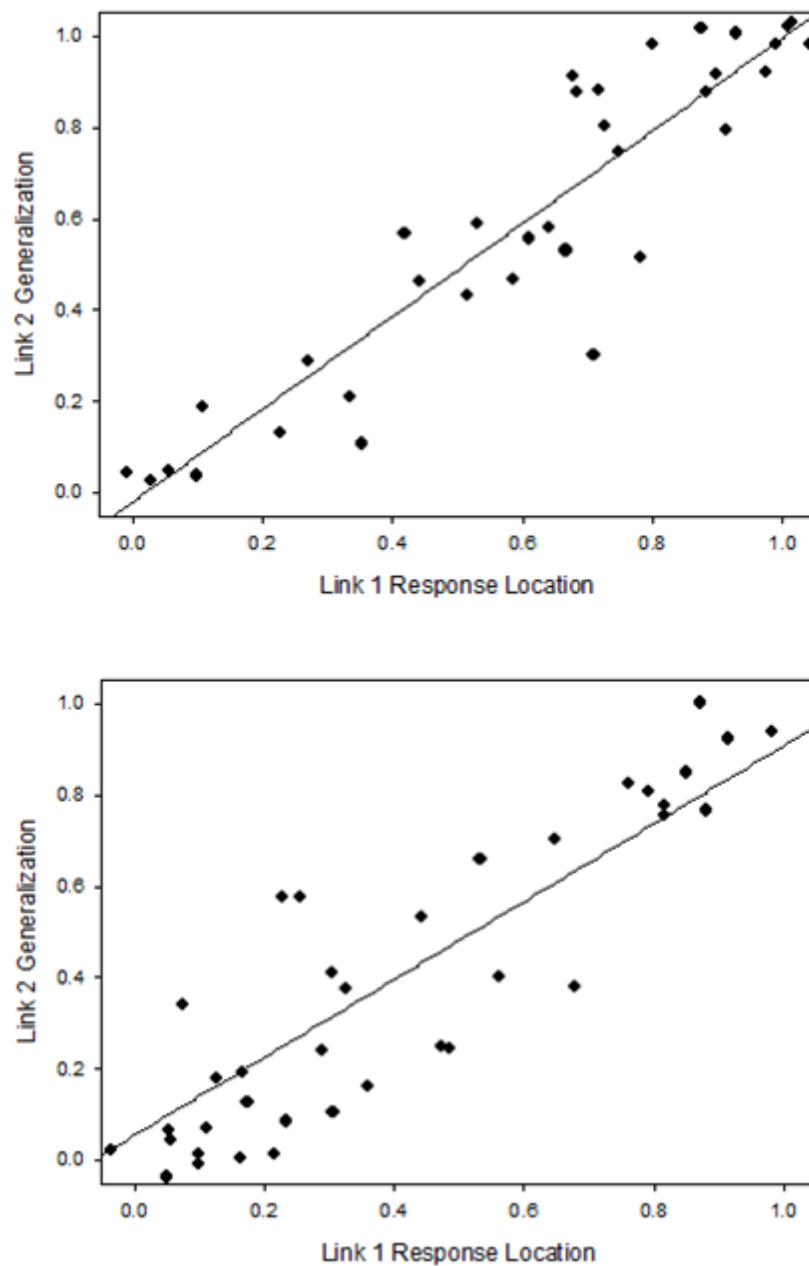


Figure 26 – Correlation between Link 1 and Link 2 reports in Experiment 8. The correlation for individual animals between Link 1 response location and Link 2 generalization data for Brightness (top panel) and Orientation (bottom panel) during Experiment 8.

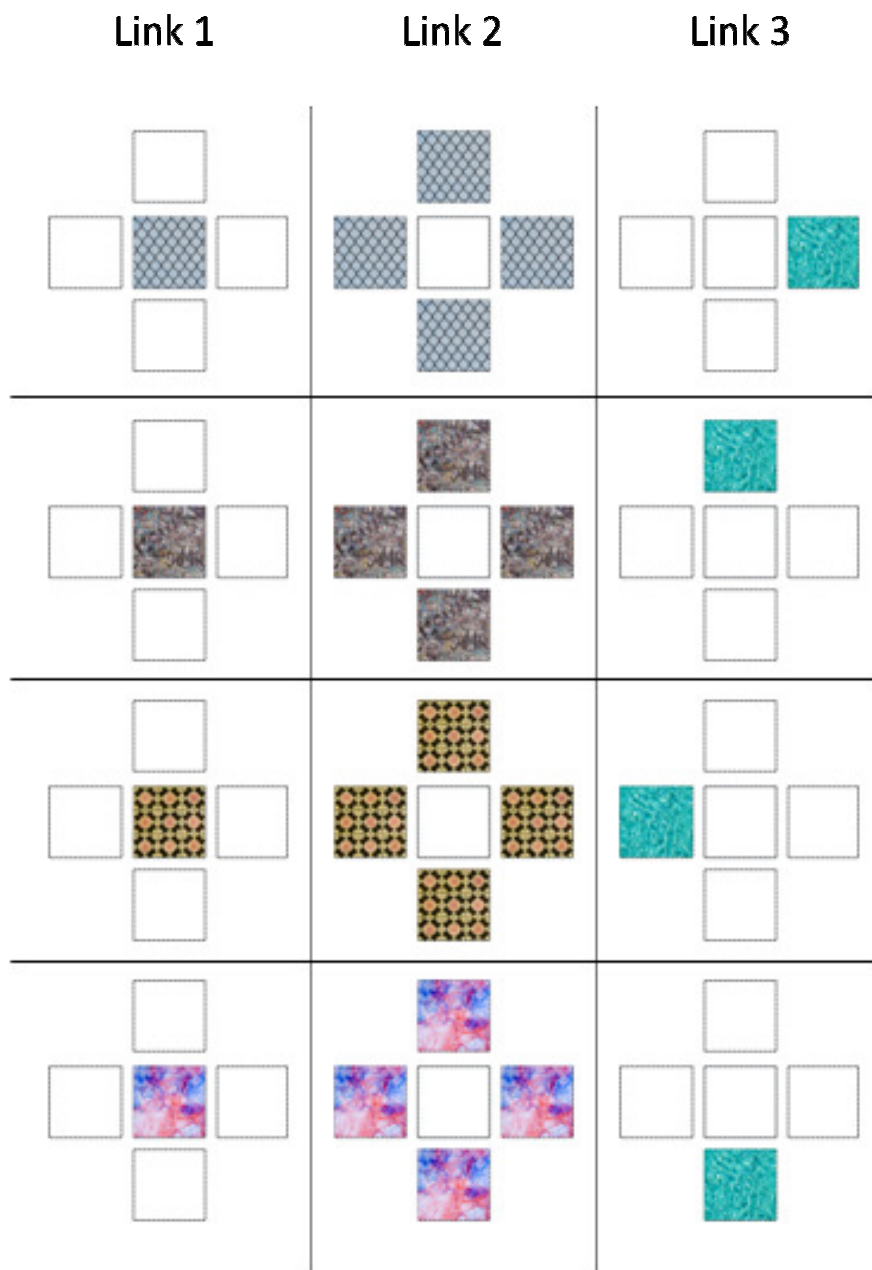


Figure 27 - Schematic Representation of the Four Key Task used in Experiment 9. Each trial involves three displays, which progress from left to right. Four representative trials are shown; one for each response location. The white keys were unrepresented to the animals; they are included simply to facilitate the reader's understanding of the design.

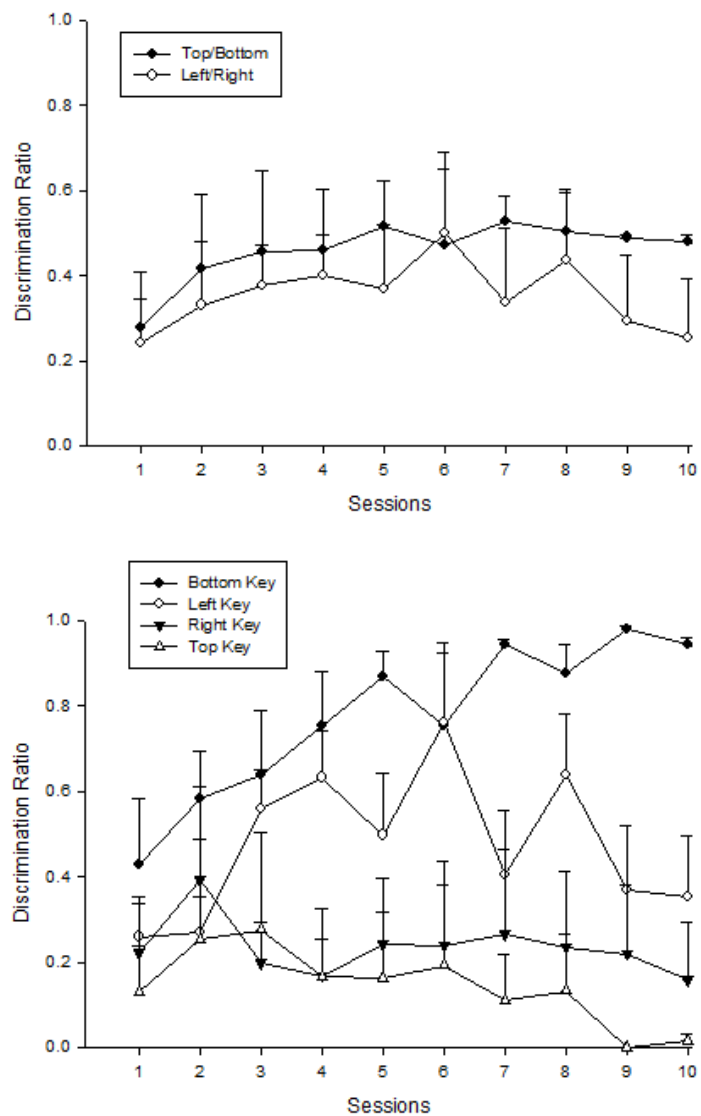


Figure 28 - Data from the Four Key Task used in Experiment 9. Overall discrimination was poor (top panel), mainly caused by the largely evident bottom key bias (bottom panel), the reason for which is unclear.

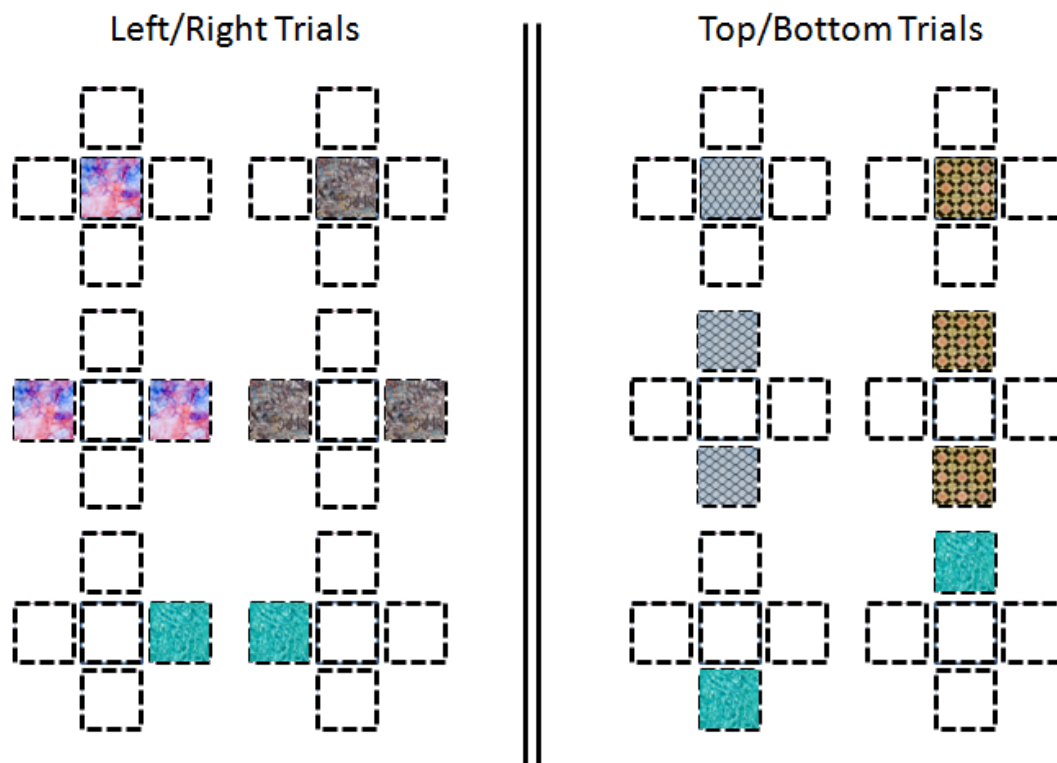


Figure 29 – Design of the two two-key tasks used in Experiment 10. Animals received trials in which the left and right keys were lit in Link 2 (left panel) or in which the top and bottom keys were lit in Link 2 (right panel). The white keys were unrepresented to the animals; they are included simply to facilitate the reader's understanding of the design.

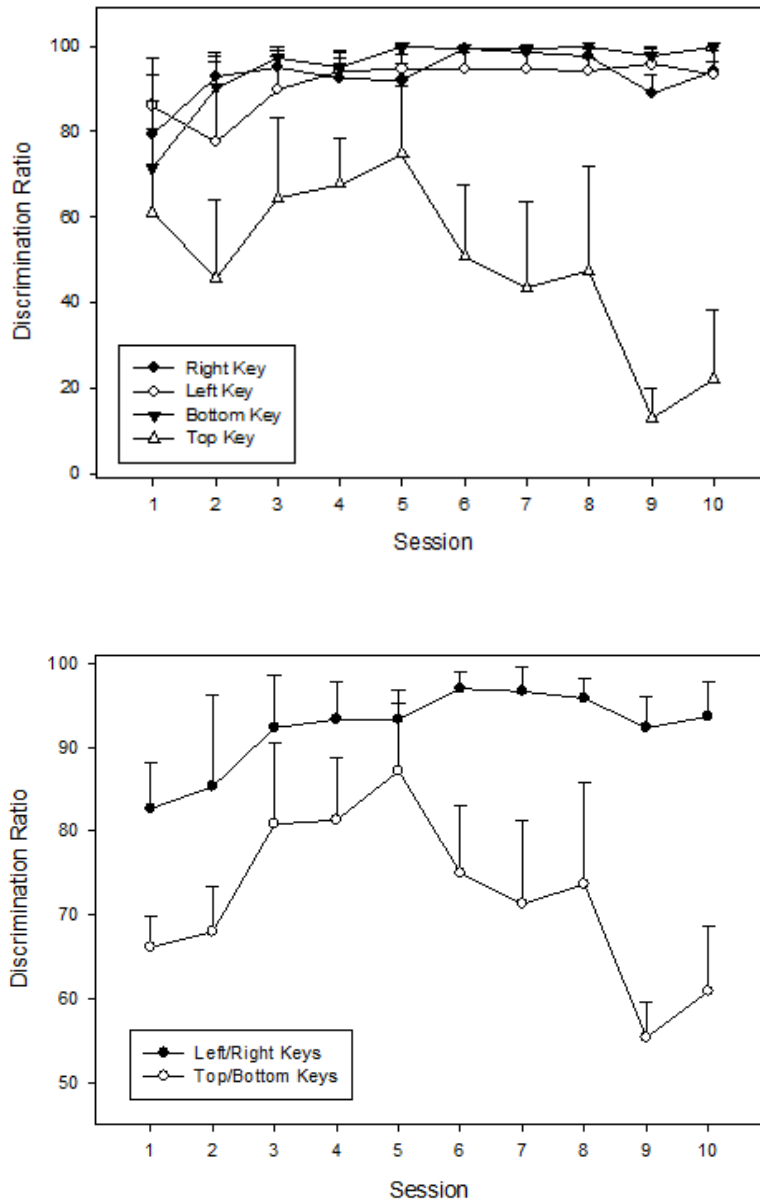


Figure 30 - Data from the two two-key Tasks used in Experiment 10. The top panel shows data from each key location; note that all start above or initially at chance, but that the bottom key bias quickly reasserts. This leads to good discrimination in the left/right discrimination, but poor discrimination in the top/bottom discrimination (bottom panel).

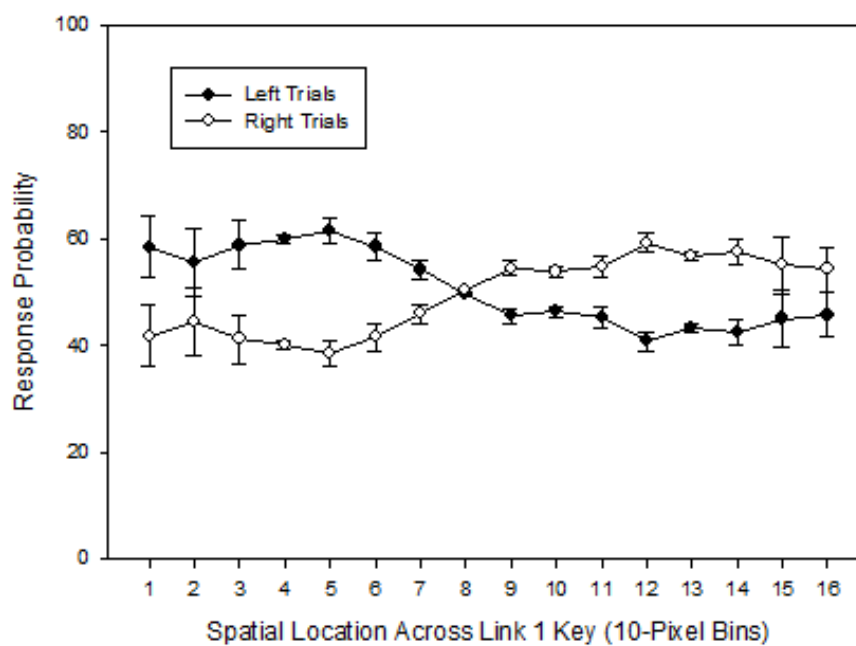


Figure 31 – Response probability across Link 1 key in Experiment 10. Data from Experiment 10 for the three pigeons that showed signs of learning the left/right task. Overall, Link 1 anticipation was poor, but key distance and key size may have been important factors.

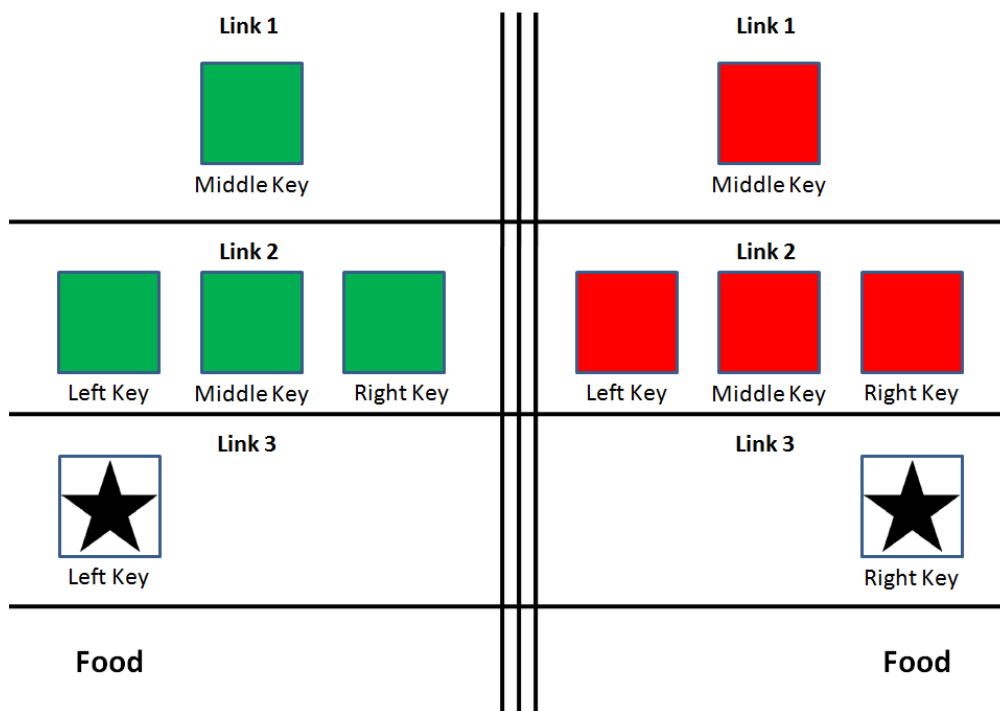


Figure 32 - Schematic representation of trials in the Three Key design used in Experiment 11. Each trial consisted of a central Link 1 stimulus followed by three Link 2 stimuli, one of which occupied the same spatial location as the Link 1 stimulus. This afforded the birds the opportunity to “stay” during Link 2 or “switch” during Link 2. See text for details.

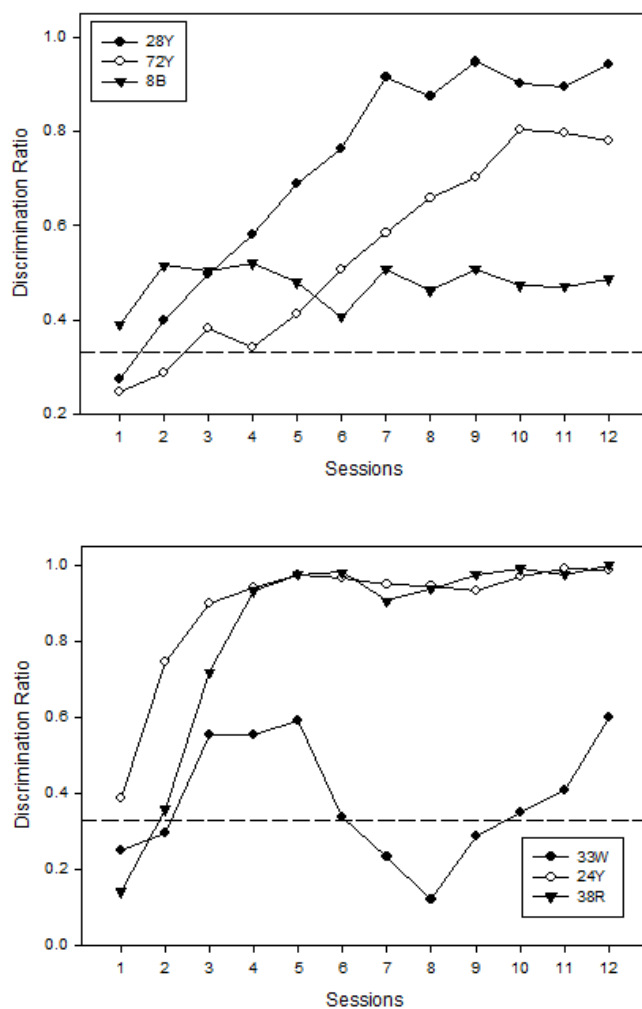


Figure 33 – Discrimination ratio for each bird in Experiment 11. Congruent responses were coded as responses that were on the same side as the Link 3 report response for that trial type; all other responses were incongruent. *Top Panel:* Non-naïve pigeons. *Bottom Panel:* Naïve pigeons.

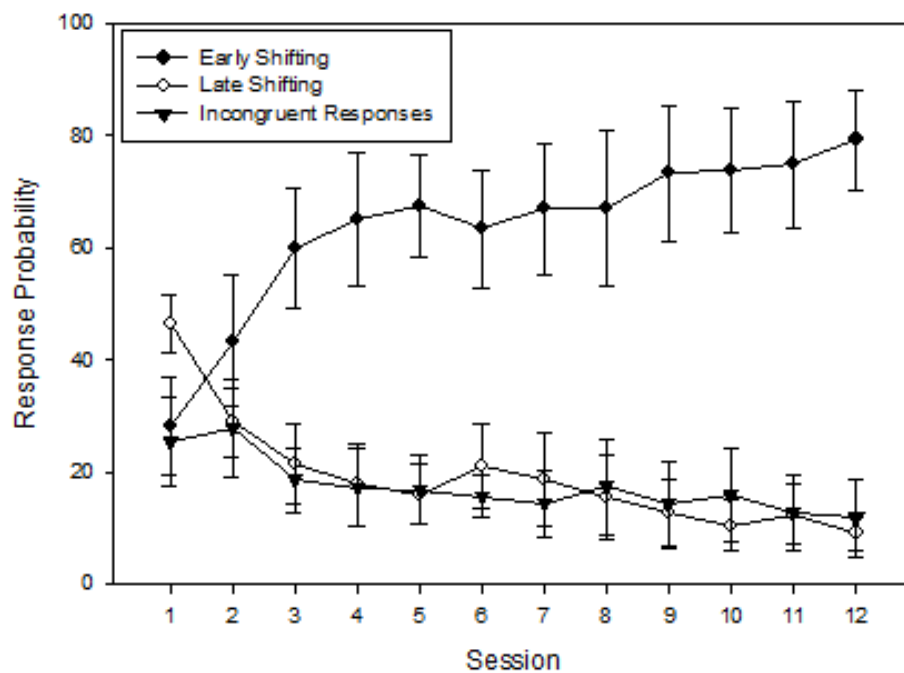


Figure 34 – Response strategies in Experiment 11.

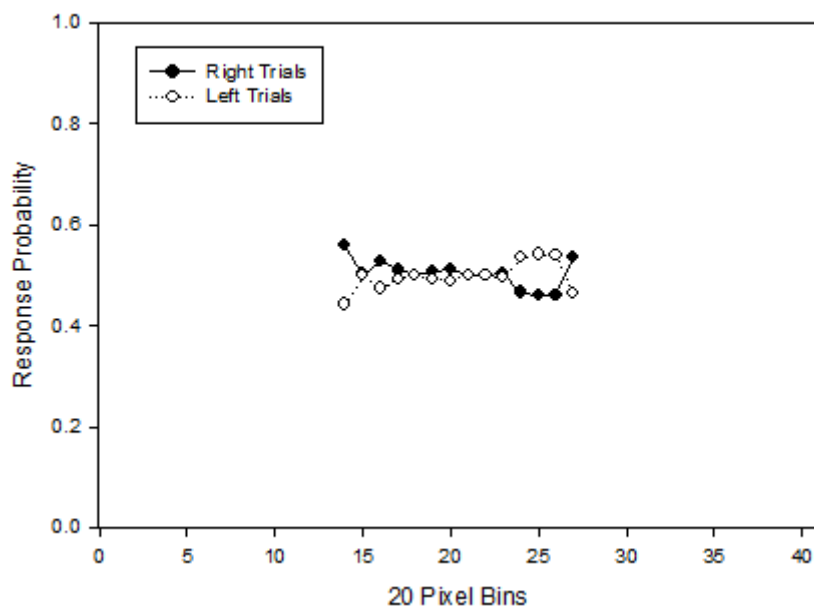


Figure 35 - Link 1 Responses during Experiment 11. There was no evidence of anticipatory responding during Link 1 in this task; possible explanations are discussed in the text.

CHAPTER 5

THE INITIAL AND TERMINAL OPERANT RESPONSE

Chapter Introduction

Instrumental conditioning differs from Pavlovian conditioning in numerous ways, but one important way concerns the measurement and choice of the behavioral response emitted by the organism and collected by the researcher. In Pavlovian conditioning experiments, the stimulus is provided by the researcher, but the response is determined “by the organism”; the researcher is left (sometimes in futility) to track and monitor the correct behavior (be it freezing, key pecking, heart rate increase, salivation, etc; see Schwartz et al., 2002; or Jenkins, 1973, for a review). Some advances in the study Pavlovian conditioning (especially those related to autoshaping or serial conditioning) have concerned the measurement of novel or otherwise overlooked behaviors. For example, Holland (1977), studying rats, found that the responses to autoshaped lights were behaviors such as rearing or magazine entry whereas the responses to auditory CSs were often startle responses, head jerks, or magazine entry. And, as has been discussed numerous times, Wasserman et al. (1978) measured the location of a pigeon’s keypeck response in addition to the rate of that keypeck response.

Dissimilar from Pavlovian conditioning, both the discriminative stimuli, the to-be-produced responses, and the available reinforcer (i.e., the three-term contingency; Skinner, 1953) are explicitly proscribed by the researcher in operant conditioning. These linkages are essentially arbitrary, and so operant responses can take many forms (but, see Moore, 1973, for a discussion of the non-arbitrary nature of many operant responses). Some operant responses are common to animals: in pigeons, pecking keys, hopper insertion (e.g., Cook & Smith, 2006), or treadle stepping (e.g., Smith & Keller, 1970); in rodents, nose poking (e.g.,

Fountain, Krauchunas, & Rowan, 1999), sand digging (e.g., Bunsey & Eichenbaum, 1996), lever pressing (e.g., Yokel & Wise, 1975), or platform finding (e.g., Morris, 1984); in chickadees or other small birds, perching or vocalization production (e.g., Sturdy & Weisman, 2006); in monkeys, eye fixation or button pressing (e.g., Mruczek & Sheinberg, 2007) ; in dolphins, paddle pressing (e.g., Smith, Schull, Strote, McGee, Egnor, & Erb, 1995); etc. Many of these responses are relatively uncommon parts of the organism's typical behavioral repertoire. As an example, rats may not naturally approach and press a lever with a single forepaw, yet will do so following operant conditioning. This list of possible behaviors is, of course, not exhaustive; virtually every conceivable behavior performed by every animal is able to be conditioned with the techniques of operant conditioning. [Although, there are many peculiar examples of behaviors that are difficult or impossible to condition, e.g., moving away from a food source to obtain food (Herschberger, 1985); teaching dogs to yawn for food (Konorski, 1967); conditioning pigeons to preen for food (Hogan, 1964), etc. A wonderful review of these violations of Thorndikian conditioning can be found in Hinde (1973), though these may often reflect differences in performance rather than differences in learning, as often expressed in that text, see Wasserman, 1981.]

Whereas a large or detailed review of the similarities and distinctions between Pavlovian and Operant conditioning are beyond the scope of this document (but are well discussed in many texts on learning, see Pearce, 2008 or Schwartz et al., 2002 for a complete discussion of these issues), we feel that it does make good sense to take a wider vantage on the experiments that have been conducted so far and consider both the nature of these presumptively anticipatory keypecks (or nose pokes, for rats) and the terminal responses that these former keypecks (or nose pokes) anticipate.

Despite the seemingly enormous variation in the kind and quality of operant behaviors that can be trained and tested with animals, in each of the eleven studies presented thus far, many of the responses produced by the animals have been of a highly similar form. In fact, we might say that the two most important responses have been equivalent: the tracked anticipatory responses (i.e., Link 1 and Link 2 behavior) and terminal responses (Link 3 behavior) have both been equivalent in each study. Pigeons have produced anticipatory keypecks toward the location of a future keypeck; rats have produced anticipatory nose-pokes toward the location of a future nose-poke.

The astute observer might therefore question if the observed phenomena are observed only when these two responses are equivalent. Skinner (1969) might not have been particularly concerned with this odd arrangement, given that his main concern with the definition of an operant was an “action on the environment” and “its probability of occurrence” rather than “its topography.” But, when the topographies of all of the presented behaviors are so strikingly similar, one might question whether the anticipatory responses would indeed be generated by responses that had different initial and terminal forms. Indeed, one might question whether the anticipatory pecks were simply fractional or preparatory in nature (Hull, 1931) or the occurrence of “mistimed” goal-directed pecks toward the location on the touchscreen of the terminal response.

Unfortunately, due to the nature of our current response apparatus and subject pool, we are limited in the nature of the responses that we can collect. In fact, both our rat and pigeon chambers were built using the same basic design specifications (Gibson et al., 2004), and so recording non-touchscreen responses was unfeasible. Thus, our current ability to answer this question in our lab is somewhat limited by our technology.

However, as we have previously mentioned, other types of responses are sometimes collected in the course of research with pigeons. One commonly collected response is the insertion of the head into the food hopper, which is a sort of odd pigeon equivalent of the rat nose poke. Using this method, the pigeon's response is measured using infrared LEDs when it directly inserts its head into a small enclosure that contains a retractable grain hopper, which is immediately activated upon the production of the choice response. Of course, pecking is involved (the pigeon immediately pecks grain following correct responses), but the functional operant is the hopper insertion response.

As previously mentioned, the Comparative Cognition Laboratory at Iowa does not currently have any such devices. But, the Comparative Cognition Laboratory at Tufts University has several of these devices installed in operant chambers that also have touchscreen devices. So, we asked if it might be possible to analyze data from a project in which both touchscreen and choice-hopper devices were used. To our knowledge, only one study (Cook et al., 2005) had previously examined a similar distribution of initial pecks toward the location of an upcoming response in a forced-choice task when hopper insertion was the terminal choice response. There, the location of pigeons' first peck at a pictorial stimulus predicted choice accuracy in a study of long-term visual memory, thus providing the researchers with a diagnostic measure for the reaction time of picture recognition. But, the spatial distribution of these pecks was not measured with a similar level of detail as has been conducted over the course of these dissertation experiments, and pecks beyond the first peck were not analyzed.

Therefore, Experiments 12 and 13 are a re-analysis of some parts of two previously published projects by Cook and Smith (2006) and Cook, Levison, Gillett, and Blaisdell (2005) that uses data collected with their operant chambers equipped with both infrared LED hoppers and touchscreens. Briefly, each of these

studies consisted of the presentation of a single picture. Pigeons were required to make a number of observing responses (i.e., FR pecks) to this stimulus prior to making a head-insertion response into one of two hoppers located on opposite sides of the chamber to indicate their classification of the object. Although the central experimental questions in each study were not particularly relevant to the broader issues presented in this dissertation, each study did involve the presentation of single object on each trial; it involved a touchscreen-based FR to these objects on which response locations could be measured; and it required a lateralized choice response, though this response was in the form of a hopper-insertion and not a keypeck response. So, we considered these studies to provide an ideal context with which to evaluate the production of anticipatory keypecks in the absence of a terminal keypeck response.

There were two other reasons to request these particular data for analysis. The first was somewhat theoretically uninteresting, but fundamentally important for future experimenters who might investigate anticipatory peck responses. Simply put, how general is this phenomenon? Can we observe it in other datasets? These two projects would provide especially nice convergent evidence because they use richer visual stimuli than the simple ones chosen for our own experiments. The second reason to request these data more specifically concerns exactly the use of feature-rich visual stimuli. Whereas previously reviewed studies (Allan, 1993; Dittrich et al., 2010) had each reported that peck location tracked the discriminative features of visual stimuli, both had run go/no-go type tasks in which this feature-tracking behavior could not interact with the production of an upcoming spatial response. So, these re-analyzed data might be able to address whether pigeons in visual discrimination tasks peck preferentially at regions of the display that mediate discrimination performance or at regions of the display that are diagnostic of their upcoming response location.

Experiment 12

As previously mentioned, this study was conducted by Cook and Smith (2006) a number of years ago at Tufts University; the data were collected for re-analysis. Therefore, a number of the methods diverge from those used in other experiments in the dissertation. Despite these differences, we thought that these data were worth including in this dissertation due to its unique ability to answer the above question about the form of the terminal operant response. A complete description of the results and methodology of this original study can be found in Cook and Smith (2006); only the relevant details will be reproduced here.

[Note: Although this analysis is being presented as a separate Experiment, I was not involved in the design, execution, or data collection of this experiment. I requested these data for re-analysis because I thought that they might answer an important methodological concern. Permission has been obtained from the authors of the original study to re-analyze these data and include them in this document.]

Method

Participants. The pigeons in this study were five male silver-king pigeons. They had performed previous visual discrimination tasks that were unrelated to the current task. They were maintained at 80-85% of their body weight, and kept in a pigeon colony with a 12-h light/12-h dark schedule with free access to water and grit.

Apparatus. Pigeons were tested in a black chamber (38 x 36 x 38 cm) controlled by a microcomputer. Stimuli were presented on a color monitor (NEC MultiSync C500; 800 x 600 resolution) visible through a window in the chamber's front panel. Pecks to the monitor were detected by an infrared LED touchscreen (Elotouch Systems, Menlo Park, CA). A ceiling houselight was illuminated except during time-outs. Identical food hoppers (Coulbourn #E14-10) were located in the chamber's right and left walls, 3 cm from the front panel.

Infrared LEDs mounted 2.5 cm in front of each hopper detected the bird's approach and indicated its choice of hopper. The right and left hoppers, respectively, contained mixed grain and safflower.

Stimuli. Fourteen colored pinwheels were used as stimuli; only trials in which two types of stimuli (the "Prototype" stimuli) were shown were re-analyzed in this Experiment (see Figure 36). These pinwheel stimuli had six identically sized colored slices that were colored according to a scheme that created two distinct perceptual categories. Prototype stimuli differed from one another in each of these colored slices, making them perfectly representative of the two categories.

Procedure.

Training. As the birds had participated in an earlier study, no additional shaping was required. Pigeons were first required to peck at a 2.5-cm central white disc to indicate trial readiness; one of the 14 stimuli was then presented. Following 10 observing pecks to this stimulus, lights inside of each hopper illuminated to indicate that they could be entered (as choices). Choices of the correct hopper produced 2.3-s access to the grain from that hopper; choices of the incorrect hopper produced a 5-s dark timeout. A 3-s ITI followed either outcome.

Sessions comprised 112 trials organized into 14 trial blocks. Correction procedures followed incorrect responses during the first block of each session; responses during correction trials were not scored and peck data from correction trials were not re-analyzed.

Analysis Plan

The learning data from this experiment (and resultant classification of the various stimuli tested in this study) have been described in detail by Cook and Smith (2006). Therefore, this report will focus on the anticipatory reports made during the final four sessions from each bird's classification of these stimuli.

Additionally, this report will focus primarily on the Prototype trials, as these represent trials that most closely resemble those tested in the earlier experiments.

Results and Discussion

During the final four sessions of each bird's categorization performance on the prototype trials, classification performance was quite high; the five birds tested had a mean classification performance on these trials of 92.81% correct.

The peck data from these correct trials were pooled for examination. The top panel of Figure 37 shows the cumulative responses emitted by the birds for trials which required either right or left hopper insertions; there was a clear bias in favor of making rightward directed anticipatory pecks on trials in which the upcoming hopper insertion would be in the right hopper, whereas there was a clear bias in favor of making leftward directed anticipatory pecks on trials in which the upcoming hopper insertion would be in the left hopper.

One large methodological disparity uncovered during the analysis of this experiment was that it appeared that there was no requirement that the birds actually direct responses at the stimuli when making their observing responses; thus, the width of the entire screen (i.e., 800 pixels) is represented in this figure. Nevertheless, most pecks were stimulus directed (i.e., centrally located, where the stimulus was displayed), with the addition that, as previously mentioned, most pecks were also spatially biased toward the location of the upcoming hopper insertion response.

The pecks on these distributions were analyzed using a repeated measures ANOVA (Space x Response Direction x Bird as a random factor). This ANOVA revealed a significant effect of space, $F(39,156) = 25.07$, $p < .001$ confirming the fact that the central locations received more responses, but the ANOVA disclosed no significant effect of Response Direction, $F < 1$, indicative of the nearly equal number of pecks recorded on leftward and rightward trials. Critically, there was a

Space by Response Direction interaction, $F(39,156) = 4.35, p < .001$. This interaction indicates that the two distributions of responses observed in Figure 37 were reliably different from one another.

The bottom panel of Figure 37 shows these same data plotted in terms of response probability. Because of the extreme paucity of responses on the area of the screen that lay outside of the actual stimulus (between 0 and 300 pixels on the left and between 500 and 800 pixels on the right), pecks between 300 and 500 pixels were grouped into 20px bins and pecks at the edges were discarded. As can be seen in this figure, a high proportion of the pecks are directed toward the side of the upcoming hopper insertion response.

Experiment 13

Cook et al. (2005) trained pigeons over a period of three years in an ambitious study of long-term memory. In that study, the pigeons were required to make an arbitrary left or right hopper insertion to each of thousands of randomly assigned photographic stimuli with highly variable content. In their report of these data, they used the first peck to the stimulus to measure reaction times after noting that “it was highly predictable from the location of their first peck to the stimulus (p. 352)” which hopper the birds would next enter. But, despite a brief characterization of the correlation of these first peck locations with the choice response and the utility of this first peck for measuring reaction time, there was little discussion or description of the pecking distributions across the entire observing response as these issues were not central to that experimental report. Therefore, as in Experiment 12, we requested these data so that we could more closely examine these distributions of responses. As in Experiment 12, a complete description of the results and methodology of this original study can be found in Cook et al. (2005); only the relevant details will be reproduced here.

[Note: The same caveats from the previously presented experiment apply. Permission has been obtained from the authors of the original study to re-analyze this data and include them in this document.]

Method

Participants. The pigeons in this study were two male silver-king pigeons, Linus and BF. They performed this visual discrimination task for 3 years. They were maintained at 80-85% of their body weight, and kept in a pigeon colony with a 12-h light/12-h dark schedule with free access to water and grit.

Apparatus. The apparatus used in this experiment was identical to the one used in Experiment 12.

Stimuli. Stimuli in this experiment consisted of 480 x 300 pixel pictures that were pulled from various image collections and the Internet. These pictures had highly variable content and were each randomly assigned to the left and right choice hopper.

Procedure.

Training. Each trial was preceded by a small white disc localized in the center of the screen; pigeons pecked this stimulus to initiate the trial. They were then presented with a random picture stimulus to which they were required to complete a set number of required FR responses (five), but up to three additional non-required pecks per trial were also collected by the researchers and could therefore be used in the re-analysis. Following these observing responses, the choice hoppers illuminated; entry of the correct hopper was followed by access to reinforcement from that hopper, entry to the incorrect hopper was followed by a brief dark timeout. Correction procedures followed incorrect responses on each trial; responses during correction trials were not scored and peck data from correction trials were not re-analyzed.

Each session consisted of two distinct phases; this experimental plan was repeated continuously over three years. Briefly, in each 120 trial session, pigeons were shown 30 “new” pictures (twice each, for a total of 60 trials) which served to increase the pool of stimuli. Once this particular set of “new” pictures had reached an 85% correct criterion for two consecutive sessions, these pictures were added to the pool of old stimuli and a novel set of “new” pictures was added. The remaining 60 trials in each session consisted of presentations of 60 old stimuli that were randomly retested from the available pool. At the time the data were re-analyzed, the birds had been trained and tested with over 1,500 images.

Analysis Plan

The complex dataset from this long experiment has been described in detail by Cook et al. (2005). Therefore, this report will focus on the anticipatory reports made during ten sessions from each bird’s classification of these pictorial stimuli. Additionally, only responses from correct trials were analyzed.

Results and Discussion

Because only two subjects were tested in this study, we first examined the observing response distributions separately for each bird. Therefore, Figure 38 shows the distributions for each of the two birds individually. Whereas one bird (BF, top panel) showed a slight bias to peck the right side of the screen and the other bird (Linus, middle panel) showed a slight bias to peck the left side of the screen, both birds produced highly characteristic anticipatory pecking distributions. When the trial required a right hopper insertion response, the birds directed the majority of their observing responses to the right of the image; when the trial required a left hopper insertion response, the birds direct the majority of their observing responses to the left of the image.

For consistency with past data analyses, we also examined the average probability that peck reports at each spatial location were made on trials with

rightward and leftward responses. As in Experiment 12, because of the small numbers of responses that occurred outside of the stimulus area, this analysis was restricted to the central 480 pixels of the screen (i.e., where the stimulus was displayed). These data are shown in the bottom panel of Figure 38. Here, there was an exceptionally strong tendency for the birds to make anticipatory reports to the stimulus during the observing response.

Of further interest when examining these distributions is the fact that unlike the diffuse color, brightness, orientation, or texture stimuli that were used in this dissertation specifically because they did not have particularly diagnostic regions that might evoke directed pecking responses, the stimuli in this experiment often contained highly salient features such as people, objects, buildings, or animals. And, presumably, in order to recognize each picture to perform the task with high accuracy (each bird was still at 73% correct after being tested from a pool of over 1,500 images), detailed pictorial content of each picture must have been encoded by the birds. But, despite the previous experimental reports reviewed earlier (e.g., Allan, 1993; Dittrich et al., 2010) that made explicit claims that pigeons localize responses at the diagnostic regions of photographic stimuli, the birds in this task did not appear to do so, instead tending to make observing responses in the direction of their next response.

An additional analysis of these data also revealed that highly conspicuous spatial drift occurred over the course of the observing response. There were two ways to analyze these drift data. The first was to plot along the abscissa the number of pecks that the bird had emitted and along the ordinate the difference between the average response location for each peck; i.e., to analyze the spatial drift in responding as a function of each discrete behavioral response. These data are shown in the top panel of Figure 39. Here, both birds showed a significant divergence in average spatial location of the eight possible observing pecks

emitted on each trial, demonstrating that although the birds were likely to make divergent pecking responses early in the trial (as discussed by Cook et al., 2005), later pecks during this observing response were even more diagnostic of the birds' choice response. A repeated measures ANOVA (Peck Number x Bird as a random factor) was conducted to confirm these effects; a significant effect of Peck Number was found, $F(7,7) = 5.72, p < .05$.

The second way to analyze this drift data was to note the average difference in response location during the time at which each peck occurred, regardless of which peck it was in the FR sequence. This kind of analysis is sensitive to the fact that the birds might choose to respond at any point once the picture is shown; the average difference in spatial location in each of these time windows should be indicative of how much discriminative information has been extracted by the birds at each interval. After visual inspection of the peck distributions it appeared that most responses occurred within the first 4 s of stimulus presentation after the initial peck to the warning signal; the timing data were thus divided into 20 200-ms bins. The data analyzed in this fashion are shown in Figure 39. Here, we can clearly see that pecks emitted very early in the sequence show little control by the upcoming report response; but, over the first five 200-ms bins (i.e., the 1 s of responding), there was a quick rise in the difference between the peck distributions on left response and right response trials. Here, the distributions become separated by about 200 pixels; over the course of the next 15 bins, the difference between the distributions slowly asymptotes near the 300 pixel mark. Again, a repeated measures ANOVA (Peck Time x Bird as a random factor) was conducted to confirm these effects; a significant effect of Peck Time was found, $F(19,19) = 22.60, p < .001$.

Thus, the data re-analyzed from Cook et al. (2005) again confirmed that the distributions of observing responses were highly evident during cases in

which the terminal response topography was different from that of the initial response. Furthermore, this analysis disclosed that these responses were likely to occur even in cases in which the pictures contained highly diagnostic regions that must have mediated picture recognition. As well, conspicuous spatial drift occurred over the course of the observing response during picture recognition.

Chapter Discussion

The main question addressed in this chapter was whether the anticipatory responses and terminal responses must have the same topography in order to observe spatially directed anticipatory responding. To answer this question, we used data collected at the Comparative Cognition laboratory at Tufts University, with operant chambers (and pigeon tasks) that allow for the measurement of both touchscreen pecks and hopper insertion responses. The data analyzed in these two Experiments clearly indicated that the anticipatory response and terminal response can take different forms. The majority of the responses made by the pigeons were spatially directed, anticipatory observing responses even when their terminal response was not a keypeck (extending the first-peck analyses by Cook et al., 2005).

These data also address a related issue: namely, if these anticipatory responses only occur during what might be labeled as sign-tracking behavior (Hearst & Jenkins, 1974), or if they would also occur during goal-tracking behavior. In most treatments of the distinction between sign-tracking and goal-tracking (e.g., Holland, 1980; Silva et al. 1992), insertion of the head into the hopper or hopper-directed activity is taken as goal-tracking and not sign-tracking. The complication in Experiments 12 and 13 was that the goal-directed action was also the functional operant, so it is difficult to parse whether this result would truly be considered a goal-tracking event. Nevertheless, we might still say that the anticipatory observing response keypecks occurred prior to a goal-tracking event

rather than to a sign-tracking event. Therefore, we might conclude that these measurable anticipatory behaviors might occur prior to any predictable, prospective event.

An additional methodological disparity is of particular note with regard to the possibility of goal-tracking. As detailed in the method, the two hoppers in each experiment each contained two different types of food reinforcers; one contained mixed grain, the other contained safflower. As discussed in the general introduction, the differential outcomes effect (Trapold, 1970) might therefore have promoted both an increased acquisition of the initial task or, of particular relevance to this dissertation, an increased likelihood to make spatially directed pecks toward the centrally displayed stimulus. According to Trapold, the sight of a particular stimulus produces the differential expectation of the particular reward (rather than of simply reward in general) that has been paired with that stimulus. That this reward has occurred in a particular spatial location may only serve to heighten the linkage between a discriminative stimulus and space, perhaps further promoting this anticipatory behavior. Indeed, previous studies that have utilized the differential outcomes effect have found that under certain conditions, this effect can promote better learning about spatial environments (Savage, Pitkin, & Careri, 1999; Legge & Spetch, 2009).

A possible follow-up study to address the influence of differential outcomes on these anticipatory reports might be to use a similar procedure with either differential or nondifferential outcomes in the food hoppers. In this experiment, two groups of pigeons could be trained to discriminate simple pictorial stimuli. After the presentation of a simple discriminative stimulus, a leftward or rightward hopper insertion response would be required. In one group of pigeons (DOE [Differential Outcomes] Group), the two hoppers would contain different types of grain; in the other group of pigeons (Control Group), the two

hoppers would contain the same type of grain. Following training, the spatial distribution of pecking responses could be examined. If the differential outcomes effect does indeed promote stronger spatial learning, then a stronger tendency to make anticipatory pecks should be seen in the DOE Group than in the Control Group.

One final methodological note is also addressed from the re-analysis of this dataset. A possible issue in many of the studies presented thus far is that a “warning signal” or “readiness key” was not used prior to the display of the stimulus. This methodological choice was made mainly for pragmatic purposes when conducting research with the rats and, for consistency, was also used with the pigeons. The issue solved by not using the “warning stimulus” with the rats was that requiring multiple responses in a similar location seemed to interfere with the temporal and spatial distribution of those responses. Therefore, using a ready signal in the same location as Link 1 (on which the spatial distribution of responding was tracked) seemed like a bad methodological choice because it interfered with one of our primary dependent measures.

But, this methodological choice left open an alternative interpretation about the spatial distribution of responding. According to this interpretation, the animal might approach the screen having already discriminated the stimulus, and so the spatial distribution of responses might be a consequence of a pre-response spatial orientation or positioning of the animal and not a particular feature of the response to the discriminative stimulus. In these re-analyzed data, however, a warning signal peck was required to initiate the trial; this peck forced the bird to be oriented in a central spatial location at the start of the trial before any pecking responses might have occurred. That these differential distributions are observed even under these circumstances seems to disconfirm this possible spatial positioning hypothesis.

However, the presentation of this warning signal may have allowed us a better opportunity to measure the conspicuous spatial drift across the spatial location of the observing responses as observed in Experiment 13. But, it is also possible that this spatial drift was due to the longer time-course required to retrieve one of the thousands of images stored in long-term memory when compared to the very small number of discriminative stimuli presented in the other experiments in this dissertation. The utilization of a warning stimulus in future pigeon experiments about this phenomenon might better enable us to distinguish between these possible alternatives.

As discussed briefly in Experiment 13, one curious feature of these observing response pecks is that they appear very strongly influenced by a secondary, upcoming response rather than directed at the diagnostic features of the currently displayed visual stimulus that mediate successful image recognition. Here, I intentionally use the term “curious” because several lines of evidence and well-known features of discrimination learning would suggest that pigeons should behave otherwise. First, previous studies (e.g., Allan, 1993; Dittrich et al., 2010) that tracked responding during the recognition of photographic stimuli in birds showed pecking directed at particular diagnostic regions of stimuli. And, the well-known feature-positive effect (e.g., Jenkins & Sainsbury 1969, 1970) suggests that birds should direct toward areas of the stimuli that are most strongly predictive of reinforcement. Importantly, these previous studies were mainly go/no-go tasks, which required no terminal “choice” response, unlike forced-choice tasks. That fact may offer additional insight into why pigeons do not direct their pecks at features of the stimuli in the current tasks.

But, the methodological difference between tasks with a choice response and those without does raise an interesting interpretive question for comparative psychologists. Simply put: why would the pigeon, in a task in which it was asked

to report the identity of a photographic stimulus, and in the *presence* of that same visual stimulus, direct pecks not at the diagnostic features of that *present* stimulus which mediated recognition, but instead at non-diagnostic regions of the image that correlated with its *future* response? From our analysis of choice task data, it was clear that certain features of the display (such as the physical location of the stimulus) influenced where the pigeons would peck; the large majority of the time, the pigeons pecked at the stimuli in these tasks despite no obligation to do so (i.e., why not make completely directional pecks off the stimulus itself?). But, the majority of the pigeons' responding was controlled by their upcoming response, not by particularly diagnostic or salient regions of the stimuli. If we call these pecks "observing responses", why do they seem so unrelated to *observing* and so influenced by the animal's upcoming choice?

This question seems closely related to the similarly interesting puzzle of how humans (and, indeed, primates in general) direct their saccades at an image, which could either be mediated by bottom-up saliency (Itti & Koch, 2000) or through top-down guidance (Becker & Rasmussen, 2008; Hollingworth, 2009). In general, studies with human participants have shown that despite the quick extraction of bottom-up information, top-down, task-related influences tend to be more influential in the control of eye movements (Land, 2009). Important data concerning this anticipatory saccade behavior in non-human primates were presented by Sheinberg, Peissig, Kawaski, and Mrucek (2006). There, monkeys were required to perform manual button-press responses to a set of visual stimuli. Although differential eye movements are often required by researchers in primate visual tasks, here, the monkeys were free to make any number of saccades in any location before they made their choice response. When examining the direction of each monkey's *first saccade* to each visual stimulus, Sheinberg et al. found a strong correlation between that initial saccade's location and the monkey's

upcoming choice response. When monkeys would next respond right, their first saccade was almost always directed toward the right; when monkeys would next respond left, their first saccade was almost always directed toward the left. In other words, even before their first saccade, and despite the fact that eye-saccades are physically critical for observing the stimulus, saccades were strongly influenced by the monkey's upcoming choice response.

Previous peck analyses have tracked the temporal emergence of stimulus control across the sequential presentation of stimuli in a go/no-go task (e.g., Cook, Kelly, & Katz, 2003). Here, we offer a way to measure the dynamic emergence of stimulus control in a choice task by using the difference in the spatial distributions of observing report responses. This technique might be coupled with a methodology such as Bubbles (Gibson, Lazareva, Gosselin, Schyns, & Wasserman, 2007), in which random areas of pictorial stimuli are revealed and correlated with choice responses and the discriminative information used by organisms in each picture can be identified. When used together, these methods might provide additional information about the time-course of how those selective features are processed.

Finally, we return to the initial question that prompted the re-analysis of these data. That the initial and terminal responses can be different and still promote differential distributions of anticipatory pecking responses may seem like an unimportant fact, but we do feel that it has theoretical significance. As discussed in the literature review (Chapter 1), many previous descriptions of anticipatory or preparatory behaviors have been “fractional” or “partial” responses that appeared to anticipate the production of a consummatory response that would be required upon receipt of the reinforcer. For example, Hull (1931) described the fractional “chewing” reactions made by rats en route to a food source. Coupling these early observations with the fact that the topographies of

our initial and terminal responses were the same, one might conclude that perhaps the responses observed in Link 1 were simply “fractional” reactions toward the location of the upcoming Link 2 key. However, it seems clear from the data in this chapter that even when the anticipatory pecking response differs from the terminal choice response, the differential distribution of pecking responses is still observed; thus, interpreting these anticipatory pecks as somehow being fractional forms of the terminal response seems highly unlikely. Instead, it would appear that the mechanism that accounts for the distributions of anticipatory keypecks in these tasks is probably the spatial representation of an upcoming choice. The possibility that such a mechanism accounts for these data is more fully discussed in the General Discussion.

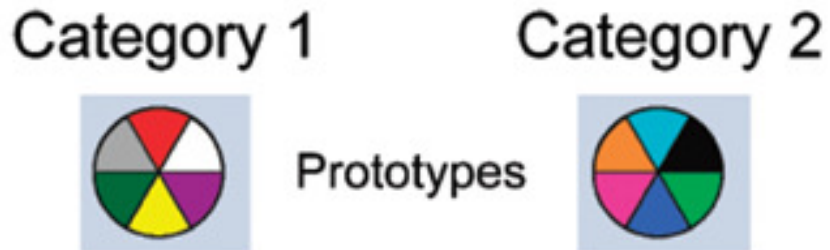


Figure 36 - Prototype stimuli re-analyzed in Experiment 12. Stimuli tested by Cook and Smith (2006); figure reproduced from Cook and Smith (2006). Different prototype stimuli were tested with different animals; these are merely representative examples.

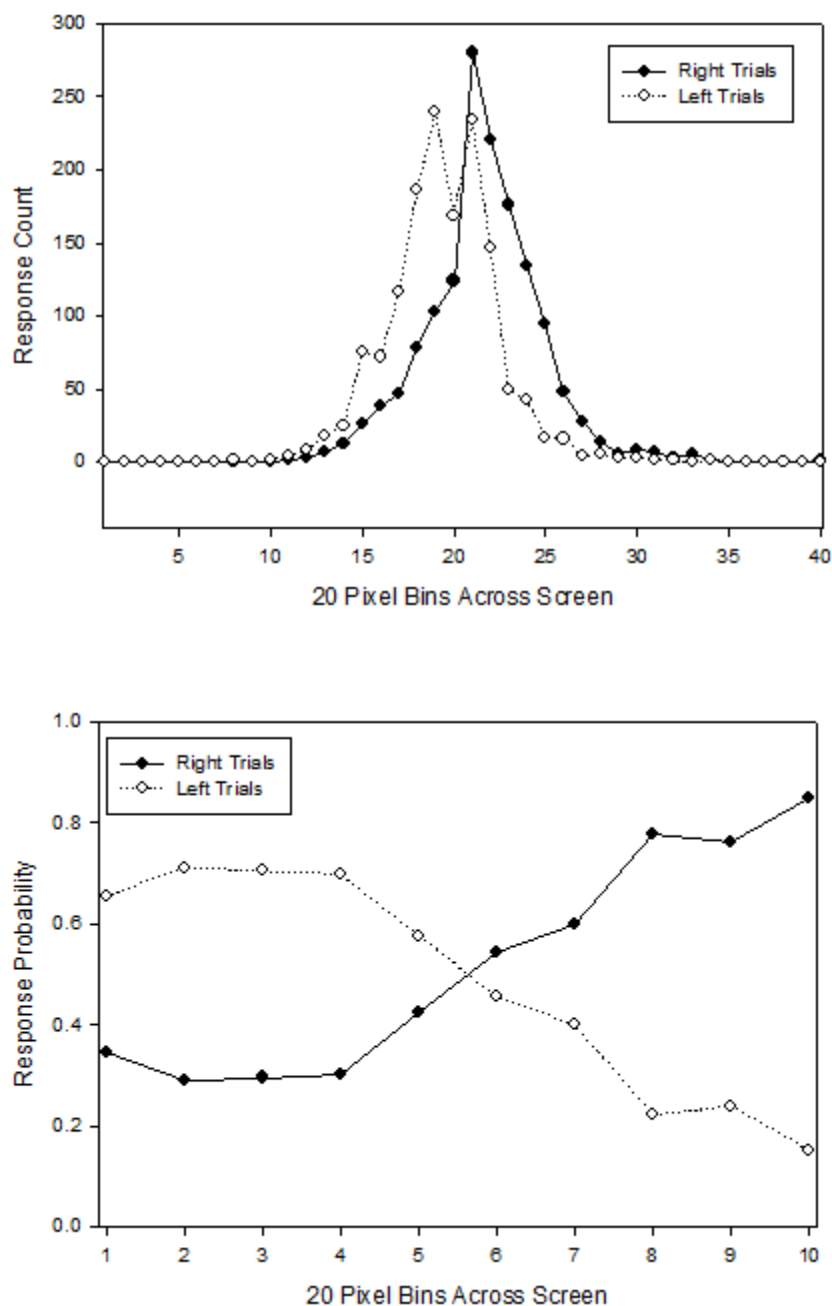


Figure 37 - Response count and probability across stimulus in Experiment 12. *Top panel:* Response counts in individual 20-pixel bins across the width of the entire screen during Prototype trials in Experiment 12, separated into trials with an upcoming rightward or leftward response. *Bottom panel:* Data from the top panel across the central 200px of the screen transformed into response probabilities, separated into trials with an upcoming rightward or leftward response.

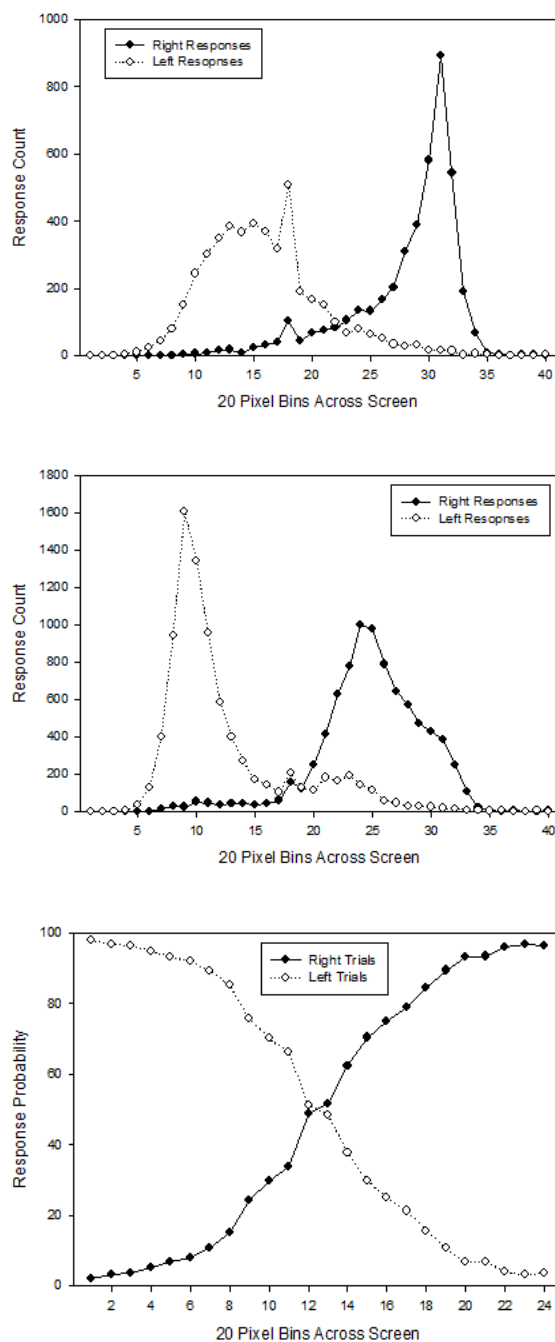


Figure 38 – Response count and probability across stimulus in Experiment 13. *Top and middle panel:* Response counts in individual 20-pixel bins across the width of the entire screen for pigeons BF and Linus individually, separated into trials with an upcoming rightward or leftward response. *Bottom panel:* Data from the top panel across the central 480px of the screen transformed into response probabilities, separated into trials with an upcoming rightward or leftward response.

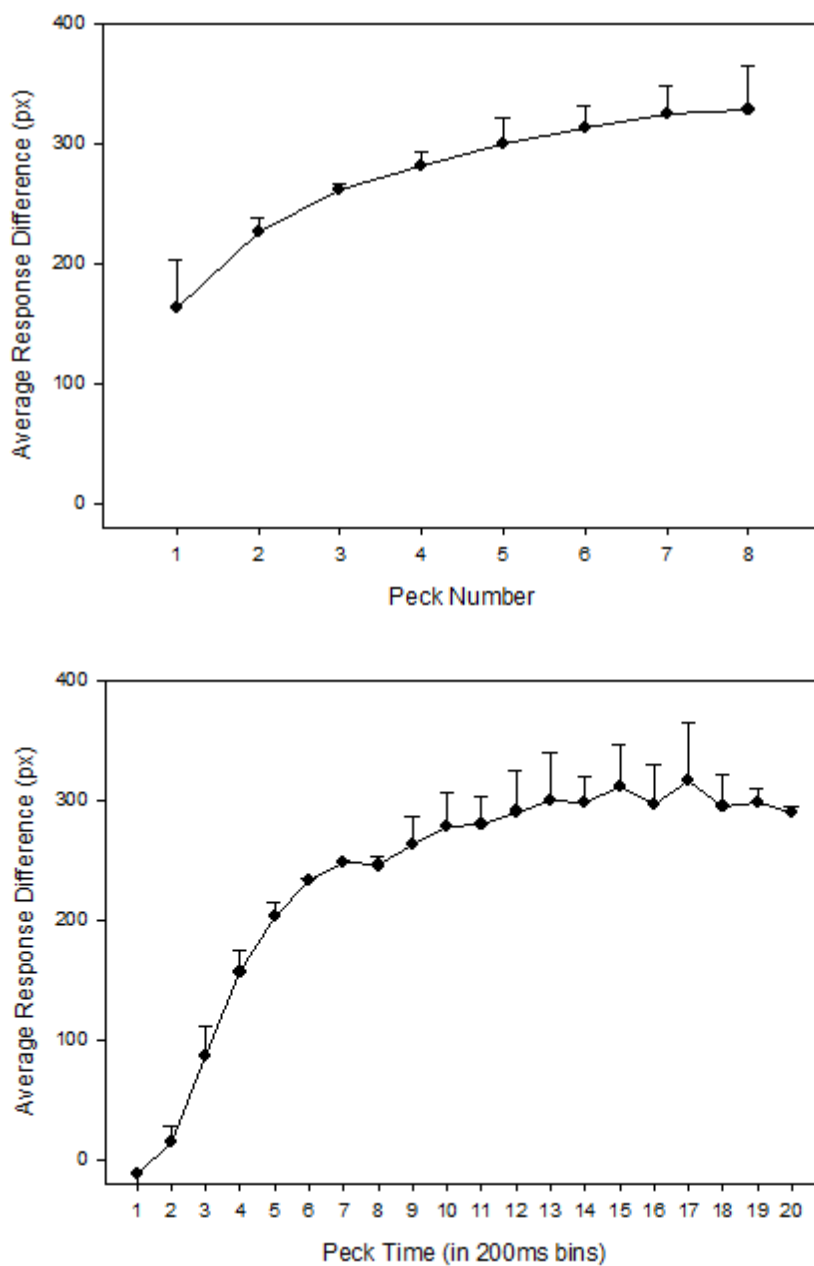


Figure 39 – Average difference between mean response distributions during left and right trials for both pigeons. *Top panel:* The x-axis is number of pecks in the FR sequence. *Bottom panel:* The x-axis is the same data coded across temporal intervals, separated into 200ms bins.

CHAPTER 6

GENERAL DISCUSSION

Spatial Anticipation: A Human Example

The experiments in this dissertation were focally aimed at investigating the measureable anticipatory behaviors that occurred before a spatially directed action. As an everyday example of such a spatially directed action, consider a sequence from the movie *Field of Dreams*. As the Black Sox materialize from the corn and run onto the field, Ray Kinsella takes a spot on the bleachers next to his daughter. A few warm-up tosses later, and the Black Sox are playing a rowdy game. As the pitcher receives the ball and a hitter steps into the box, Kinsella turns to his daughter to teach her some of the finer points of baseball. “Watch Joe,” he says, pointing to Shoeless Joe Jackson, the left fielder. “Watch his feet as the pitcher gets the sign and starts to pitch.” The camera zooms in on Shoeless Joe’s feet. As the pitch is delivered (off screen), Joe begins to lean toward his right, and then takes a few halting steps to the right. Then, we hear the crack of the bat. Suddenly, he takes off at full speed in that same direction. “A good left fielder,” Kinsella explains, “knows what pitch is coming.” We see Joe track down the fly ball with an outstretched hand, catching the hard shot because of his good first move. Kinsella continues, “And he can tell from the bat’s angle which way the ball’s heading.”

Kinsella is no magician or mind reader; he is merely a student of the game. To see which direction Shoeless Joe will run *even before he does so*, and *even before the ball is in flight*, he watched Joe’s feet. And of course, despite the exaggerated portrayal for the movie audience, Shoeless Joe was not particularly unique in his behavior; most, if not all good outfielders telegraph their “jump” with these preemptive movements. For Kinsella, it did not take much detective

work to know where Joe was heading. Drift to the right, and Joe's first move will be right. Drift to the left, the Joe's first move will be left.

Ray's explanation for this behavior was that Joe had developed a keen sense over many successive at-bats that afforded him the ability to instantaneously combine information about pitch-selection and bat-angle into a fielding advantage. This advantage allowed him to anticipate the location of the ball and start to move there in advance of the ball being hit. Of course, the temporal dynamics of the situation constrained the amount of complex or conscious planning in which Shoeless Joe could engage. Even if he had perfect knowledge of the pitch type, the pitch takes less than four tenths of a second to reach the plate and the swing only a fraction of that. The discriminative information was available only for a mere instant. But still, Joe combined that available information into a blindingly fast first move – so fast, in fact, that he starts before the ball is ever hit.

The experiments presented in this dissertation were aimed at investigating the same sort of anticipatory phenomenon in pigeons and rats that Kinsella observes in Shoeless Joe. In these experiments, we presented pigeons or rats a cue in the form of a centrally located discriminative stimulus that contained information about an upcoming spatial event. When we measured their response to this centrally located stimulus, we were able to measure signs of the upcoming discrimination behavior even before a spatial choice was available. The experiments presented in Chapter 2 demonstrate this anticipatory tendency. In this first set of experiments, we presented evidence that the spatial associations learned during serial conditioning (e.g., Wasserman et al., 1978) shift forward in time to a centrally located key; this temporal shift to the first stimulus occurs in concert with choice performance to the second stimuli (see Figures 2 and 6). Both in pigeons and rats, this spatial shift is so strong that within only 10-12

nondifferentially reinforced sessions, 85-95% of the responses made to the left side of the Link 1 key were on trials in which the animal would respond left, and 85-95% of the responses made to the right side of the Link 1 key were on trials in which the animal would respond right (see Figures 3 and 7).

Prospective Coding, Anticipatory Behavior

These anticipatory, pre-choice movements are then demonstrated in a variety of experiments and in two species of animal, occurring even when the terminal response is not the same as the initial response. One question that concerns the nature of these movements is whether they reflect the influences of *prospective* coding on the current response. Do these observable, incipient behaviors constitute evidence for the anticipation of a goal? Would that anticipation constitute evidence for prospective coding?

Although literature about this issue was reviewed in the general introduction, we return to this issue now because it seems central to the broader implications of this dissertation.

The Etymology and Usage of Anticipation and Prospecion

In the Skinnerian tradition (e.g., Skinner, 1989), the similarity or difference in the usage of a set of terms can often be informed by tracing the etymological roots of these terms. “Anticipation” and “prospecion” offer a nice example of this strategy, for despite both being classical examples of English words borrowed from Latin, the terms “anticipation” and “prospecion” have divergent etymologies. “Anticipation” comes from two Latin roots, “ante-” (before) and “capere” (to take); the original Latin term “anticipatus” literally meant “to take into possession beforehand” (i.e., to take care of something ahead of time). “Prospecion” is an English derivative of “prospect”, from the Latin “prospectus” (a view or outlook), from the verb “prospicere” (to look forward upon). The two Latin roots here are “pro-” (forward) and “specere” (to look

upon). Thus, the root terms of “anticipation” and “prospection” are quite different. The former is built on a root, “capere”, that implies an action; the latter is built on a root, “specere”, that implies a perception.

The point of this foregoing etymological discussion is that despite the fact that the two terms both imply a future orientation, modern usage in the psychological literature seems to have preserved their etymological distinction: “anticipation” seems to denote *behavior*, e.g., “anticipatory behavior”; whereas “prospective” seems to denote *cognition*, e.g., “prospective memory”. As evidence for this, in a search of the PsycNET database, there is only a single paper (ironically, by de Kort, Correira, Alexis, Dickinson, & Clayton, 2007, on food-caching by scrub jays) that notes “prospective behavior” as a keyword, but there are 549 papers that note “prospective memory” as a keyword. Similarly, there is only a single paper that notes “anticipatory memory” as a keyword, but there are 39 papers that note “anticipatory behavior”. Surely, other combinations of the root terms would yield similar results.

Of course, despite the fact that psychology is literally “the study of the mind” (from the Greek *ψυχή* [psyche]), we often describe it to students as “the study of behavior”. We tell students this strange definition at complete odds with the root meaning of the word because we recognize that our only avenue for understanding cognition is through monitoring behaviors. Thus, despite the fact that “anticipation” primarily denotes behavior, it is clearly being measured for the purpose of revealing some cognitive state of the organism. And, despite the fact that “prospective” primarily denotes cognition, it is only measurable through overt behavior. The point here is that although the terminology is certainly not equivalent and there is an extant preference to use one term to denote behavior and the other to denote cognition, they are inextricably linked for the purposes of psychological investigation.

Prospection, Anticipation, and Learning Theory

We go about our lives executing actions that appear planned and structured, as if they have been performed not because of some past history but because of some future intention. William James (1890) observed that “the whole sting and excitement of our voluntary life... depends on our sense that in it things are really being decided from one moment to another, and that it is not the dull rattling off of a chain that was forged innumerable ages ago” (p. 453; see Wegner & Wheatley, 1999). This idea is similar to that of Tolman (1932), whose “purposive behaviorism” suggested that we ought to describe behaviors in terms of their goals and objectives rather than rote connections between stimulus and response.

At the same time, as behavioral scientists, we must recognize the enduring psychological paradox of perhaps our only stable law of behavior, Thorndike’s Law of Effect (1911). This law claims a profound truth: our actions are driven by their past association with consequence and not in service of any future goal. Thus, Thorndike claims that we go through life accumulating experiences about the stimuli that signal the onset of various events, and, as we learn about those stimuli, begin to react to them accordingly and form memories about their occurrence. After successive presentations, our actions begin to be influenced by these representations in memory, such that our current actions appear to anticipate the onset of these future events.

The later theorist William Estes expressed the possibility that behaviors are not coded merely as particulate units of S-R or S-S associations. In this analysis, he notes that “a striking simplification in the interpretation of many learning phenomena is achieved at a stroke if we conceive the result of an organism’s experiencing a sequence of events to be, not simply the strengthening... of the constituent stimulus-response connections... but rather the

establishment in memory storage of a representation of the entire sequence, so that later recurrences of earlier members of the sequence lead to anticipation of the later members (1969, p. 186).” This analysis suggests that, rather than the organism individually representing individual components of a chain of responses, the organism might form some kind of representation of the entire sequence, whereby a prospective code for future stimuli or responses might influence the production of the current response. Whether the entire sequence must be represented for such anticipatory actions to occur is a matter of theoretical debate, but the experiments in this dissertation clearly show that the location of upcoming spatial responses do influence current responding.

Here, we are able to measure pecking or nosepoke responses that shift in the direction of an upcoming response. It seems clear that the direction of a future, upcoming response has influenced these anticipatory responses. Does this necessitate attributing the behavior to a “prospective” code? Thorndike might argue that despite actions appearing goal-directed, these behaviors are in fact only performed because they have succeeded in producing positive effects in the past, and are therefore not performed with any “prospective” goal in mind.

Of course, with the broader development of animal cognition and neuroscience, learning theory has grown more sensitive to the broader range of associations that are present in learning situations than only the S-R connections that Thorndike explored. For example, we no longer believe that the actions of animals are performed without regard for the goal of these actions; consider devaluation studies (Adams & Dickinson, 1981; Colwill & Rescorla, 1985), or the differential outcomes effect (Trapold, 1970). Or, consider the neurological evidence reviewed; Watanabe (1996) and Matsumoto, Suzuki, and Tanaka (2003); both reported that different neurons activated depending on different types of anticipated reward. Given this more modern outlook, it is apparent that animals

can be sensitive to and anticipate the onset of particular upcoming stimuli in the environment and perform responses that work toward achieving a particular goal. Behavior of that sort certainly *seems* to be the product of prospective codes.

A Disconnect between Animal and Human Prospection?

But even if we are no longer so uncomfortable with the concept of prospective or goal-oriented behavior in animals, there seems to be a qualitative difference, at least definitionally in the literature, between prospective memory (or anticipatory behavior) in animals and prospective memory (or anticipatory behavior) in humans. Simply put, there seems to be a large gap between what animal researchers might call prospective and what human researchers might call prospective.

In the animal literature, the term prospective is widely used to denote coding strategies in which the animal responds with a strategy that appears to reflect an active psychological representation of the upcoming goal rather than a representation of current or past stimuli (reviewed extensively in Chapter 1). But, in the human clinical literature, the term prospective is most often used to describe tasks that involve “conscious planning” and instructions to complete a particular action within a particular timeframe, often after an intervening delay. For example, Hertzog (2008) defines prospective memory as “remembering to perform an intended act at an appropriate time and place when enactment must be delayed” (p. 103).

As an example of such a clinical or prospective task from the human clinical literature, a particular group of patients (or normal subjects) might be asked to remember to complete an important subgoal (e.g., “Remember to refill the car’s gas!”) while participating in a driving simulator (Kerns, 2000); the experimenter might then make note of how often the participant engages in this planned action while completing the main task (e.g., “Drive from point A to point

B.”). Dismukes (2008) collected anecdotes of behaviors that he termed “prospective” from a number of students who were assigned to record behaviors that *they* thought were prospective, in an attempt to measure “naturally occurring” prospective codes. Examples of these were tasks like “Remember to buy toothpaste when at drugstore” or “Take the car to the garage before 5 p.m.”. Again, the content and quality of these anecdotes are ones that involve “remembering to remember” to do an action in the future.

How similar are these human/clinical prospective tasks to the ones in this dissertation, or even the ones from the animal literature reviewed in Chapter 1? Should we have new terminology to denote the behaviors of patients in car-simulators or individuals remembering to buy toothpaste when compared to the behavior of pigeons or rats remembering a specific sample or responding in a particular location? What about more subtle examples of our own behavior that might be the product of different environmental contingencies than the delayed execution of explicit instructions provided by an experimenter, but may yet yield anticipatory behaviors?

Possible Resolutions in Motor Planning & Prospective Perception?

One area of research which might aid us in bridging the divide between these divergent definitions of propection might be found in the motor planning and execution literature. Here, participants typically perform well-defined tasks with explicit experimenter instructions. But, certain researchers have paid close attention to the differential kinds of movements that participants make as they execute behaviors in service of a specific goal given to them by those instructions. For example, participants might sequence their behavior differently or grip an object differently depending on what they are told to do with it next.

As a wonderful example of such clearly goal-influenced motor planning in everyday life, consider the scenario described by Rosenbaum, Meulenbroek, and

Vaughan (2001). The authors recount watching a waiter filling glasses of water that were inverted on the table. To pick up a glass before pouring, the waiter uses a very awkward thumbs down posture with his hand, inverting his arm in a way that would be uncomfortable to maintain and clearly not the posture the waiter would have chosen if he were asked, say, to move the glass from one place setting to another (cf. Marteniuk, MacKenzie, Jeannerod, Athenes, Dugas, 1987). After picking up the glass with this posture, the waiter then “flips” the glass so that it is right side up, simultaneously inverting his grip to a much less awkward one, pours the water into the glass, and places the glass on the table. Rosenbaum et al. (2001) note that “the waiter tolerated initial discomfort and instability for the sake of later comfort and stability” (p. 103). Here, the waiter’s movements are governed by what Rosenbaum et al. (1990) called the “end-state comfort effect”; clearly, the early actions taken by the waiter anticipate the later actions (or, the *goal* of the preceding behavior), despite the sufficiency of the opposite motor behavior for executing the task.

This anecdote was experimentally tested by Rosenbaum, Marchak, Barnes, Vaughan, Slotta, and Jorgensen (1990). To visualize what Rosenbaum et al. did in this experiment, imagine a light dumbbell that is lying flat on the floor and having to stand it, end-side-up, onto one of two target platforms. The two targets and the dumbbell are arranged such that they are horizontally aligned; the dumbbell is located equidistant from the two platforms, and the cylindrical portion of the dumbbell forms a straight line between them. When participants were asked to manipulate this object by moving it from the starting location to the right platform, participants grasped the object using an *overhand* grip, so that their thumb and index finger would be closer to the top of the dumbbell when the object was rotated and placed on the platform, which is a more comfortable grip in which to hold and place the object than the alternative (thumb down) grip. But,

when participants were asked to manipulate this object by moving it from the starting location to the left platform, participants grasped this object using an *underhand* grip, so that, once again, their thumb and finger would be near the top of the dumbbell once it was rotated for placement. Here, the goal location that participants were required to move the object toward influenced the way that they grasped the object. Additionally, the way that they grasped the object was driven by *end-state* comfort; participants moved the object in such a way as to maximize comfort at the end of their planned movement. Thus, the early grasping behavior of participants was diagnostic of their final movement pattern and reflective of their represented goal.

These end-state comfort effects are also strongly resistant to the effects of bimanual interference. Here, at issue is the natural inclination of people to use symmetrical movements when performing bimanual tasks and the strong inference that is usually generated by asking participants to make two different movements with each limb. But, when participants were asked to perform an analog of Rosenbaum et al. (1990)'s task with two objects by Weigelt, Kunde, and Prinz (2006), they again showed strong end-state comfort effects, even when the task given required the asymmetrical movement of the hands. Thus, participants performed anticipatory behaviors toward an upcoming goal state even in the face of what might be considered a strong bias against making asymmetrical hand movements in order to do so.

Another example of the end-state comfort effect can be found in Cohen and Rosenbaum (2004), in which participants were required to move a tall cylinder, which resembled a tall toilet plunger, from a mid-level shelf (start position) located roughly near each participant's stomach to either a higher or lower shelf (target position). The question here is whether participants will vary their grip height on the cylinder in order to make the initial lift from the start

position comfortable or whether they will grasp the object in such a way as to make the placement of the object on the target position comfortable. Cohen and Rosenbaum found that participants were again governed by an end-state effect; participants tended to grasp objects differentially depending on the height of the target shelf. Similar end-state effects are seen in numerous other examples, e.g., wheel turning (Rosenbaum, van Heugten, & Caldwell, 1996) and abduction-adduction (Zhang & Rosenbaum, 2008).

These motor-planning behaviors seem to “bridge the gap” between the human and animal prospection literatures because whereas they clearly reflect the influence of a future goal on current behavior, they do so in a way that appears not to involve complex planning or memory monitoring. Despite many possible alternative strategies and the presumptive lack of any complex, conscious planning on the part of the participants, participants act in such a way as to gain comfort toward the end of the action. In this way, the behavior in these examples resembles the behavior of the birds in Experiment 11 (see Figure 33), which shift response location before they are required to do so. Although the temporal and spatial constraints are such that shifting in Link 2 or Link 3 will ultimately produce the same result, the birds shift well in advance of when they are required to shift, anticipating their next response.

In fact, humans engage in all sorts of apparently anticipatory actions that seem to require little in the way of conscious planning, reminiscent of Shoeless Joe from the start of this chapter. Some of these studies can be found in the Sports Psychology literature, which have shown that baseball players (Paull & Glencross, 1997; Ranganathan & Carlton, 2007), cricket players (Abernethy & Russell, 1984), tennis players (Goulet, Bard, & Fleury, 1989), and badminton players (Abernethy & Russell, 1987) use discriminative information about an opponent’s pre-swing movement to anticipate the location of the next shot or the

location of the next pitch. In baseball, for example, expert players start their pre-swing step an average of 100ms *before* the ball has been released by the pitcher, while novice players start their pre-swing step an average of 50ms *after* the ball has been released by the pitcher (Ranganathan & Carlton, 2007). There is no doubt that expert players react in advance to cope with the incredible temporal constraints on completing a successful swing.

These studies indicate a further linkage between anticipatory actions and prospective memory, and additional anticipatory behaviors that disclose prospective codes can be found in the human literature on perceiving events. One of these effects has been typically termed “representational momentum” (see Schutz-Bosbach & Prinz, 2007, for a review). In these tasks, subjects are asked to view an object as it moves (or rotates, or oscillates) from one position to another on the screen. The object is then suddenly removed and the subject is asked to make a decision about where the object was at the time it was removed. In this case, subjects make errors indicating the prospective coding of the object’s motion path; they produce “localization errors” that indicate their anticipation that the object will have been displaced farther along its current trajectory than it actually was. One key result occurs during movement oscillations (Kerzel, Jordan, & Musseler, 2001), in which an object moves left to right (and back again) in a smooth sequence. When participants are asked to judge the position of the removed object at the end-points of the oscillation, subjects produced *negative* localization errors, indicative of their anticipation of the continuation of the oscillatory sequence rather than their blind adherence to the current trajectory of the object. These studies provide critical evidence that not only is the production of movements controlled by the anticipation of their goals, but the perception of objects is controlled by the prospective coding of their likely future location.

Similar studies have also been conducted by animal researchers. For example, Neiwirth and Rilling (1987) trained pigeons to discriminate a clock-hand stimulus that rotated around the clock at a constant rate. On some trials, the clock-hand was obscured for a portion of the rotation and then re-appeared in a location consistent with constant motion; on other trials, the clock-hand was obscured and then re-appeared in a location inconsistent with constant motion. Pigeons were able to differentiate these two conditions, and importantly, displayed errors similar to the errors of human participants described above. Pigeons too showed “representational momentum”; they were more likely to make forward errors than backward errors. This result suggests that animals, too, code perceptual events prospectively.

Further evidence for the interaction between perception and goal-directed behavior can be found in the studies of Mechsner and Prinz (2003; reviewed by Schutz-Bosbach & Prinz, 2007). Here, participants were asked to turn two manual cranks in order to spin two flags on a table. Before describing the results of this study, it is necessary to review the following fact: it is very difficult to produce, with each hand, two independent, arrhythmic circling patterns. To prove this to yourself, try making two circles to yourself in the air with your index fingers at the same rate (this should be easy); now, try making one circle at some set speed while making the other at $\frac{3}{4}$ of that speed. Of course, we could arrange even more difficult conditions under which you would find these arrhythmic circling patterns nearly impossible to perform (Kelso, 1994). But, if situated in an experiment and told that the goal of the experiment is to move the flags at equivalent rates (even if this requires nearly impossible circling patterns), participants are able to accomplish bimanual coordination tasks that they would find nearly impossible without the perceptual information. Thus, the linkage between an available perception and a directed goal greatly simplifies a very difficult task.

One large difference between our current task with animals and many of the tasks and behaviors that we have discussed with humans is the ability to measure this prospective shift over the course of successive sessions. Whereas early sessions with the pigeons do not entail much prospective shifting, later ones do. The use of tasks with humans that focus on *learning* and those that do not utilize experimenter instruction may provide us with an even better understanding of the development for these anticipatory or prospective effects over the course of a particular discrimination problem.

Additionally, psychologists who utilize similar approaches which focus on learning and motor planning might be able to provide key evidence to ongoing debates on the nature of prospective memory in development as well as clinical populations. Do children undergo systematic changes in their ability to process prospective events, and what biological or cognitive change occurs that allows children to be better monitors of prospective events? Do these prospective memory systems develop independently or concurrently with those that mediate anticipatory behavior? Kerns (2000) notes that the development of prospective memory appears linked with other tasks that measure executive functioning. In a similar vein, Einstein and McDaniel (1990) suggest that certain types of prospective memory tasks may be particularly resistant to the effects of age-related decline; what makes these memory systems resilient to common age-related deficits while other memory systems undergo progressive degradation? Additional theoretical development that more precisely specifies the differences between the divergent tasks used by these various areas will be useful for disambiguating the complex issue of how prospective coding strategies emerge, both within the smaller timescales represented by individual experiments or behaviors and at larger timescales in terms of developmental maturation.

Resolving the Distinction

The point of the preceding discussion of different forms and definitions of anticipatory behavior and prospective memory was to note that the concepts of propection and anticipation are different in multiple literatures. As well, it is unclear if the same psychological or cognitive mechanisms govern “instructed” and “non-instructed”, “planned” vs. “unplanned”, or “conscious” vs. “unconscious” behaviors. Indeed, it is even unclear to what extent those behaviors that we *think* are planned or organized prospectively are actually executed with conscious thought; as noted by Wasserman, people are “quite content to accept highly elaborate explanations of human behavior, almost pathologically disposed to create the most complex interpretation, even when simpler ones would do. We prefer the explanation that attributes the most highly advanced cognitive capacities to people.” (Buchen, 2009)

So, whereas some prospective tasks with humans are generally similar to tasks that might fall under the realm of “metacognition” in animals, others truly involve the retention of prospective elements of an upcoming event. In the clinical psychology literature, there is an apparent conflation between concepts such as prospective memory, metacognition, episodic memory, and executive functioning. That these terminologies are blurred makes it difficult to develop a cohesive theoretical model or integrate multiple experiments. Some reconciliation of the definitions used in these two literatures may serve to increase the amount of contact between these literatures. As the cognitive and neurobiological mechanisms that govern anticipatory behavior or prospective coding in humans and animals become better specified, the utility and application of animal models toward the treatment of human clinical populations will become clearer.

Clinical Relationships

I would like to briefly focus on two clinical areas in which prospective memory or anticipatory behavior seem importantly implicated. The first of these areas will be addiction and drug seeking; the second will be schizophrenia.

Addiction and Drug Seeking

In some ways, there seems to be little better human example of a self-destructive yet prospectively mediated behavior than drug addiction, especially drug *seeking* behavior. We are constantly faced by a barrage of media showing us the extreme degradation, social humiliation, and spiral into poverty that faces the severe drug addict. What behavior could possibly be more self-destructive and self-punishing than those behaviors in which severe addicts will engage in order to get their next “fix”? These behaviors are often extremely costly to the individual, and yet done with a completely future orientation in mind.

The possible neurobiological connection between sign-tracking and drug abuse (Tomie, Grimes, & Pohorecky, 2008) and possible parallels between anticipatory behavior and drug seeking behavior may make an animal model of anticipation useful for the study of drug seeking behavior. Two questions immediately come to mind. First, perhaps pre-existing individual differences, genetic manipulations, or induced neurobiological differences would help explain some component of drug seeking. With areas that govern prospective planning inhibited, would the ability of animals to effectively seek drugs be limited or altered? Conversely, does the influence of drugs negatively impact the ability to code for events prospectively, especially those that do not relate to the addiction? Put another way, do resources that might be devoted toward engaging in other prospective goals (such as finding food or shelter) become subsumed by prospective goals related to the addiction?

A second set of questions could be more focally directed at the work presented in this dissertation. Here, we might ask what effect the substitution of drug rewards or intracranial stimulation for the primary reinforcer in the current three-link anticipation task would have on the generation of anticipatory behavior. We might expect several changes in behavior. For example, we might expect an even stronger function of the Link 3 stimulus as a conditioned reinforcer, which may serve to heighten the propensity to make anticipatory reports in both Link 1 and Link 2. This result might be expected due to the further increased contiguity between the Link 3 stimulus and the delivery of primary reinforcement, as well as perhaps the increased value of the primary reinforcement itself.

Despite what we believe to be considerable optimism regarding adapting the current procedure to the study of drug seeking or using drug rewards instead of food reinforcement, a note of caution must be made. Despite persuasive arguments that drug addiction and drug seeking share many characteristics of Pavlovian conditioning (Tomie et al., 2008), there is a dearth of evidence that currently supports the idea that drugs can serve as reinforcers in autoshaping. Whereas the currently existing evidence suggests that drugs or alcohol may be effective in certain experimental paradigms (e.g., Krank, 2003; Tomie, 2001), those experiments paired ethanol or amphetamine intake with saccharin infused liquid (in order to make the solution palatable). Thus, it is unclear if the drug or the saccharin was responsible for the shaping.

Additionally, Kearns and Weiss (2004) reported that whereas cocaine infusions were more than adequate to support operant behavior in rats, they found little to no evidence that cocaine would support autoshaped lever pressing, despite the fact that a concurrently run control group that received food pellets autoshaped quickly. But, important procedural differences (such as trial-spacing and frequency) may play an important role with drug reinforcers. For example,

unpaired US presentations hamper the development of the autoshaped response, and it may be that the persistent high that might develop from the repeated presentation of cocaine reinforcement may effectively serve as unpaired trials with a low inter-trial interval. When these trial-spacing issues were resolved by Uslaner, Acerbo, Jones, and Robinson (2006), significant sign-tracking of a lever for cocaine infusions occurred. But, even still, these sign-tracking responses were restricted to movement in the area of the lever and not actual lever presses. So, one important suggestion for the use of cocaine or drug reinforcement in this paradigm would be the use of a very long inter-trial interval to make certain that any remaining cocaine from the previous trial had been substantially eliminated, and the careful use of visual observation during the initial phases of training.

One possible advantage for the usage of a cocaine or drug reward is that the use of a non-spatially-localized reward such as the delivery of an addictive drug might eliminate any latent goal-tracking behavior that might interfere with responding during the task. In a preliminary neurobiology experiment with rats that performed a task identical to the one given in Experiment 2, rats given infusions of muscimol (a GABA agonist which inactivates a region of cortex) into their prefrontal cortex showed (in addition to much weaker anticipatory responding) substantial levels of a behavior not normally observed: they returned to the food-hopper mid-sequence, as if to obtain their reward after only one or two responses instead of the required three. Thus, rats were performing additional goal-tracking responses when a system that might mediate their prospective memory for spatial locations had been removed. Rats that were reinforced with non-localized drug infusions (as opposed to pellets delivered to a feeder located in a particular spatial location) might not evidence this kind of goal-tracking response.

The utilization of tasks such as the one presented in this dissertation that appear to tap into mechanisms of prospective, goal oriented processing might be beneficial for the study of drug addiction or drug seeking behavior. Additionally, the substitution of addictive substances or drug reinforcers for food reinforcement in the current discrimination may be a similarly interesting avenue to pursue.

Schizophrenia

Beyond speculation about the possible role of prospective mechanisms and drug abuse, an existing connection between prospective memory and disease mechanisms can be found in recent schizophrenia research (Kraus, Keefe, & Krishnan, 2009). Current research has shown that schizophrenic patients have difficulty utilizing prospective memory, both those that are cued (Kumar, Nizamie, & Jahan, 2005) and are not cued by external events (e.g., Elvevag, Maylor, & Gilbert, 2003). Based on this evidence, schizophrenics might have difficulty both responding to a cue to remember a particular event (e.g., despite setting an alarm to remember to take their medicine at 5pm, schizophrenics might fail to respond to the signal) or remembering an event without that external cue (e.g., remembering to take their medicine at 5pm).

But again, the majority of the tasks investigated in this literature involve the kind of planning and execution that typifies the clinical definition of prospective memory. Are schizophrenics also impaired in the kinds of prospective coding tasks that typify those conducted with animals? Would schizophrenics perform differently on the types of motor-planning tasks previously described, or perform differently than normal controls on the three-step anticipation task described in this dissertation?

One study by Jarrett, Phillips, Parker, and Senior (2002) investigated a previously discussed perceptual component of prospective coding, the “representational momentum” effect, in schizophrenic patients. Here, Jarrett et al.

used a slightly different version of the task in which patients were shown two sequential pictures and asked if they were “same” or “different”; pictures were either sequences that might have occurred forward in time (e.g., a person holding a cup of coffee as Picture A; the same person dropping the cup of coffee in Picture B) or sequences that might have occurred backward in time (e.g., coffee dropping in Picture A, coffee holding in Picture B). Despite the predictions of the study’s authors, participants with schizophrenia made more errors in the forward than in the backward condition, indicating representational momentum.

But, future studies using simpler stimuli (such as the moving clock-hand of Neiwirth and Rilling or oscillating ball of Kerzel et al.) and a lower reliance on conceptual information may show differences in this patient population.

Therefore, the creation of tasks with non-verbal instructions that more closely mimic learning paradigms may be particularly useful in this research area.

Similarly, the future development of animal models of prospective processing may be especially important for our understanding of how this disorder affects cognitive mechanisms. Again, the transition from current tasks, that typically rely more on “high-level” report mechanisms or conceptual information, to more basic tasks, that can be replicated and conducted with animals, may have important implications for understanding the neurobiology of this complex disease.

A further complicating factor here appears that whereas high-level clinical disorders such as depression have been modeled in animals by focusing on specific symptoms like anhedonia or behavioral responses to certain classes of drugs after stress challenges, schizophrenia is a complex disease and a number of its symptoms have been independently modeled in animals (e.g., inattention, behavioral stereotypy, locomotion, and the presence of particular neurobiological factors). But, it appears that the performance of these animal models on prospective memory tasks have not been well addressed by these animal

researchers. So, one possible clinical relationship between the current work and possible future work may be to assess anticipatory behavior with current models of schizophrenia in animals.

Anticipation in Ethological and Historical Traditions

In his famous tribute to Lorenz, Tinbergen (1963) characterized ethology as “the biological study of behavior” (p. 411). He drew a distinction between the ethologists and animal anatomists, the former being those who observed the behavior of animals by asking “Why do these animals behave as they do?” It turns out that there is a modestly strong relationship between the behavior quantified in this dissertation and two areas one might characterize as ethological, one being “Intention Movements”, the second being the distinction between “Appetitive” and “Consummatory” behaviors. Therefore, I will next discuss these earlier measurements of anticipatory behavior and their relationship to the phenomena observed in this set of experiments.

Intention Movements

An interesting ecological link between the anticipatory behavior observed in these experiments and behavior observed in nature is in the “intention movements” of many animals, especially birds (Daanje, 1950). These movements are partial or incomplete versions of full movements that often precede complete locomotor activity; they were named intention movements by early researchers (e.g., Heinroth and Lorenz) because these incomplete movements would often serve as discriminative cues for the ethologists studying them. For example, the Griffon Vulture adopts a crouched position with a curved neck and outstretched beak before it is about to take flight; the Robin bows once or twice before it is about to take flight; the Little Owl ducks upon being frightened (Daanje, 1950). When studying, say, a Robin, the ethologist could predict the bird’s next movement based on these partial “intention movements”.

Interestingly, these intention behaviors appear also to be noticed *by other conspecifics*, such that the “intention movement” may become a ritualized behavior that gets subsumed into a mating, contact, or communication ritual. In this way, the “intention movement” that serves as a cue for the meticulous researcher has also come to serve as a discriminative stimulus for an observant conspecific.

For example, consider the flight of a flock of pigeons (Davis, 1975). If, as little kids are wont to do, you were to run up to a large flock of pigeons and wave your arms wildly about, they will all suddenly disperse. Presumptively, this case is mediated by the large discriminative stimulus (i.e., you) running at the flock, and an independent reaction from each observer. Setting this obvious case aside and paying close attention to the flock, it is clear that many birds will take off and land into the middle the flock of birds without eliciting an entire flock movement. So the flight of one individual bird does not always elicit large flock behaviors. But let’s consider a further, perhaps more peculiar situation. Suppose one individual pigeon in this flock could be selectively startled by the sight of a cleverly hidden predator or a highly specific stimulus. Would the rest of the flock take flight as a result of this single bird’s frightened escape, or would they remain behind, unaware of the specific stimulus that triggered the first bird’s actions?

It turns out that, if an individual pigeon is startled into sudden flight, the entire flock flies with it. This behavior is, of course, highly adaptive: if one pigeon notices a concealed or quickly approaching predator, the individual movement of that more perceptive pigeon can serve as a signal to the rest of the flock to flee. To experimentally address this question, Davis (1975) arranged a large room with a gridded floor which could be selectively electrified in particular places. When an individual pigeon was shocked, it took flight; but, so too did all of the other pigeons in the flock, despite not feeling the shock or having any

outward indication that it occurred. One possibility is that the “communication” to the other birds to flee in this case is mediated by something about the flight movements themselves, but in fact, this turns out not to be the case. The key difference between the case in which a pigeon flies away and the flock stays put and the case in which a pigeon flies away and the flock concurrently flees is in the pre-flight intention movement that is performed by the pigeon that makes a “planned” flight as opposed to those that make startled flights. These pre-flight movements cue birds that a flight is about to occur; therefore, the entire flock does not flee. Other examples of such intention movements serving as communication signals between conspecifics are numerous (Daanje, 1950; Leger, 1993), occurring in animals as far ranging as dogs (Bekoff, 1977) and ants (Holldobler, 1971).

The point of discussing intention movements here is that they bear some resemblance to the behaviors observed in the observing responses in Link 1. This resemblance is that they could be interpreted as fractional movements that belie the next movement of the animal with some discrete behavior that allows a careful researcher to predict the location of the animal’s next response (see Figure 26). But, in another sense, the behaviors observed in this dissertation differ dramatically from these ethological intention movements in that the anticipatory Link 1 responses occur in a highly constrained situation with decidedly unnatural behaviors, produced through the arbitrary and artificial linkages of successive stimuli (though, in fairness, the developmental or learned trajectory of many intention movements is unclear). Additionally, these anticipatory behaviors occur even when the topography of the initial and terminal behaviors are different (see Figures 37 and 38), quite different from intention movements, in which the anticipatory and final forms of the behaviors often have highly similar topographies.

So, the most striking similarity between the intention movements of early ethologists and the behaviors observed in this dissertation (and those observed by other researchers that study the pre-choice movements of adult or infant human participants) is that each are viewed as a behavioral marker that predicts the future behavior of the organism and both are interpreted as bearing some mechanistic relationship with the current cognitive state of the organism. Whereas obviously our definitions of cognition and the potential usage of these movements as dynamic windows into cognition has changed since the time of Lorenz and Daanje, the basic point remains the same: often, without the use of any sophisticated neural measurements (e.g., fMRI activations or electrophysiology), behavioral measurements are sometimes sufficient to provide similar kinds of insight into cognitive processes and at the very least can provide these neurobiological methods with an important source of convergent evidence.

Appetitive / Consummatory Behaviors

A further linkage between the historical, ethological tradition and the experiments described in this dissertation concerns the distinction between “appetitive” and “consummatory” behaviors. As noted by Sachs (2007, 2008) in a highly critical review of the continued use of this terminology, the appetitive/consummatory distinction has fallen dramatically out of favor and is typically paid little attention in modern neuroscience, insinuated by Sachs to be because of these terms direct linkage with outdated models of neural function (e.g., Lorenz’s 1950 psycho-hydraulic model). But, despite the inescapable linkage of these terms with now defunct theories, the historical roots of these terms were much more purely behavioral. The behavioral etymology of these terms is well described by Ball and Balthazart (2007) and bears reviewing here before discussing their possible relevance to the current dissertation. The distinction between “appetitive” and “consummatory” behaviors originated with

Sherrington (1906), although the terminology was formally introduced by Craig (1917). The main concern noted by these early ethologists was that whereas many behaviors seemed somewhat random, undirected, and unpredictable, other behaviors appeared more focused, directed, and stereotypic. The former behaviors were termed “appetitive” whereas the latter behaviors were termed “consummatory”, though there were many additional implications of these terms. For example, one of the main distinctions between appetitive and consummatory responses was that “consummatory” responses were generally assumed to be “innate” responses.

Consider the behavioral example provided by Ball and Balthazart (2007) of quail mating; the male quail engages in a series of vocalizations, it engages in “searching” behaviors for a female quail, and it produces “strutting” displays that are somewhat decoupled from the general stimulus of female presence. When a female is actually present, the male is less likely to engage in some of these behaviors (Potash, 1974). Yet, the actual act of copulation follows a relatively fixed pattern, in which the male grabs the female’s neck, mounts her, and attempts to contact their two cloacae. In Ball and Balthazart’s view, the former behaviors (e.g., vocalization, strutting) are “appetitive”, whereas the consummation of the sexual act is “consummatory”. Thus, the appetitive behaviors of these animals somewhat less focused, not elicited by particular stimuli, and non-stereotypic; the consummatory behaviors of these animals are highly focused, elicited by particular stimuli, and highly stereotypic.

These notions of appetitive and consummatory responses were utilized by other learning theorists to explain other types of behaviors, such as feeding behaviors. Consider the analysis provided by Wasserman (1981) of the pigeon feeding behavior as such an example. Appetitive behaviors include “becoming active and seeking food”; consummatory behaviors are those that come later, once

the bird has “[Spotted] a kernel of grain, the bird approaches it, pecks and seizes it in his bill, and finally swallows it” (Wasserman, 1981, p. 39).

These behaviors actually have a curious relationship to autoshaping, in that the apparently stereotypic or “innate” behavior of grain consumption is actually a learned response that changes over successive presentations of food and non-food in the developmental history of the organism. For example, Hogan (1973) presents a series of elegant observations about the behavior of newly hatched chicks and their consumption of food. When reared in social isolation (i.e., without contact with the mother hen or other chicks), chicks peck at (and eat) sand or food indiscriminately during their first two days of life. Only during their third day of life, after sufficient experience pecking at grains and being nourished, do they start to peck primarily at grain (although they still direct some number of pecks at sand). The connection to autoshaping is that the same relationship develops between the autoshaped keylight and the food reinforcer; the pigeon learns to approach and peck the autoshaped keylight because of its successive pairings with food reinforcement.

It is worthwhile to consider whether the notions of “appetitive” and “consummatory” behavior are applicable within the current experimental context, and whether they might provide a valuable framework for analyzing these effects. To start, there is some degree of similarity in the appetitive-consummatory distinction and the anticipatory movements seen before the response to the terminal link stimuli. The pecking responses during Link 1 and Link 2 are directed in the location of the Link 3 stimulus; resembling the “searching” behaviors that precede the consummatory response. The pecking responses during Link 1 are slower than those in Link 2 or 3 (see Figures 4, 11, 19, and 22); in that sense, one could say that the Link 1 pecks are less stereotypic and more “appetitive”, whereas the fast responses seen during Links 2 and 3 are more

stereotypic and “consummatory”. And, in terms of IRT, the faster responses in Link 3 have a lower variability than those in Links 1 and 2. Additionally, in a previously unreported analysis, we examined the standard deviation of the pecking responses to the Link 1, Link 2, and Link 3 stimuli during Experiment 1 independently for each trial type; there was a strong trend for the standard deviation of pecking responses to decrease across each successive link (a pattern of behavior shared by three of the four birds, with the fourth bird showing little difference between the standard deviation in each link). This pattern of behavior further implies that responding grows more stereotypic or consummatory toward the end of the response sequence. But, we chose not to report this analysis because the stimuli differ in the Links (there is the unlikely but possible concern that the star stimulus might attract particularly concentrated responding because it consists of a figure on the key rather than a diffuse color). In any event, a number of factors confirm the concept of increased narrowing or behavioral stereotypy the closer the pigeon gets to reinforcement.

But, despite these aspects of the “appetitive” vs. “consummatory” distinction being observable in our dataset, the terminology itself seems unfavorable because it implies a qualitative distinction between behaviors observed early in the trial and behaviors involved later in the trial; or behaviors observed early in acquisition and later in acquisition. There may be a clear link between concepts; researchers have realized that the qualitative distinction between these terminologies is only a generalization and that a quantitative distinction may be of greater value. Similarly, my preference is for a model of this behavior that implies a quantitative shift in behavior, rather than a qualitative shift in behavior.

Nondifferential vs. Differential Reinforcement

Although the three-link procedure utilized in this dissertation (see Figure 1) is somewhat complicated to explain to humans, it is simple to explain to animals. After all, after only ten training sessions of about 100 trials each, both rats and pigeons were quickly shifting their response location in anticipation of a stimulus, even with no explicit requirement that they engage in this behavior (see Figures 2 and 6). Whereas a very small number of subjects failed to learn these tasks, the many that did so did not require any differential reinforcement to shift their choice behavior from one key to another in Link 2 or from one side of the stimulus to the other in Link 1.

The particulars of nondifferential and differential reinforcement were not a central issue to this dissertation, but deserve discussion because relatively few tasks offer the ability to reinforce the animal for any choice that it might make while simultaneously obtaining such unequivocally clear discrimination performance. Tasks or models that utilize nondifferential reinforcement might be construed as “Hebbian” or “statistical learning” tasks; they involve the organism or model learning about the collocation or contemporaneous concurrence of some set or pair of stimuli, but might be interpreted as not directly teaching that relationship. Examples of such tasks involve contextual cueing (Chun & Jiang, 1998) or the serial reaction time task (Nissen & Bullemer, 1987), in which participants are asked to respond to a target or sequence embedded within a fixed pattern. This pattern is “implicitly” presented to the subject; i.e., there is no signal for the participant to use or recognize this pattern. These kinds of tasks are also called “unsupervised learning” tasks. In animal learning tasks similar to the ones presented in this dissertation, the clearest examples of nondifferential reinforcement come from the autoshaping studies of Wasserman et al. (1978) and Rescorla and Cunningham (1979). Here, reinforcement is completely unlinked to

the animal's behavior; reinforcement is given every trial, regardless in which behaviors the animal chooses to engage.

Tasks that involve differential reinforcement are ones in which the subject is explicitly taught to use some feature of the task or display; this task may or may not involve the use of verbal instructions. For example, subjects might be taught, but not instructed, to respond "same" or "different" to a set of items by rewarding them with a pleasant chime and "points" when they are correct and a timeout/buzzer when they are incorrect (e.g., Castro, Young, & Wasserman, 2006). These tasks are also called "supervised" learning tasks.

The differences between these situations in which participants have been given nondifferential (unsupervised) or differential (supervised) training on a set of items have been of recent theoretical interest (e.g., Love, 2002). The fact that our task incorporates some aspects of nondifferential training may allow us to capitalize on the differences between these training procedures and lead to some interesting discoveries about learning in differential and nondifferential situations.

As an example of such an inquiry, we (Brooks, Ng, Buss, Marshall, Freeman, & Wasserman) attempted to train rats on a version of our three-link task in which stimuli from distinct perceptual categories (e.g., "cars" and "humans") were used as the stimuli, but the rats failed to make congruent Link 2 report responses. However, after the addition of a delay for incongruent responses (between Links 2 and 3, as in Experiment 5), the rats began to learn. Interestingly, these rats were the same rats that had earlier received training with the brightness and orientation stimuli in Experiments 7 and 8; there, they performed anticipatory reports without the addition of any such differential component. Thus, the addition of a differential delay to the task aided the rats in learning the more complex category task, but this delay was unnecessary in teaching a task with presumptively more basic stimuli. The particulars of how the addition of this

delay interacts with learning despite the delivery of reinforcement on every trial may warrant further study.

Additionally, the current procedure could be easily modified to one in which differential reinforcement was provided based on the animal's response. In that new task, pigeons could receive reinforcement for responding during Link 3 only if they chose the congruent side during Link 2. Or, Link 3 could be skipped altogether; reinforcement could be delivered immediately upon making the "correct" or "incorrect" choice during Link 2. This change may or may not further promote anticipatory responding. The data analyzed in Experiment 12 were from an experiment in which differential reinforcement was given to the animals; there, we observed a highly similar trend toward making anticipatory reports during the observing response, but it is difficult to say whether this trend was stronger or weaker than any others in the dissertation because the design of the experiment and stimuli used were so very different. Similarly, the data from Experiment 13 are from a task in which differential reinforcement was given; there, anticipatory reports were exceptionally strong. But again, it is again difficult to make any general statements about the nature of reinforcement because so many other parameters of the tasks were different. Indeed, in these latter tasks, differential outcomes were given as well as different reinforcement, an even further distinction between these and other procedures presented in this dissertation.

Still, it is not hard to imagine an investigation into the power of the "approach" response or spatial contiguity could be conducted with differential reinforcement in which the Advantage/Control/Disadvantage design used in Experiments 4, 5, and 6 was adopted. Here, the differential contingency would be differential reinforcement; reinforcement would be given following Link 3 responses only if the correct choice was made by the animal in Link 2, whereas a timeout and correction procedure could be given if an incorrect choice was made.

In the Advantage condition, responses congruent with the Link 3 location would be reinforced whereas incongruent responses would be punished; the opposite would hold true in the Disadvantage condition. If timeouts or correction procedures were used, it would be difficult or impossible to implement the Control condition that was run in Experiments 4, 5, and 6 because on 50% of the trials the animals would be subjected to a probabilistically unavoidable timeout; if correction procedures and timeouts were not used, it would be possible to design the experiment exactly as before.

It may be a fruitful exercise to attempt to replicate some of the tasks used in this dissertation both with and without differential reinforcement to compare the effects of differential reinforcement on anticipatory behavior.

Returning to Dynamics

In the last section of my dissertation, I would like to return to the general point at which this investigation started; namely, the nature of pre-choice behavior as a dynamic process. In the introduction, I initially referenced mouse movement and eye movement studies conducted by Spivey et al. (2005) before progressing to pecking responses by pigeons and nosepoke responses by rats. In the way of a brief reminder to the reader, these studies by Spivey used the graded drift in spatial responding as a proxy for the amount of activation of a particular concept or category. The inference made by Spivey et al. (2005) was that the participants' mouse movement drifted toward a spatial location because the partially activated conceptual information activated a spatial response location (concurrently displayed to the participant), thus providing the researcher with a behavioral index of the degree or time-course of the concepts' activation.

Whereas most of the stimuli presented to the pigeons and rats in this dissertation were highly discrete and did not result in the same degree of conspicuous spatial drift across time (although, see Experiment 13; Figure 39),

one might wonder whether a similar prospective mechanism might create the differential Link 1 response distributions. Quite simply, could the activation of a prospective memory location cause a kind of spatial “drift” or “pull” in responding to a centrally located stimulus? To answer this question mechanistically, this final section in my general discussion will be presented in the form of a computational model that may serve as a starting point for the development of a unified framework of the general results presented in this dissertation.

Description and Justification of the Basic Model

For pragmatic purposes, this model will be presented as a “sketch” of a computational framework rather than a complete computational account. Specifically, I will attempt to sketch a basic computational model for these results and describe certain components of this model in detail, along with testing the central question at hand, which is whether such a mechanism could account for such spatial drift in observing responses. It is my hope that this outline of a framework for modeling these experimental results may, with greater development, come to elicit a number of more directed, theoretical questions about the nature of anticipatory pre-choice behavior and the nature of prospective memory and/or its neurobiological underpinnings.

While a traditional associative account may have good success explaining the shifts in Link 2 behavior that arise from the presentation of particular stimulus features combined with the function of the Link 3 stimulus as a conditioned reinforcer, it would likely have difficulty, without substantial modification, to account for the shifts in behavior observed in Link 1. Similarly, additional assumptions would be required to specify the linkage between activation and behavior in an associative account. Therefore, this computational or theoretical “sketch” will be done using the general principles of *dynamic field theory* (DFT).

The DFT (Erlhagen & Schöner, 2002; Schutte, Spencer, & Schöner, 2003) is a formal mathematical framework which utilizes concepts from dynamical systems to model embodied cognition. It makes good sense to use the DFT as a starting-off point for a mathematical model in this case as one might say that many recent implementations of the DFT are inherently spatial in nature; in these cases, the environmental (or biological, or computational) substrate that couples relevant dimensions between tasks is a spatial representation. This representation is useful because the task and behaviors that I have been investigating are also primarily spatial. Second, dynamic systems often deal with responding along a continuous dimension. When dealing with pigeons and rats, there is little annoyance offered by the sometimes “discrete choices” afforded to humans by movement of say, the left or right limbs (Erlhagen & Schöner, 2002); the pigeon has one beak with which to localize pecks and a continuous spatial dimension (location on the touchscreen) in which to respond. Thus, there is a good marriage between the necessarily continuous nature of response collection and the continuous nature of the model’s output. Lastly, the DFT has mechanisms to deal with how memory might guide the spatial location of a response. This mechanism is of fundamental importance because the proposed mechanism for the shifts in anticipatory behavior observed is a mnemonic code for an upcoming spatial location. Because similar spatial responding driven by memory has been modeled in the past (e.g., Schutter, Spencer, & Schöner, 2003), this modeling framework should be amenable for simulating the current set of experiments.

In DFT, tasks are modeled as fields of activity that update on a moment-to-moment basis. The rule by which fields are updated is reproduced below from Schöner (2007) with most of the complex mathematical expressions removed:

$$\tau \dot{u}(x,t) = -u(x,t) + \text{resting level} + \text{input} + \text{field interaction}$$

In simple terms, this formula states that the change in the activation of a given

unit at any given timestep is a summation of four components: (1) the previous activation of the unit; (2) the resting level, or default state of the field; (3) any additional current input to that unit; (4) interactions between the units on both the same and different fields, according to the specifications of an interaction kernel. Whereas each of these parameters is important, the interaction term is crucial. This interaction specifies that nearby units are *excited* by field activity whereas far units are *inhibited*. Because of these properties, it is possible to establish self-sustaining peaks of activation in which the propensity to respond at one location is likely to suppress the propensity to respond at other locations (see Schöner, 2007). Thus, the model can make discrete “decisions” between multiple inputs (Erlhagen & Schöner, 2002).

The basic model that I will sketch will consist of four dynamic fields, though the first two that I will describe will be of primary importance for modeling this task. The first field will be a two-dimensional field that can be thought of as either representing the current spatial working memory of the animal or as a form of behavioral readout. One dimension of this field will be horizontal *spatial location* and the second dimension will be *activation strength*. When peaks of activation build in this field above threshold, we can interpret these peaks as the direction that the animal will direct its response. The main test of our model will come from the behavioral readout provided by this field when simulating both Link 1 and Link 2 behavior. If memory for prospective response locations can influence the peaks that form in this field, then we should see the peaks that form in this field during Link 1 “smear” or “drift” in the direction of a prospective response location. And, with the same set of parameters, we should see a strong preference for building a peak in the prospective response location in Link 2 despite the presentation of multimodal input to the model.

The second field in this dynamical system will be a three-dimensional field that represents memory for a specific feature of stimuli in space. So, one dimension in this field represents a particular feature (such as color), one dimension represents space (as in the first field), and one dimension represents activation level. Activation in this second field can be interpreted as memory for where particular features are located or have been located in the past. The differential subthreshold activation of color-space location within this field is critical for modeling this behavior, because in order for the animal to make differential spatial responses based on the color of the stimulus on each trial, the animal must have represented particular prospective locations depending on the color of the stimuli shown. Therefore, despite the previously noted difficulties in adapting a traditional associative account to modeling these data, the model presented using the DFT is still fundamentally associative in nature; the primary means by which the model learns and accounts for shifts in responding is through the association between features of the stimuli (such as color or orientation) and the location of that stimulus in space.

In this type of model, the first and second fields are *coupled* along the spatial dimension, such that activation passes between them. The third and fourth fields in this dynamical system are inhibitory fields that facilitate and maintain the stable localization of peaks of activation, the details of which are described in greater detail in other publications that have utilized this modeling framework (e.g., Johnson, Spencer, & Schöner, 2008; Simmering, Spencer, & Schöner, 2006).

Simulating an Experiment

To explicate further how we might model the current task using this framework, we will simulate Experiment 1 as an example. Rather than model learning (which is complex using these frameworks and is not really the central

mechanistic question addressed by this simulation), we will deal with one presumptive end-state performance in which a strong prospective memory has formed for the left location on trials in which red stimuli are shown and a similarly strong prospective memory has formed for the right location on trials in which green stimuli are shown (as in Experiment 1, see Figure 1).

To simulate this end-state performance, we will make a parametric change. In this modeling framework, the main parametric manipulation that will be done to represent the pre-existing prospective memory of response locations will be in the form of a *preshape* to the color-location field. This *preshape* can be thought of as a pre-existing long-term memory for responding in a particular location (e.g., Thelen, Schöner, Scheier, & Smith, 2001) or for particular task parameters (Erlhagen & Schöner, 2002). Whereas this normally might be formed through experience in a long-term memory field (Spencer, Perone, & Johnson, 2009; Erlhagen & Schöner, 2002), here, its presence will be set in a static fashion to probe the dependence of the Link 1 and Link 2 biases on the metric details of the memory traces that form during learning.

The values used and rationale for this *preshape* bear some further explanation. *Preshapes* are typically added to DFT models to account for particular spatial or featural parameters of the task (Erlhagen & Schöner, 2002). The *preshapes* here will be given at the left and right locations, as these are the locations occupied by the conditioned reinforcing stimuli that occur in Link 3. Furthermore, based on the results of Experiments 1, 2, 4, 5, and 6, it seems fair to assume that the spatial and temporal contiguity between the Link 2 and Link 3 stimuli facilitate the formation of differentially *preshaped* activation at each spatial location depending on the color of the Link 1 and 2 stimuli. So, in the location that will next be occupied by the Link 3 stimulus (i.e., the congruent location), we will assume a strong *preshape* in the color-space field for that

location, indicative of both memory for a possible upcoming response location as well as that location's contiguity with a strong conditioned reinforcer. In the incongruent location, we will assume a relatively weak preshape in the color-space field for that location, indicative of the memory for another possible upcoming response location but with no heightened activation conferred to it due to the lack of contiguity with the Link 3 stimulus. Examples of these color-location preshapes can be found in Figure 40. A complete description of what occurs when the values of these preshape parameters are changed will follow in the discussion of the results of the simulations.

Over the course of an individual trial, two discrete stimuli (to represent Links 1 and 2) will be presented to this model via activation in the first field. The stimuli themselves will be graded Gaussian activations at the location occupied by the response keys. These stimulus presentation will occur in four discrete time-steps over the course of each trial. In the first time-step, a differential preshape will be presented to the color-space field dependent on the color of the stimulus, but no stimulus will be presented. In the experiment, this preshape-alone input accounts for the differential mnemonic codes that have been established over time that might influence observing behavior (see above). In the second time-step, the Link 1 stimulus will be presented to the model in the form of a peak of activation at the center key location (see Figure 41, top panel). This stimulus will be given some time to form a self-sustaining peak and drift toward a prospective response location if such an event might occur. In the experiment, this stimulus presentation and subsequent peak formation is the equivalent of allowing the bird to respond to the central Link 1 location.

In the third time-step, all stimuli will briefly be removed from the model, existing peaks will be squelched, and the model will be returned to preshape conditions. In the experiment, this is the equivalent of removing the Link 1

stimulus along with any continued propensity to respond to the center key, which was unobserved in any of the experimental data. In the fourth time-step, the two Link 2 stimuli will be presented to the model in the form of two Gaussian peaks of activation at the two sidekey locations; again, these stimuli will be given time to interact (i.e., compete) so that the model will make a response decision and form a single stable peak (see Figure 41, bottom panel). In the experiment, this is the equivalent of presenting the colored Link 2 sidekeys and the animal responding to only one of them.

Data from trial simulations of the model are shown in Figure 42. In one of these simulations, a red/left preshape was presented to the model before the presentation of red stimuli in Link 1 and Link 2; responses to these stimuli are represented in red. In the other trial run, a green/right preshape was presented to the model before the presentation of green stimuli in Link 1 and Link 2; responses to these stimuli are plotted in green. Taking Link 2 behavior first, it is clear that despite the bimodal and equivalent input to both stimulus locations, the preshape is sufficient to drive strong responding at only one of these response locations. Thus, the model “commits” to responding to the congruent key, just like the birds and rats. In other words, it takes a multimodal input (i.e., two lit keys) and converts it into a unimodal response (Erhlagan & Schöner, 2002).

Link 1 behavior during these simulated trials is also interesting. Here, there is clear evidence of peak drift after the presentation of a symmetrical central stimulus. Trials in which a red trial was presented evoke more leftward response activation during Link 1; whereas those in which a green trial was presented evoke more rightward response activation during Link 1. This result confirms the main mechanistic explanation of the behavior set forth by the model; that a prospective response location built in long-term memory based on the contiguity of the conditioned reinforcer with one of the Link 2 responses is sufficient to

cause response drift in Link 1. Thus, one possible mechanistic explanation for the “anticipatory” behavior is the representation of the prospective goal in spatial memory based on the contiguity of conditioned reinforcement.

This peak drift during the first stimulus presentation (i.e., Link 1) is similar to the peak drift observed in the model developed by Schutte, Spencer, and Schöner (2003). That simulation modeled the A-not-B task described by Piaget (1954), in which children will erroneously return to a previously reinforced location despite being clearly shown a toy being hidden in a novel location. In their model, a preshape that formed through the repeated presentation of a toy located at a particular location (A) influenced the subsequent response of the model when a toy was then presented at a novel spatial location (B). On the trial in which the stimulus was presented at Location B, a self-sustaining peak that formed upon stimulus presentation drifted across time closer toward Location A (see Figure 1 of Schutte et al., 2003, for a graphical representation of this peak drift). This peak drift in working memory was interpreted as being one possible mechanism that could explain the error that children commit.

Figure 43 examines the spatial drift in my current model in more detail, because this figure includes time as a principal axis. Presented in this figure is a single trial using the red/left preshape. In this figure, warmer colors represent stronger activation and cooler colors represent weaker activation. The trial begins with the preshape toward the bottom of this figure (the period of initially blank responding) and proceeds toward the top of the figure (see the Y-axis, which represents time). The first ridge of activation in this figure is caused by the presentation of the first stimulus. Notice that there was a small amount of time directly after the stimulus presentation in which this activation was relatively diffuse, but centered toward the Link 1 key (reflective of the Gaussian nature of the input). But, when a peak (or ridge) built in response to the stimulus, it went

through a very short period of spatial drift toward the preshape location. It should be noted that little spatial drift beyond what is initially driven by stimulus dynamics occurs; the peak did not drift wildly to the left or progressively shift throughout the trial, it eventually settled into a relatively stable state. This spatial observation is quite similar to what is observed with pigeons; despite the observation of differential spatial response in Link 1, we observe little “drift” in behavior like that observed by Spivey et al. (2005) apart from that observed in Experiment 13 (see Figure 39). And, in a sense, this is a desirable result: the birds can only respond to the Link 1 stimulus, so a model that reported responding at other locations would not seem to have very high face validity. One possibility for this observed behavior both in the pigeons and the model is due to the parameters of the task (i.e., “task space”), and in particular, the strong nature of the Link 1 input. Given these parameters, it might be that spatial drift is unlikely to occur once a stable peak of responding has formed, and for the birds, most responding only begins “post-drift”.

Continuing to analyze Figure 43, the next blank period was the time at which the peak formed in Link 1 was squelched (as the key is no longer available) and the prospective preshaped locations were re-presented to the model in preparation for Link 2. There was then a small period of “indecision” on the part of the model as it chose between the available Link 2 response locations. This “choice” was entirely driven by the interaction between the preshape and the presentation of the stimuli at the Link 2 locations. But, once a peak was formed at this location, it grew progressively stronger and stable while the other response location continued to be inhibited. Thus, rather than a probabilistic choice rule (e.g., Luce, 1986) for determining spatial decision making, the dynamic interaction between the inputs is responsible for resolving the multimodal input into a unimodal decision (see Erlhagen & Schöner, 2002).

The final analysis of this DFT sketch concerns the presentation of two different preshapes to the model; one of these was relatively strong and the other was relatively weak. The data from this comparison can be seen in Figure 44. Both preshapes were sufficiently strong to be able to alter the spatial location of Link 1 responding (though the shift in the Link 1 response location during the weak preshape was *very slight*), but it is evidently clear that the stronger preshape creates a stronger Link 1 peak drift than the weaker preshape. This parametric difference was presented to demonstrate the importance of this preshape parameter for influencing the spatial distribution of Link 1 responses.

Interpreting Other Experiments Using This Model

Beyond explaining only the spatial shift in Experiment 1, conceptualizing the task using this DFT model may offer explanations for what occurs during other experiments in this dissertation. Whereas the true test for any good model of a psychological process must ultimately be its ability to predict novel experimental results, re-evaluating the presented results using this framework may help to tie together some of the diverse experiments that we have presented.

For example, consider the relatively weak spatial anticipation observed in Experiment 3. In that experiment, orientation cues were used in Link 1 and color cues were used in Link 2. Conceptualizing this task according to the DFT model, the switch of the feature dimensions in Link 1 and Link 2 may dramatically influence the way the preshape (or prospective memory) is able to interact with the stimulus presented to the bird (or input presented to the model) presented in Link 1. In the DFT model, using two separate feature dimensions in the stimuli (such as orientation and color) will necessitate using two separate feature-space fields to represent the two separate features. This change will be prompted by the previous use of DFT models to account for the binding of different features of visual stimuli (Johnson, Spencer, & Schöner, 2008). One of these feature-space

fields would be for the interactions between color and space (as before); the other would be for the interactions between orientation and space. The use of two separate feature fields (one color-space field, one orientation-space field) may result in the prospective preshape being present in only one of these fields, being sufficient to drive highly accurate Link 2 discrimination (as is observed in the Experiment 3), but insufficient to cause any spatial anticipation during Link 1 (also observed in Experiment 3). In effect, conceptualizing the task in this way might suggest that the pigeons were not binding orientation, color, and Link 3 stimulus into a complete sequence of events, but instead may be importantly controlled by the particular features used in the stimuli. Future investigations may utilize a similar task (as well as a spatial response) in order to test how animals or children respond when the features of the Link 1 and Link 2 stimuli are different or similar.

This model may also offer some additional insights into the behavior of the rats when different spatial locations were presented in Experiment 7, as well as accounting for generalization performance in Experiment 8. Whereas a precisely similar study has not been modeled by the DFT before, a similar study modeled by Erlhagen and Schöner (2002) may be worth mentioning. In that simulation, which modeled the timed movement initiation paradigm described by Ghez, Favilla, Ghilardi, Gordon, Bermejo, and Pullman (1997), the spatial location of inputs was varied. There, close spatial inputs tended to result in the formation of a unimodal peak that took time to resolve into a unimodal distribution centered on the correct spatial location, whereas far spatial inputs tended to result in the formation of two bimodal peaks that took little time to resolve into unimodal distributions centered at the correct spatial location. So, one possibility is that the presentation of close inputs in our task makes resolving the

inputs into discrete response locations more difficult, creating more incongruent responses in Link 2 and lower Rho values in Link 1.

Similarly, the generalization in Experiment 8 could be simulated by presenting the model with intermediate values of the stimuli used during training. So long as the inputs along the feature fields are sufficiently broad, intermediate values of the stimuli should result in peaks forming at one or the other of the two trained response locations. As stimuli progressively shift along the feature dimension, the likelihood of peak formation occurring at each of the alternative response locations should progressively shift. This result should also explain the tendency of the animals to respond predominantly “left” or “right” in Link 1 rather than at an intermediate Link 1 location, consistent with descriptions of other generalization data (Migler, 1964).

In summary, the development of this model may offer a possible mechanistic explanation for the shift in response location seen during Link 1 and may offer possible explanations for the behavior seen during Link 1 and Link 2 in the other tasks presented in this dissertation. It may also help serve as a generative model, predicting or modeling new results or task parameters. Future experiments with this model in mind will be required, of course, to test this possibility.

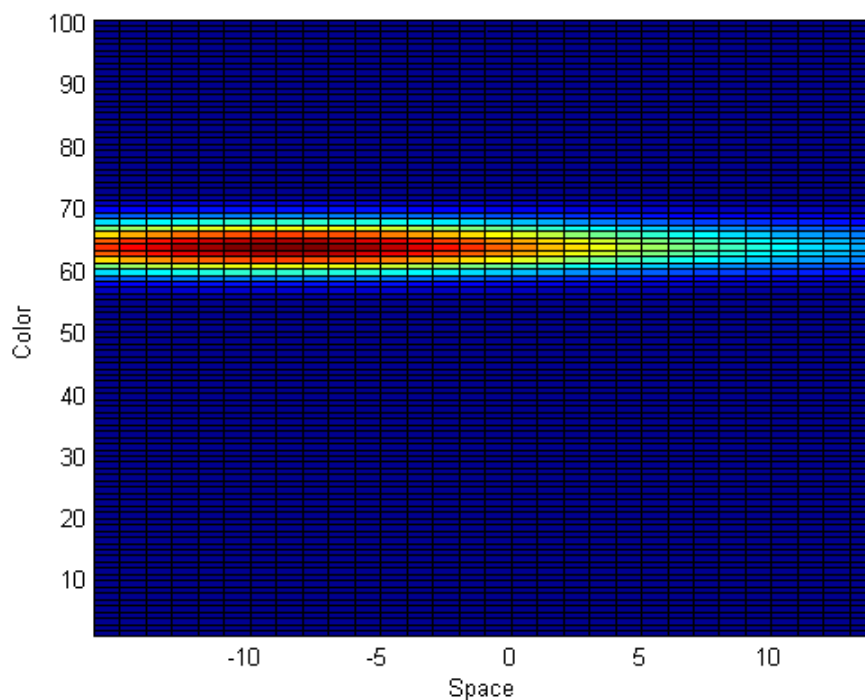


Figure 40 – Example preshape input for the DFT model on trials with a red stimulus. On red trials, subthreshold activation is added at locations previously congruent with conditioned reinforcement. The location of the preshape on the color parameter is somewhat arbitrary.

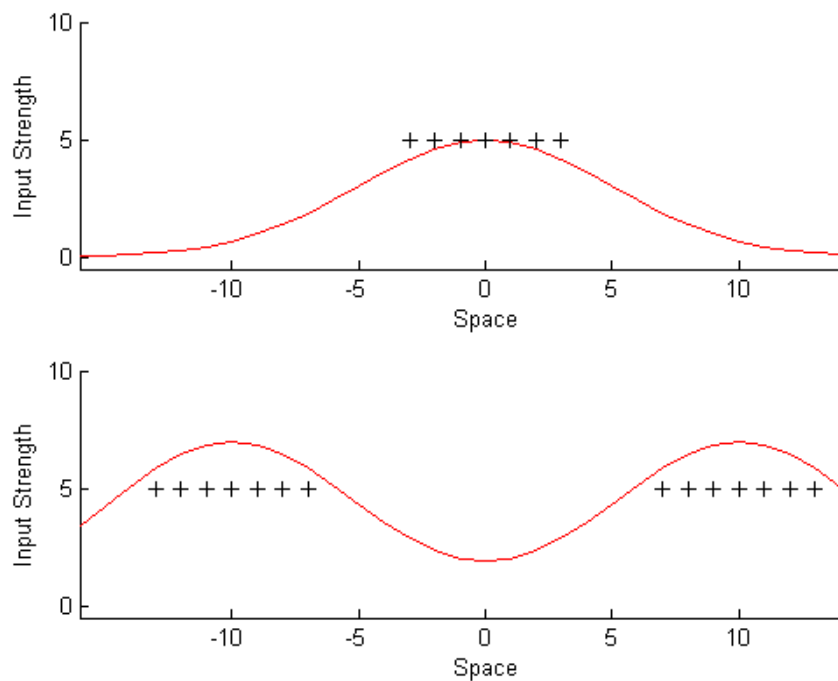


Figure 41 – Task inputs to the dynamic field model for red trials. Black crosses denote the actual location of keys on the screen; actual inputs take the form of symmetrical Gaussian distributions centered on the key locations.

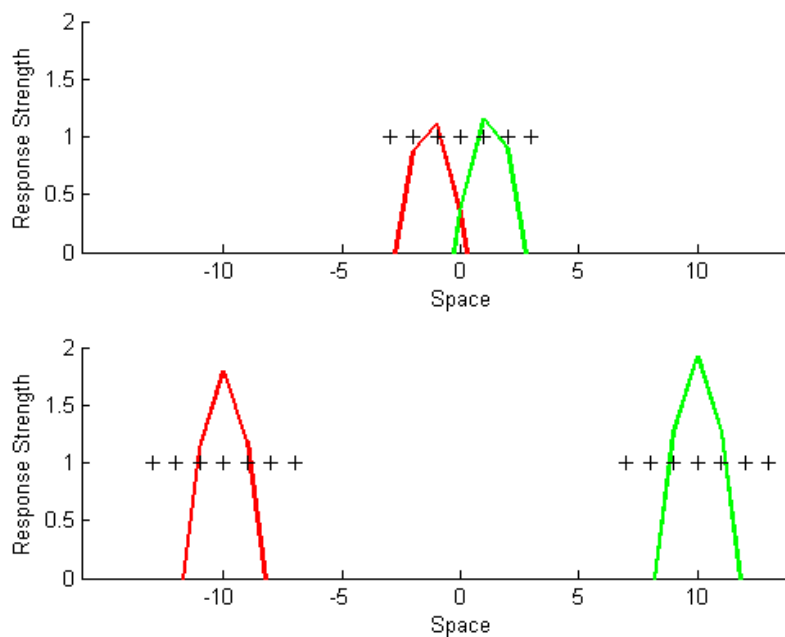


Figure 42– Field response strength in the DFT model. Activation is separated for red trials (shown in red) and green trials (shown in green) during Link 1 (top) and Link 2 (bottom) after using the preshape parameters and input parameters previously described. Black crosses denote stimulus locations.

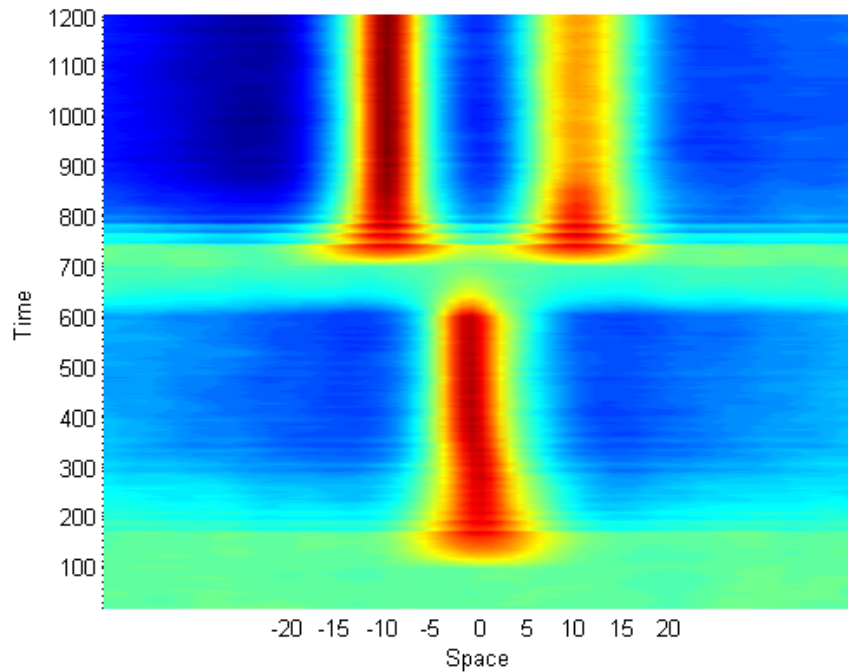


Figure 43 – Activation in the response field as a function of space and time during a Red (left) trial. In this plot, warmer colors represent higher activation, while cooler colors represent lower activation. Darkest reds represent the formation of a stable peak. The first stimulus is presented to the model near time=100; the second stimulus is presented near time=700. See text for additional details.

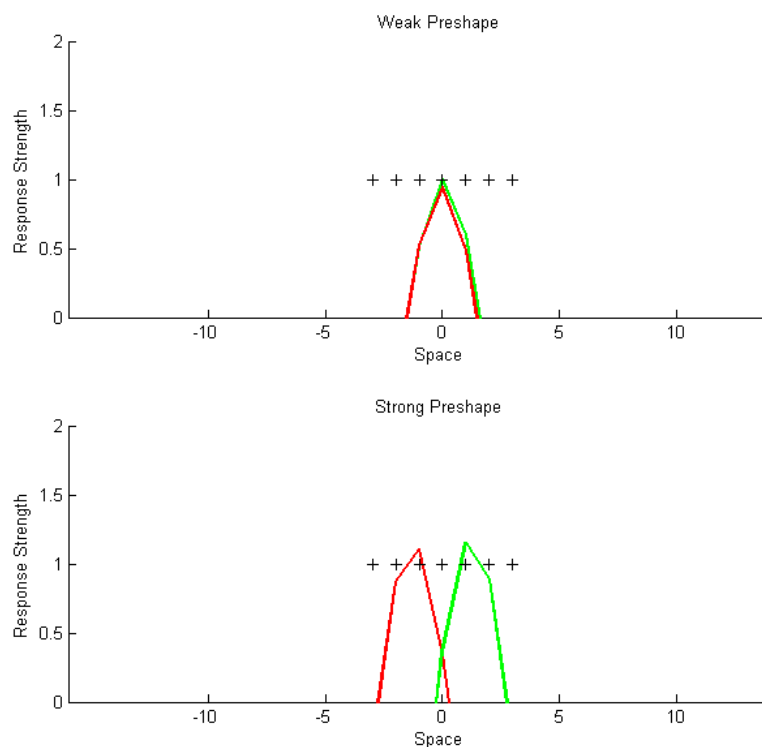


Figure 44 – Response strength for Link 1 after either a weak preshape (top panel) or strong preshape (bottom panel) in a prospective response location. Stronger preshapes produce more clearly divergent Link 1 peak drift.

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APPENDIX

Touchscreen Behavior

It occurred to me while writing this dissertation that some important technical information should be conveyed to those who might be interested in continuing some of these studies, interpreting any of the data presented in this document, or running future studies in which touchscreen responses are measured with a similar level of detail. The most critical of this technical information is the “behavior” of touchscreens commonly used in operant chambers, both in our lab at Iowa and the Comparative Cognition Laboratory at Tufts. We use similar devices; the “behavior” of both types of devices is the same. [N.B.: Future experimenters that find themselves analyzing the “behavior” of their equipment should *also* begin to question their sanity.]

The issue here is really quite simple: despite advertisements and proclamations to the contrary, touchscreen devices do not *really* have pixel-by-pixel resolution. This is similar to the fact that computer keyboards or response boxes do not have millisecond resolution despite the fact that they are used in dozens of studies that report reaction time in milliseconds, or that modern computers have cycling processor clocks that constrain the display of stimuli to particular time periods, which alters the presentation times of stimuli. Not to belabor the point, but as a practical example of a similar problem, unless the hardware that the researchers are using has been *incredibly* optimized for millisecond stimulus presentation, any paper that claims to present stimuli for 250-ms and then record and report responses collected by a standard US keyboard in milliseconds, what should really be inferred is that the researchers programmed the stimuli to occur with 250-ms intervals but the computer added a bit of random

noise, and the researchers collected responses accurate to the nearest millisecond but the keyboard added a bit of variability.

For computers and response boxes (or keyboards) the reasons are particular to the experimental conditions under which these experiments are run. For touchscreens, the reason for the lack of pixel-specific resolution lies in, as best I understand it, the fact that every touch is passed through a set of low-level software filters that attempt to determine where on the screen the peck (or your finger) contacted; these filters are predisposed to returning particular grid locations rather than returning pixel locations uniformly distributed throughout all possible pixels. Of course, these issues are usually hidden from human researchers because our index fingers span the width of multiple pixels.

A good example of this “touchscreen behavior” can be found in the analysis of a small sampling of data. This small sample of data was actually taken from the Tufts touchscreens, but the same issues persist in the Iowa touchscreens as well (or, as best I know, *any* touchscreens). First, consider the top panel of Figure 45; these data have been pooled into 20 pixel bins, and the data look relatively “normal” (i.e., they show “leftward pecking” on “left” trials and “rightward pecking” on “right” trials).

Now consider the data in the bottom panel of Figure 45; these data have *not* been pooled into 20 pixel bins, and show a very strange “sawtooth” pattern of responding. Clearly, this is not due to the way pigeons respond: Pigeons are not innately predisposed to peck in five- or ten-pixel increments! Instead, the touchscreen is predisposed to report some locations more than others.

The reason I presented data from Tufts screens (which are infrared models) rather than data from Iowa screens (which are pressure-sensitive models) is because the Iowa touchscreens (at least, those used to test pigeons) further exacerbate this problem by being pressure sensitive, which, over time, results in

certain areas of the screen being more sensitive to pecking responses than other locations.

The point here is that anyone who initially examines the raw data without having read this appendix and without thinking to average or pool the data as I have may be *disturbed* by the very strange pecking distributions that they obtain and the very real discontinuities reported by the touchscreen. But, now I have given you sufficient warning as to expect them.

These issues can be solved in two ways. The first is to pool the data, as I have, into bins of responding. This averages across these odd spatial proclivities of the touchscreens for reporting certain gridded locations on the touchscreens more than others. If this is the solution, care should be taken that the bins are appropriately reflective of the size of the stimuli; for example, in most of my experiments which used 250-px stimuli, I used either 10 or 25 pixel bins so that extraneous areas would not be included.

The second way to resolve the problem is to convolve the pecking data with a Gaussian filter. This would similarly average the spatial location of pecks, but do so in a more graded fashion. The issue with this method is that the size of a filter sufficient to resolve these touchscreen issues will create the appearance of a large number of pecks outside the region defined by the stimulus.

Either way, the results will be dealt with similar to how these issues are dealt with by human researchers that claim to present stimuli with precise timing; by averaging across multiple trials and binning RTs. But, this issue may turn out to be of more critical concern to pigeon researchers that ask their experimental subjects to localize pecks toward very small regions of touchscreen displays (e.g., small keys spanning 5-pixels) and using these pecks to collect RT data, as the pigeons have very likely completed an relatively high arbitrary number of

“misses” before a correct response is registered due to touchscreen sensitivity issues.

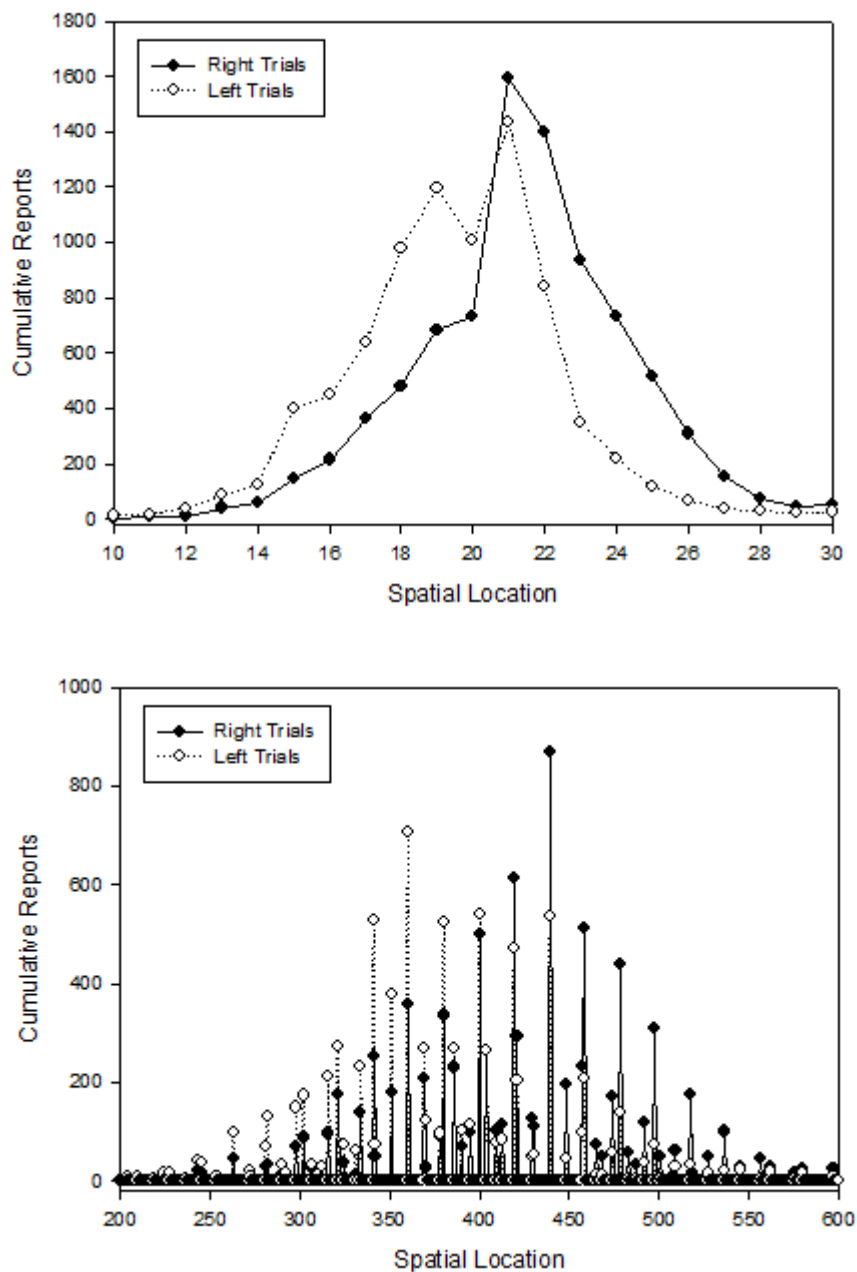


Figure A1 - Data on “touchscreen behavior”. *Top panel:* Touchscreen data that has been pooled into 20px bins. *Bottom panel:* Spatial location across the entire screen, unpooled. Note the “sawtooth” pattern.