

TOPOGRAPHICAL FEATURES OF CONDITIONED INHIBITION  
IN DISCRIMINATED AUTOSHAPING IN PIGEONS

BY

GLORIA D. ELDRIDGE

A Thesis

Submitted to the Faculty of Graduate Studies  
in Partial Fulfillment of the Requirements  
for the Degree of

DOCTOR OF PHILOSOPHY

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Winnipeg, Manitoba

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## Topographical Features of Conditioned Inhibition in Discriminated Autoshaping in Pigeons

In understanding the stimulus control of behaviour, it is necessary to determine not only how and why organisms respond in the presence of some stimuli, but also how and why they fail to respond in the presence of other stimuli. The concept of excitation is often invoked to account for responding in the presence of a particular stimulus and the concept of inhibition is often invoked to account for at least some instances of not responding. Behavioral inhibition is a generic term which refers to all behavioral processes which lead to response suppression. The term includes both learned and unlearned sources of inhibition, and as such, may conceal differences in mechanisms and features of different types of response suppression.

### Conditioned inhibition

This thesis concentrates specifically on conditioned or associative inhibition. Conditioning refers to operations which manipulate spatiotemporal relationships among environmental events and to changes in behaviour which occur as a result of those operations. Conditioned excitation occurs when a stimulus which does not initially produce a given response is placed in a particular temporal relationship with a stimulus (unconditioned stimulus or US) which does produce a response (unconditioned response or UR). As a result of the spatiotemporal arrangement of the two stimuli, the formerly neutral stimulus (the conditioned stimulus or CS) comes to elicit a response (the conditioned

response or CR). Conditioned inhibition is defined with respect to conditioned excitation. There are many definitions of conditioned inhibition; however, most definitions share two major features: (a) the inhibitory stimulus acquires the capacity to suppress responding controlled by an excitatory stimulus, and (b) the capacity to suppress responding is acquired through conditioning. For example, Hearst (1972, pp. 6-7) defined a conditioned inhibitory stimulus as a "multidimensional environmental event that as a result of conditioning...develops the capacity to decrease performance below the level occurring when that stimulus is absent." Other defining features of conditioned inhibition are that (a) the suppressive effect is due to a negative relationship between a stimulus and a reinforcer, not between a response and its consequence, (b) the conditioned inhibitory stimulus is a discrete external stimulus which is added to a situation in which all other conditions are held constant, and (c) the suppressive effects are removed when the stimulus is removed. Moreover, the conditioned inhibitory stimulus is defined by its effects on conditioned excitation and not by the operations used by the experimenter (Miller & Spear, 1985).

The term "conditioned inhibition" is used to refer to response suppression by a conditioned external stimulus. However, there is some confusion between "conditioned inhibition" as described above and the "conditioned inhibition procedure," one of a number of procedures for producing conditioned inhibition. To conform to common usage, I will use "conditioned inhibition" to refer to conditioned response suppression and "conditioned inhibition procedure" to refer to the specific procedure (described below).

There is considerable evidence which suggests that a negative correlation between a stimulus and a reinforcer is necessary to produce conditioned inhibition (e.g., Hearst, 1972; Hearst & Franklin, 1977; Kaplan, 1984; Rescorla, 1969; Wasserman, Franklin, & Hearst, 1974). However, there are numerous strategies for producing conditioned inhibition (see Fowler, Kleiman, & Lysle, 1985; LoLordo & Fairless, 1985; Rescorla, 1969, 1982; Williams & Overmier, 1988). Procedures which have been demonstrated to produce conditioned inhibition include (a) differential conditioning, (b) Pavlovian conditioned inhibition, (c) explicitly unpaired stimulus presentations, (d) inhibition of delay, (e) long forward trace conditioning, (f) cessation training, (g) backward conditioning, and (h) excitatory extinction.

In differential conditioning, one stimulus (CS+) is paired with the US and another stimulus (CS-; the putative inhibitor) is not paired with the US. The Pavlovian conditioned inhibition procedure is similar in that the CS+ alone is paired with the US, but a compound of the CS+ and the CS- is not paired with the US. In the explicitly unpaired procedure, the CS- and the US are presented randomly and independently of one another, except for the requirement that they must remain separated from one another by long variable time periods. In inhibition of delay, a very long CS is paired with the US. The early portion of the long CS becomes inhibitory and the portion closer to the US becomes excitatory (Schwartz, 1978). In long forward trace conditioning, the CS- is paired with the US, but with an extended interval between CS- offset and US onset. The CS- will become inhibitory if the trace interval is long enough to preclude CR acquisition (Hinson & Siegel, 1980). In cessation training, the CS-

is presented during the US and overlaps US termination. In backward conditioning, the CS- is presented at US offset. Finally, in excitatory extinction, the CS- is presented in compound with a CS+ during extinction of the CS+.

### Measurement of conditioned inhibition

Identifying a stimulus as a conditioned excitor is relatively easy; it requires monitoring the development of responding to the conditioned stimulus as conditioning proceeds. Identifying a stimulus as a conditioned inhibitor is more complex. It requires demonstrating (1) that the putative inhibitory stimulus suppresses responding maintained by an excitatory stimulus, and (2) that the response suppression was the result of conditioning. A conditioned inhibitor is defined solely as a stimulus which has response suppressive properties. By implication, the putative inhibitory stimulus elicits no directly observable or measurable responses and can be detected only through its effect on behaviour controlled by an excitatory stimulus. Consequently, traditional measures of conditioned inhibition have been indirect post-conditioning tests, that is, observations of the interaction between inhibitory and excitatory stimuli in the control of behaviour after conditioning. More recently, there has been evidence that an inhibitory stimulus may control observable and measurable responses, in particular, withdrawal from the stimulus (Hearst, Bottjer, & Walker, 1980; Hearst & Franklin, 1977; Kaplan, 1984; Wasserman, Franklin, & Hearst, 1974). Withdrawal from an inhibitory stimulus has the potential to be an important direct measure of conditioned inhibition in that it is an observable response and can be monitored directly throughout conditioning. In the following section, I will

describe the major measures of conditioned inhibition and control conditions for associative effects.

Summation test. In a summation test for inhibition, the putative inhibitory stimulus is presented simultaneously with a known excitatory stimulus. The logic of this test is that inhibition will suppress excitatory responding. Inhibition is inferred from a reduction in the level of excitatory responding (as measured by the amplitude, duration, frequency, intensity, or latency of the response) during the stimulus compound, relative to control conditions. Summation tests are usually conducted post-training, although test trials may be interspersed with acquisition trials to give a longitudinal analysis of the development of inhibition. However, summation tests are conducted without reinforcement to prevent excitatory conditioning from accruing to the inhibitory stimulus on compound test trials. Therefore, interspersed test trials during acquisition may yield a discrimination between reinforced acquisition trials (CS+ alone) and unreinforced test trials (CS+ and the putative inhibitor).

The most commonly used summation test involves presenting the putative inhibitory stimulus in compound with a known conditioned excitatory stimulus (CS+). The CS- is considered a functional inhibitor if responding to the CS+ and CS- compound is suppressed relative to the CS+ alone or to other control conditions. An increasingly common summation test involves observing the reduction in the level of an operant response when the putative inhibitor is presented. In this procedure, the putative CS- is presented periodically during a baseline of ongoing operant behaviour, for example, bar-pressing for food or

to avoid shock. The putative inhibitor may be trained in the same environment in which the operant training occurred (termed "on-the-baseline") or in a different environment (termed "off-the-baseline"). However, in both situations, the CS- is considered a functional inhibitor if operant responding is suppressed during presentation of the CS-, relative to control conditions. A rarely used form of the summation test involves presenting the putative inhibitory stimulus simultaneously with the US. The presence of inhibition is inferred from a reduction in the UR during the stimulus compound. This procedure can detect only very strong inhibitory effects because a weak inhibitor would be unlikely to reduce the UR significantly.

Reacquisition test (also called Retardation test). In this test, the putative inhibitor is paired repeatedly with the US to transform the CS- into a conditioned excitor. The logic of this test is that if the CS- has acquired inhibitory properties opposite to those of conditioned excitors, then the CS- will resist efforts to transform it into a conditioned excitor. If acquisition of conditioned excitation to the CS- is retarded relative to acquisition to a novel stimulus which is also paired with the US, the CS- is considered a functional inhibitor.

Disinhibition. Disinhibition is often considered the "inhibition of inhibition" (Brimer, 1972). The logic of the disinhibition test assumes that excitation is a precursor of and is conditioned prior to inhibition, that inhibition is less stable and more vulnerable to disruption than excitation, and that a given stimulus may be simultaneously excitatory and inhibitory. In disinhibition, a

novel stimulus is superimposed on the putative inhibitory stimulus. This is similar to external inhibition, where a novel stimulus is superimposed on an excitatory stimulus. Superimposing a novel stimulus on an excitatory stimulus usually results in a decrease in responding. However, superimposing a novel stimulus on an inhibitory stimulus results in an increase in responding, which is presumed to reflect reinstatement of the excitatory response which had been suppressed by the inhibitory stimulus. The novel stimulus blocks the action of the inhibitory stimulus, allowing underlying excitatory control to be revealed. Thus, a novel stimulus may have two effects — response suppression or facilitation — depending on whether it is superimposed on an excitatory or inhibitory stimulus, respectively (Brimer, 1972).

Inhibitory stimulus generalization gradients. Inhibitory gradients share the same assumptions as summation tests and are often considered to be summation tests (Rescorla, 1969). In gradient tests, features of the putative inhibitory stimulus are varied systematically and presented in a compound with a known excitatory stimulus. Responding is assessed in the presence of each stimulus compound and compared to responding in the presence of the excitatory stimulus alone. Responding in the presence of each compound stimulus is reduced, with minimal responding occurring to the compound containing the putative inhibitory stimulus. Generalization gradients reveal dimensional control by features of a putative inhibitory stimulus; however, a flat gradient cannot be assumed to reflect the absence of conditioned inhibition. It may indicate only that the particular feature which was varied did not control responding. In addition, reduced responding in the presence of the compound

containing the putative inhibitory stimulus may reflect only reduced excitation relative to other stimulus compounds and not inhibition. Gradient tests do not generally correlate well with other measures of conditioned inhibition.

Superconditioning. Superconditioning refers to the rapid acquisition of a CR to a neutral stimulus presented in a compound with a putative inhibitory stimulus, relative to acquisition to a neutral stimulus presented in a compound with a stimulus which did not receive prior inhibitory training (Revusky & Garcia, 1970; Rescorla, 1971). The logic of this test is that the putative inhibitor produces a negative expectation for the occurrence of the US, making the unexpected occurrence of the US more significant than if it occurred without the putative inhibitory stimulus (Rescorla & Wagner, 1972). However, Miller and his colleagues (see Miller & Matzel, 1988) suggest that superconditioning may be due to overshadowing of the target CS by the other stimulus in the compound, rather than to inhibition.

Withdrawal from CS-. In the measures described in the previous section, inhibition is not observed directly but is inferred from changes in the level of excitatory responding when the inhibitory stimulus is combined with an excitatory stimulus. Withdrawal from the CS- differs from other measures of inhibition in that it is a direct, observable measure. When operationally defined as, for example, "mean distance from the CS-," or "the proportion of time spent away from the area of the CS-," withdrawal can be directly observed and does not require that inhibition be inferred from changes in the level of another variable. In addition, withdrawal from the CS- may have important implications

for understanding the process of conditioned inhibition. Withdrawal from the CS- might suggest that, in some cases at least, an inhibitory stimulus suppresses responding by controlling a response which interferes with responses controlled by the excitatory stimulus.

The logic of using withdrawal as a measure of inhibition appears to derive from two sources: (1) observations of approach and withdrawal responses in the autoshaping paradigm, and (2) the conception of inhibition as somehow opposing the effects of excitation. First, positive sign-tracking (approach to a stimulus which is correlated with reinforcement) and negative sign-tracking (withdrawal from a stimulus which is correlated with the absence of reinforcement) are robust phenomena in discriminated autoshaping (see Hearst & Jenkins, 1974; Tomie, Brooks, & Zito, 1989). Second, the apparent symmetry between "pull toward" a stimulus correlated with reinforcement and "push away" from a stimulus correlated with the absence of reinforcement parallels the symmetry between positive CS-US contingencies (excitation) and negative CS-US contingencies (inhibition). If approach is engendered by an excitatory CS-US contingency, then it appears logical to assume that withdrawal could similarly be engendered by an inhibitory CS-US contingency. And indeed, negative sign-tracking in discriminated autoshaping has become so well-documented that some researchers (e.g., Bottjer, 1982; Kaplan, 1984; Tomie & Kruse, 1980) have used withdrawal from a CS- as the sole measure of conditioned inhibition.

However, this may be somewhat premature. For example, Matzel, Gladstein, and Miller (1988) review evidence (e.g., Tait & Saladin, 1986) which suggests that a conditioned stimulus may function simultaneously as an excitor and an inhibitor, depending on the tests employed. Equating excitatory control with approach to the CS+ and inhibitory control with withdrawal from the CS- would not be sufficient for a stimulus with both excitatory and inhibitory properties. Moreover, LoLordo and Fairless (1985) argue that before accepting withdrawal from the CS- as a valid measure of inhibitory control, it is necessary to demonstrate that withdrawal correlates positively with traditional measures of conditioned inhibition, such as summation and reacquisition. At present, there is suggestive but not entirely convincing evidence of a positive relationship between withdrawal and traditional measures of inhibition. This will be discussed in more detail below.

Combined tests for inhibition. Rescorla (1969) and Hearst (1972) recommend that both summation and reacquisition tests be used to assess putative conditioned inhibitors. However, in actual practice it is unusual to find that more than one test for conditioned inhibition has been used, perhaps because most of the conditioned inhibitory training procedures described earlier are well established. Rescorla (1969), Hearst (1972), and Matzel, Gladstein, and Miller (1988) argue that both summation and reacquisition tests are necessary to eliminate the possibility that suppression of responding is due to attentional changes rather than to conditioned inhibition. For example, a CS- may be considered inhibitory if responding is reduced in the presence of the compound CS+ and CS- in the summation test and acquisition to the CS- is

retarded in the reacquisition test (both relative to appropriate control conditions). However, if conditioned inhibition training resulted in increased attention to the CS-, the summation test might show suppression of responding to the compound CS+ and CS-, whereas the reacquisition test might show facilitation of acquisition to the CS-. Conversely, if conditioned inhibition training resulted in decreased attention to the CS-, the summation test might show no suppression to the compound CS+ and CS-, but the reacquisition test might show retarded acquisition to the CS-. Indifference to the CS- would presumably result in no changes on either test (Hearst, 1972).

Control procedures. Rescorla (1969) and Hearst (1972) suggest that there are three comparisons necessary to control for associative effects in conditioned inhibition: (a) novel stimuli, (b), unpaired stimuli, and (c) associatively neutral stimuli (i.e., stimuli which are neither excitatory nor inhibitory). A novel stimulus, presented alone or in compound with another stimulus during testing, controls for response suppression due to changes in stimulus control. For example, in the summation test, it is possible that the reduction in responding to the compound CS+ and CS- is due to a generalization decrement and not to a reduction in the response-eliciting properties of the CS+ produced by the inhibitory stimulus. To control for this possibility, the CS+ is also presented in combination with a novel stimulus. The CS- is considered inhibitory if responding during the compound CS+ and CS- is suppressed relative to the compound CS+ and novel stimulus. Similarly, in the reacquisition test, the rate of reacquisition to the CS- may be compared to the rate of acquisition to a novel stimulus.

It is also possible that response reduction during the summation test may be due to the effect of presenting the CS+ in compound with a stimulus which has been presented repeatedly without the US, rather than to the effect of conditioned inhibition. To control for this possibility, response reduction during the CS+ and CS- compound is compared to response reduction during a compound of the CS+ and a second stimulus which has been presented repeatedly without the US — the "CS-alone" or "habituated" stimulus. In the reacquisition test, the rate of reacquisition to the CS- may be compared to the rate of reacquisition to the habituated stimulus.

Finally, an associatively neutral condition is required as a baseline for a comparison of the effects of both conditioned inhibition and conditioned excitation. The Truly Random Control (TRC) procedure arranges a zero correlation between the CS and the US, thereby creating a stimulus which is associatively neutral (Rescorla, 1967). In the TRC procedure, the CS and the US are presented randomly and independently of one another such that the probability of the US is equal in the presence and the absence of the CS. The logic of the TRC procedure rests on the assumption that correlation, rather than contiguity, between the CS and the US is the critical aspect of conditioning.

#### Theories of conditioned inhibition.

The concept of inhibition was introduced because of observations of decreases in conditioned responding which did not reflect changes in associations. Specifically, spontaneous recovery, disinhibition, and

reinstatement after extinction suggested that the loss of the conditioned response did not necessarily reflect a corresponding loss of association. Therefore, Pavlov (1927) was led to postulate an opposing process — inhibition — to account for the loss of responding (Bolles, 1985). Pavlov (1927) theorized that associative excitation and inhibition resulted from the creation of new neurological connections in the brain.

In contrast, Skinner (1938) noted that condition inhibition was inferred from a reduction in responding in the presence of an excitatory stimulus and argued that "The property of the mere direction of the change does not establish a useful class of data. . . Excitation and inhibition refer to what is here seen to be a continuum of degrees of reflex strength, and we have no need to designate its two extremes" (Skinner, 1938, pp. 17 - 18). In the absence of direct measures of inhibition, he suggested that a reduction in excitation may be a more parsimonious explanation for observed decrements in responding. Many contemporary authors (e.g., Bolles, 1985; Donahoe & Palmer, 1988) also argue that the concept of inhibition may be unnecessary. They suggest that what is being observed in tests of inhibition (e.g., summation, reacquisition, and disinhibition) may simply be the behavioral outcome of ambiguous stimulus control (Bolles, 1985; Donahoe & Palmer, 1988; Skinner, 1938). Baker and Baker (1985) suggest that the apparent difference between inhibition and excitation (aside from differences in the procedures which produce those effects) may be due more to existing theories than to actual empirical differences in the phenomena. They conclude that there is little empirical evidence of consistent differences between excitatory and inhibitory

conditioning. Similar to Matzel, Gladstein, and Miller (1988), Baker and Baker (1985) conclude that theories which characterize excitation and inhibition as mutually exclusive properties of stimuli have generated research which has ignored the potential similarity between excitation and inhibition.

Although interest in behavioral inhibition as a process complementary to excitation had been common among Eastern European learning theorists (e.g., Konorski, 1948; 1967) since Pavlov, it is only relatively recently that this interest has been shared by Western experimental psychologists (Hearst, 1972). Rescorla (1969) presaged a resurgence of interest in the study of inhibition and influenced much of contemporary work on conditioned inhibition through a theory proposed in 1972 with Wagner. The Wagner and Rescorla theory (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972) was based on Rescorla's (1969) contingency model of conditioning. According to this model, conditioned inhibitory associations are formed to the CS when the probability of US occurrence in the presence of the CS is less than the probability of US occurrence in the absence of the CS, that is,  $p(\text{US}/\text{CS}) < p(\text{US}/\text{no CS})$ . A comparison between these two probabilities determines whether the association to the CS is positive (excitatory) or negative (inhibitory). Conditioned excitation and conditioned inhibition are assumed to be additive and to lie on a single continuum which is symmetrical around a zero point, or point of associative neutrality. Conditioned excitation is represented by a range of positive values on that continuum, whereas conditioned inhibition is represented by a range of negative values. Wagner and Rescorla (1972, p. 307) argued that "The theory appeals to no special inhibitory process . . . To

speak of inhibition in the context of this model is simply to speak of a range of values along the associative-strength continuum." Conditioned inhibition and excitation are assumed to be equivalent and are described by a single general rule, but inhibition acts in opposition to excitation. (Konorski, 1972; Rescorla, 1969; Rescorla & Wagner, 1972; Wagner & Rescorla, 1972).

Initially, Rescorla maintained that a conditioned inhibitor specifically opposed behaviour controlled by an excitor for the same US (Rescorla, 1969). However, by 1982, he noted that "an inhibitor is most effective when used in conjunction with the excitor used to establish its inhibition" (Rescorla, 1982, p. 288), which suggested that an inhibitor had suppressive effects on responses to other excitors. More recently, it has become well accepted that stimuli may have both inhibitory and excitatory properties, which has led Rescorla to suggest that inhibition may not always be the opposite of excitation (Rescorla, 1985; 1987). In at least some instances, inhibition may be one of a class of modulators which may control responding to another stimulus. In this view, inhibition may be the logical opposite of facilitation, rather than excitation, and both inhibition and facilitation may modulate responding to an excitor (Rescorla, 1985; 1987).

There are, of course, other contemporary conceptions of inhibition. For example, Fowler, Kleiman, and Lysle (1985) argue that conditioned inhibition is not autonomous or equivalent to excitation, but rather is a "slave" of excitation. Inhibition is functionally dependent on the presence of excitation and operates

only to the extent that excitation is maintained. This view is consistent with that of early learning theorists (e.g., Pavlov, 1927).

Comparator theories (e.g., Gibbon & Balsam, 1981; Jenkins, Barnes, & Barrera, 1981; Miller & Matzel, 1988; Miller & Schachtman, 1985) attempt to account for reductions in conditioned responding without postulating the concept of inhibition. As one example, Scalar Expectancy Theory (SET; Gibbon & Balsam, 1981) proposes that two expectancies are generated in the autoshaping situation, one reflecting the rate of food delivery during the CS, and the other reflecting the overall rate of food delivery. These two expectancies interact to determine behaviour in the presence of the CS. A CR (i.e., keypecking) emerges when the ratio of C/T approaches two, where C is the mean duration between US occurrences and T is the mean duration of the CS between US occurrences. Suppression of responding occurs when the expectancy for the US is greater when the CS is absent than when the CS is present (Gibbon & Balsam, 1981). The theory does not explicitly rule out the concept of inhibition, but simply relates the probability of a CR to a ratio of the two expectancies.

The Comparator Hypothesis (Miller & Schachtman, 1985) developed, in part, from Rescorla's (1969) contingency theory, and in part from "a strong sense that differential acquisition contributed less than was traditionally assumed to the differences in behaviour observed between individuals (Miller & Matzel, 1988, p. 54). According to Rescorla, a conditioned excitatory or inhibitory association is formed from a comparison between the  $p(\text{US/CS})$  and

the  $p(\text{US}/\text{no CS})$ . A comparison between these two probabilities yields a single associative value, where conditioned excitation is represented by a range of positive values and conditioned inhibition is represented by a range of negative values. Response strength is assumed to be monotonically related to associative strength (Rescorla & Wagner, 1972). In contrast, the Comparator Hypothesis is a "qualitative response rule stating that the response to a CS will be a direct function of the CS-US associative strength and an inverse function of the strengths of the associations between the US and other cues that were present during training of the CS" (Miller & Matzel, 1988, p. 61). According to the Comparator Hypothesis, the  $p(\text{US}/\text{CS})$  and the  $p(\text{US}/\text{no CS})$  result in independent associations which are positive (excitatory) because the probabilities themselves are positive (or zero).

Similar to Rescorla's model, "conditioned inhibition" occurs when the  $p(\text{US}/\text{CS}) < p(\text{US}/\text{no CS})$ . However, in the Comparator Hypothesis, "conditioned inhibition" is the consequence of a comparison between two independent positive associations - one between the US and the CS and the other between the US and the context or background. "Conditioned inhibition is viewed as the behavioral consequence of the positive association between a CS and US being weaker than the positive association between the context and the US" (Miller & Schachtman, 1985, p. 52). In other words, the context becomes a better predictor of the US than the presence of the CS. The CS is not inhibitory, but rather the context is more excitatory as a result of being paired with the US. According to this model, association inhibition does not exist and conditioned inhibition is simply a behavioral consequence of associative

excitation. In addition, an implication of this model is that a single stimulus may have the potential to function both as a conditioned inhibitor and a conditioned excitator (Matzel, Gladstein, & Miller, 1988).

There is no current consensus on the status of conditioned inhibition. Research and conceptualizations of conditioned inhibition range from Pavlov's (1927) early theorizing about inhibition as an opposing process which operates to suppress excitatory responding, to Skinner's (1938) position that the concept of inhibition is superfluous, to current theories which question the validity of the construct of inhibition (e.g., Baker & Baker, 1985; Bolles, 1985; Donahoe & Palmer, 1988; Miller & Schachtman, 1985; Miller & Matzel, 1988).

#### Sign-tracking and conditioned inhibition in discriminated autoshaping

Sign-tracking is a term coined by Hearst and Jenkins (1974) to describe the tendency of an organism in an appetitive situation to approach stimuli associated with reinforcement and to withdraw from stimuli associated with non-reinforcement. The term "sign-tracking" developed from their analysis of the phenomenon of autoshaping, which was first described by Brown and Jenkins (1968). In autoshaping, pigeons were observed to approach and peck at a keylight (CS+) which signalled the response-independent presentation of food (US). Subsequent research showed that approach and key pecking in autoshaping are controlled by an interaction between stimulus-reinforcer (Pavlovian) and response-reinforcer (operant) relationships (e.g., Eldridge & Pear, 1987; Woodruff, Conner, Gamzu, & Williams, 1977; Tomie, Brooks, & Zito,

1989). A positive stimulus-reinforcer correlation is a necessary condition for the development of approach and key pecking in autoshaping (Wasserman, Hunter, Gutowski, & Bader, 1975); however, approach and key pecking are sensitive to, and modifiable by, their consequences (Eldridge & Pear, 1987; Schwartz & Williams, 1972; Tomie, Brooks, & Zito, 1989).

Observations of discriminated autoshaping, where one stimulus (CS+) is followed by feeder operations, and a second stimulus (CS-) is not followed by feeder operations, suggested that not only do pigeons approach and peck the CS+, but they also withdraw from and do not peck the CS- (see Gaffan & Hart, 1981; Hearst & Franklin, 1977; Kaplan, 1984; Wasserman, Franklin, & Hearst, 1974). For example, pigeons approached a keylight which was positively correlated with food, withdrew from a keylight which was negatively correlated with food, and showed no consistent approach to or withdrawal from a keylight which had a zero correlation with food (Wasserman, Franklin, & Hearst, 1974). By comparing the position of the bird at the start of each trial with its position throughout the trial, Wasserman, Franklin, & Hearst (1974) concluded that pigeons in the negative contingency condition both passively and actively avoided the CS-. In other words, birds on the opposite side of the chamber as the illuminated CS- remained distant from the CS- and birds on the same side of the chamber as the illuminated CS- moved away from it. Control conditions such as keylight-alone presentations and backward pairings of keylight and food produced no consistent approach or withdrawal responses.

Hearst and Franklin (1977) and Kaplan (1984) systematically varied operations presumed to increase inhibitory control and showed that withdrawal from the key was a direct function of increasingly negative correlations between keylight and food presentations. In addition, Hearst and Franklin (1977) used a line-tilt generalization test and demonstrated that pigeons did not simply approach another stimulus which was more positively correlated with food, but actively withdrew from the CS-. Similarly, Kaplan (1984) reported that pigeons actively approached the CS+ when it was presented on the opposite side of the chamber from the pigeon's position at CS+ onset and actively withdrew from the CS- when it was presented on the same side of the chamber as the pigeon's position at CS- onset. In a related point, Eldridge and Pear (1987), Matthews and Lerer (1987), Matthews, Bordi, and Depollo (1990), and Silva, Silva, and Pear (in press) documented consistent withdrawal from the inter-trial interval stimulus (ITS) in autoshaping.

In summary, approach toward stimuli positively correlated with appetitive reinforcers and withdrawal from stimuli negatively correlated with appetitive reinforcers are well-documented in autoshaping. In addition, the strength of the tendency to approach toward or withdraw from a stimulus appears directly related to the strength of the correlation between the stimulus and food presentations, strong negative (inhibitory) correlations resulting in marked withdrawal and strong positive (excitatory) correlations resulting in marked approach and keypecking. Therefore, withdrawal from a CS- in discriminated autoshaping may function as a direct measure of conditioned inhibition and

may provide information about the way in which a conditioned inhibitor suppresses responding.

As mentioned earlier, however, several questions remain before wholeheartedly embracing withdrawal from the CS- as a reliable measure of conditioned inhibition. First, does withdrawal from the CS- correlate positively with traditional measures of conditioned inhibition? (LoLordo & Fairless, 1985). Second, how can withdrawal be quantified? With respect to the first question, the evidence suggests that some measures of withdrawal may correlate positively with traditional, indirect measures of conditioned inhibition such as summation or reacquisition. However, there are few studies to date which employed appropriate control groups for associative effects and which used established tests for conditioned inhibition in addition to measures of withdrawal (LoLordo & Fairless, 1985). In one example, Wasserman, Franklin, and Hearst (1974) demonstrated that pigeons withdrew from a stimulus negatively correlated with reinforcement and approached a stimulus positively correlated with reinforcement. Birds receiving CS-only presentations or backward pairings neither approached toward nor withdrew from the keylight stimulus. Acquisition of keypecking to the CS- was retarded when compared to a novel stimulus in a reacquisition test. Thus, measures of withdrawal in this study were compared with one test for conditioned inhibition (reacquisition) and two appropriate control conditions (CS-only and backward pairings).

Wasserman and Molina (1975) showed that withdrawal from the CS- correlated positively with outcomes on a reacquisition test for conditioned

inhibition: retarded acquisition and lower asymptotic levels of keypecking to the former CS- compared to a novel stimulus. Similarly, Hearst and Franklin (1977) observed both retardation of acquisition and withdrawal from the CS- when groups who were trained with highly negative correlations of CS and US were compared with appropriate control groups. Withdrawal from the CS- and decreased responding during summation tests or retardation during reacquisition tests have also been reported in a number of studies which did not include appropriate controls for associative effects (e.g., Gokey & Collins, 1980; Tomie & Kruse, 1980; Wilkie & Ramer, 1974). The studies described above suggest that (1) the CS- functions as a conditioned inhibitor in discriminative autoshaping according to traditional, indirect measures of conditioned inhibition, and (2) that withdrawal from the CS- as a measure of conditioned inhibition may correlate positively with indirect tests of conditioned inhibition. However, more comparative research is required before one could argue definitively that withdrawal from the CS- is an appropriate measure of conditioned inhibition (LoLordo & Fairless, 1985).

With respect to the question of how withdrawal from the CS- can be quantified, although withdrawal has both spatial and temporal features, the most commonly used measure to date is primarily temporal: the proportion of time the subject spends in a particular area of the experimental chamber. Most of the studies described above measured withdrawal via specially constructed operant chambers with two response keys on opposite sides of the front panel of the chamber and a tilt floor balanced on the midline of the chamber between the two keys (e.g., Kaplan, 1984). During a CS+ or CS- trial, one of the two

keys was illuminated. The type of trial (CS+ or CS-) and the position of the key illuminated were alternated randomly. The bird's weight closed microswitches beneath the tilt floor which recorded time spent on each side of the chamber. Total time spent on each side of the chamber was compared to total time the CS+ or CS- was illuminated on that side of the chamber. An approach-withdrawal index was calculated to yield a ratio of the time the bird spent on the same side of the chamber as the CS+ or CS- to the total time the CS+ or CS- was illuminated on that side. For each stimulus (CS+ or CS-), a ratio greater than 0.5 represented approach to the stimulus, a ratio less than 0.5 represented withdrawal from the stimulus, and a ratio near 0.5 represented no consistent approach to or withdrawal from the stimulus. Strong approach or withdrawal tendencies were indicated by greater or lesser ratios and varied with the degree and direction of the correlation between CS and US (see Kaplan, 1984).

Although this measure of withdrawal is sensitive to manipulations in the strength of conditioned inhibition (Kaplan, 1984), it fails to capture fully the spatial aspects of withdrawal or the interaction of spatial and temporal aspects. For example, it would be possible for the pigeon to straddle the line between the two halves of the chamber and by weighting one foot or the other be said to approach toward or withdraw from the lighted key. In addition, increased distance away from the lighted key is not measured once the bird has moved across the dividing line in the chamber. There may be important spatiotemporal features of withdrawal (e.g., a recurring sequence of movements toward or away from the lighted key) which may not be detected by a simple measure of position. In addition, the two-key tilt-chamber separates the CS- and CS+,

which prevents an analysis of the interaction of approach and withdrawal tendencies which might be observed if the CS- and CS+ were presented on the same key.

Matthews and Lerer (1987), Matthews, Bordi, and Depollo (1990), Eldridge and Pear (1987), Pear and Eldridge (1984), and Silva, Silva, and Pear (in press) used more sophisticated spatiotemporal measures of position to analyze response topography during autoshaping and other response-independent schedules of reinforcement. For example, Matthews and his colleagues (Matthews & Lerer, 1987; Matthews, Bordi, & Depollo, 1990) used an experimental chamber whose floor consisted of nine panels, each balanced on four microswitches. Closure of any of the switches signalled that the panel was depressed and provided an indication of the position of the bird in the chamber, allowing a more detailed spatiotemporal analysis of behaviour on response-independent schedules of reinforcement. Similarly, Pear and his colleagues (Eldridge & Pear, 1987; Pear & Eldridge, 1984; and Silva, Silva, & Pear, in press) used a computer-controlled tracking system that continuously recorded the position of a pigeon's head as the bird moved freely in the experimental chamber during autoshaping. With this technique, Pear and his colleagues provided detailed spatiotemporal analyses of response topography during both the CS+ and the ITI in autoshaping, documenting both approach toward the CS+ and withdrawal from the area of the key and feeder during the ITI. The studies by Matthews and his colleagues and Pear and his colleagues suggest that a more detailed spatiotemporal analysis of response topography during the CS+, the CS-, and the ITI in discriminated autoshaping would

supplement the less detailed spatiotemporal measures of withdrawal used in earlier studies (e.g., Kaplan, 1984) and provide additional information about withdrawal as a measure of inhibitory control.

### Design of the study

This study examined withdrawal as a spatiotemporal feature of conditioned inhibition. The continuous-recording apparatus used by Eldridge and Pear (1987) and Pear and Eldridge (1984) in their examination of response topography during autoshaping and omission training was used to provide a detailed topographical analysis of approach and withdrawal during Autoshaping, Discriminated Autoshaping, a Random Presentation control condition, and Summation and Reacquisition tests for conditioned inhibition. In addition to visual examination of topographical recordings from all phases, a spatiotemporal measure of withdrawal (mean distance from the response key) was compared with traditional measures of conditioned inhibition from summation and reacquisition tests.

This study used a single organism research design. A basic feature of single organism research design is that experimental conditions can be manipulated within a small number of subjects, using repeated measurements and employing each subject as its own control. Experimental conditions are introduced sequentially within subjects rather than across subjects and each condition serves as a baseline comparison for the next sequential phase (Kazdin, 1982; Johnston & Pennypacker, 1980; Sidman, 1960). In the present

study, each of the four birds in the experimental series was exposed sequentially to: Baseline, Autoshaping, Discriminated Autoshaping, Summation Test, and Reacquisition of autoshaping. The Baseline condition was designed to assess naturally-occurring movement patterns prior to the introduction of feeder or stimulus presentations. The Autoshaping phase was designed to provide a baseline for comparison of approach and withdrawal responses in Discriminated Autoshaping, and a comparison of the rate of acquisition during Reacquisition of autoshaping. Each bird was exposed to both Summation and Reacquisition tests of conditioned inhibition. Rescorla (1969), Hearst (1972), and Matzel, Gladstein, and Miller (1988) argue that both tests are necessary to rule out attentional explanations for response suppression.

Two control conditions were employed in this study: (1) comparison of the CS- with a Novel stimulus in both Summation and Reacquisition, and (2) comparison of Discriminated Autoshaping with a Random Presentation procedure, similar to Rescorla's (1967) Truly Random Control procedure. The Random Presentation procedure, in which keylight stimuli and feeder operations occur randomly and independently of one another, is assumed to produce an associatively neutral stimulus against which to compare the effects of the positive and negative CS-US contingencies in Discriminated Autoshaping. Although it would have been desirable to expose all birds to the Random Presentation procedure prior to Autoshaping, numerous investigators have reported reduced approach and keypecking when Autoshaping is preceded by a Random Presentation phase (e.g., Tomie, Hayden, & Biehl, 1980; Tomie, Murphy, & Fath, 1980; Wasserman, Franklin, and Hearst 1974) .

Therefore, the Random Presentation condition was introduced in a separate control series after Autoshaping. The two birds in the control series were exposed sequentially to: Baseline, Autoshaping, Random Presentation, Summation Test, and Reacquisition of autoshaping. Rescorla (1969) reported that other control conditions (e.g., CS preexposure or novel stimulus presentations) had little effect on the development of condition inhibition; therefore, other control conditions were not included in this study.

The continuous-recording apparatus described by Eldridge and Pear (1987) was used to provide a continuous record of response topography in all experimental and control conditions. The apparatus recorded the coordinates of a virtual point on the pigeon's head in three-dimensional space 30 times per second. These data were quantified in terms of the mean distance of the pigeons' head from the response key during all stimulus presentations; representative topographical data were also presented. In addition, the number of stimulus presentations with a key peck and response rate during stimulus presentations were recorded. All data were analyzed by visual inspection.

Four major questions were addressed in this study: (1) Do traditional indirect tests of conditioned inhibition show evidence of inhibitory control by the CS- under the conditions of this study? (2) How do spatiotemporal measures of withdrawal from the CS- relate to traditional indirect measures of inhibitory control? (3) What is the relationship between spatiotemporal measures of behaviour during the CS- and the ITI? (4) How do patterns of approach toward

and withdrawal from keylight stimuli during the Random Presentation control condition compare with patterns of approach and withdrawal in Autoshaping?

## Method

### Subjects

Subjects were six experimentally naive unsexed White King pigeons, maintained at approximately 80% of their free-feeding weights throughout the study. Pigeons were approximately 2 years old at the start of the study and ranged in free-feed weight from 400 to 700 g. In order for the apparatus to track their movements in the chamber, their heads and necks (excluding the beaks) were blackened with paste shoe polish prior to each session. The birds were housed in individual cages in a colony room regulated by a 12:12 hr light:dark cycle. Water was freely available in the home cages at all times.

### Apparatus

A specially constructed apparatus recorded the position of the bird's head every 1/30th s as the bird moved freely in the experimental chamber. The inner dimensions of the experimental chamber were 57 by 57 by 38 cm. The front wall, which contained the response key and food hopper, was constructed of white opaque Plexiglas and aluminum painted white. The left wall was also made of white opaque Plexiglas, the other two walls were clear glass, and the

lid was clear Plexiglas. An external aluminum frame supported the walls and lid. The floor was an aluminum mesh fitted over an aluminum drop pan.

The translucent plastic response key measured 2.8 cm in diameter and was located on the front wall with its center 36 cm from the right glass wall of the chamber and 27 cm from the aluminum mesh floor. Four RM-387 bulbs behind the key transilluminated the key with white light at all times except during feeder presentations, when the key was darkened. Three 200 mcd light-emitting diodes (LEDs) behind the key projected discrete circles of coloured light 6 mm in diameter onto the key. The LEDs were placed in a triangular configuration with the yellow light at the top, the red light at the left, and the green light at the right edge of the key. Peak and dominant wavelengths for each LED were: red, 635 and 628 nm; yellow, 585 and 583 nm; and green, 572 and 565 nm. A force of approximately 0.18 N on the key closed a switch for electronically detecting key pecks. A feedback relay at the rear of the key produced a brief "click" following each switch closure.

A 5-cm diameter feeder aperture was located near the center of the front wall with its bottom edge 12 cm above the mesh floor. An electronically operated food hopper containing commercial pigeon food was raised into the aperture during reinforcement presentations. The feeder aperture was illuminated continuously by two 1820X bulbs in series with a 3352-ohm resistor except during feeder presentations when the resistor was isolated from the circuit. Thus, the intensity of the feeder light increased during feeder presentations. Each feeder presentation was 4 s in duration. During feeder

presentations, the keylight was darkened and the feedback relay on the key did not operate.

The chamber was located in a room separate from the one containing the programming and recording equipment. The chamber was illuminated through the transparent sides and lid by light from four banks of ceiling lights in the experimental room. Each bank contained three 40-watt 4-foot fluorescent Cool White bulbs. These lights were relay controlled and were automatically turned on at the beginning and off at the end of the session. Ventilation was provided by air spaces in the top and bottom of the chamber. Room ventilation was through a ceiling register. The experimental room was 3.1 by 3.1 m and was painted flat white to minimize reflections. A speaker and white noise generator provided a constant masking noise in the room.

Two video cameras were oriented perpendicularly to the two adjacent glass walls of the chamber. The cameras were connected to an electronic video-acquisition module that scanned down the image from each camera every 1/30th s until it encountered the highest dark region of a critical width and computed the three spatial coordinates of the point at the center of this region. Because the bird's head was the only dark area in the otherwise white and brightly illuminated chamber, this center point was defined as the position of the pigeon's head. The XZ coordinates were computed from the output of one camera, and the Y coordinate from the other. Thus, the video-acquisition module computed changes in the position of an hypothetical point on the pigeon's head in three-dimensional space as the pigeon engaged in key-

pecking and other activities in the chamber. The chamber was turned at an angle of approximately 10 degrees to the cameras to prevent interference from the aluminum frame of the chamber, excluding from view two narrow segments of the periphery of the chamber. Both cameras were connected to a television monitor and a selector switch permitted visual observation from either camera throughout all sessions.

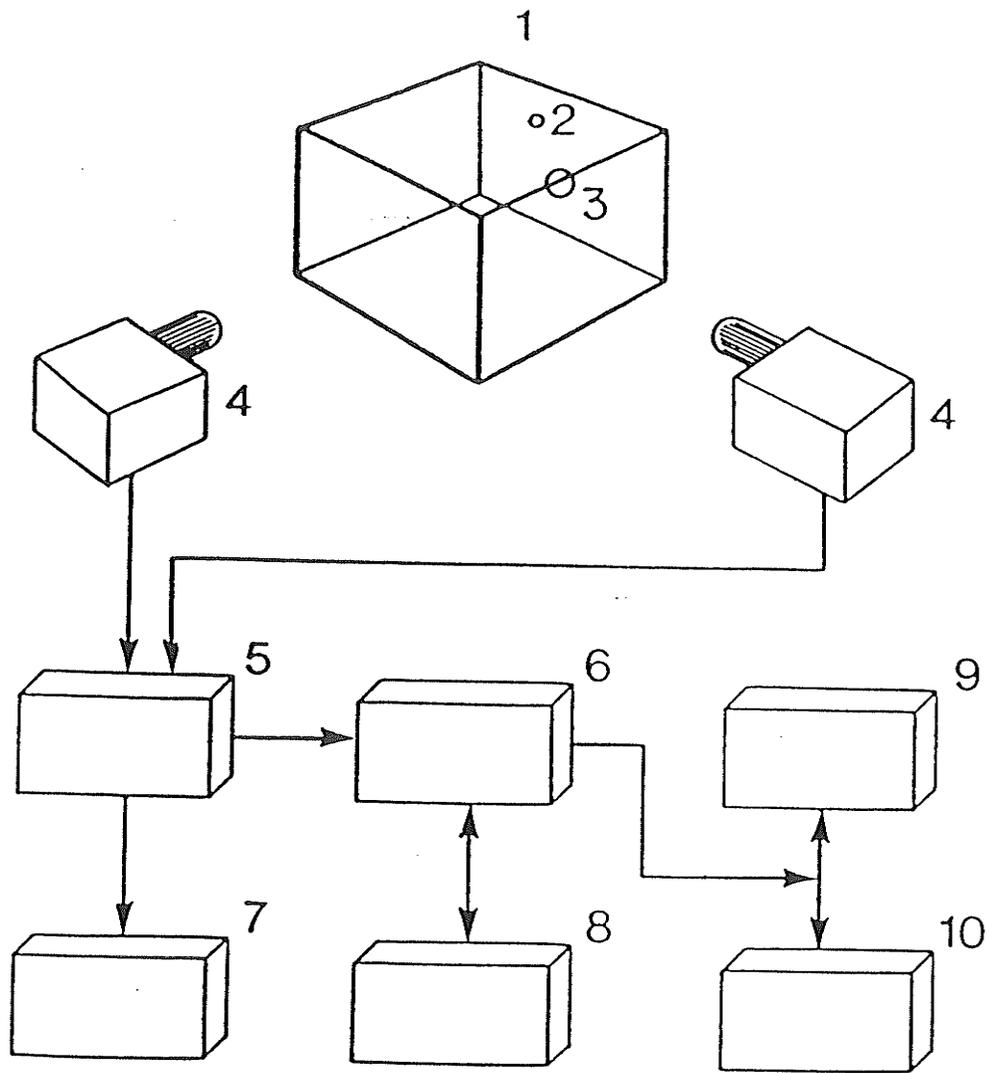
The video-acquisition module was connected to a Cromemco Z-2D microcomputer, which was programmed to control experimental sessions, to average incoming data in blocks of three (one data point for every 1/10 s), and to store data on floppy disks for subsequent analysis. Graphed data were displayed on a Hazeltine 1500 CRT screen and printed on an Epson dot matrix printer. Figure 1 shows a block diagram of the system.

### Procedure

General experimental procedures. Sessions were conducted 7 days per week at the same time each day provided that the bird's weight was within 5% of its 80% free feed weight. On its return to its home cage following each session, the bird was fed the additional commercial pigeon food required to maintain its body weight at the 80% level.

Stimulus presentations. The white keylight was illuminated during all intertrial intervals and stimulus presentations and was darkened only during feeder operations. Stimulus presentations consisted of a 6-mm diameter circle

Figure 1. Block Diagram of the apparatus.



- |                             |                  |
|-----------------------------|------------------|
| 1. Chamber                  | 6. Microcomputer |
| 2. Response Key             | 7. TV Monitor    |
| 3. Food Aperture            | 8. Disc Storage  |
| 4. TV Cameras               | 9. CRT           |
| 5. Video-Acquisition Module | 10. Printer      |

of coloured light projected in a unique position onto the white key. The stimuli were: (a) yellow circle at the top of the key, (b) red circle at the left side, and (c) green circle at the right side. For two of the birds in the experimental series, the yellow circle was the CS+ and the green circle was the CS-. For the other two experimental birds, the green circle was the CS+ and the yellow circle was the CS-. For one bird in the control series, the yellow circle was the CS+ and the green circle was the random stimulus (RS). For the other control bird, the green circle was the CS+ and the yellow circle was the RS. For all birds, the red circle was the novel stimulus (N). With four birds in the experimental series and two in the control series, it was not possible to counterbalance colours completely across the CS+, CS-, RS, and N; therefore, colours were counterbalanced across the CS+, CS-, and RS and the N remained constant for all birds. The CS+, CS-, and RS were presented separately during conditioning phases. The CS-, RS, and N were combined with the CS+ during Summation Tests. For all phases, stimulus presentations were 8 s in duration and were separated by a variable intertrial interval (ITI) with a mean of 60 s and a range from 30 s to 90 s. See Table 1 (experimental series) and Table 2 (control series) at the end of this section for a summary of hues of key stimuli and numbers of sessions for each bird in each phase.

Magazine training. Prior to baseline sessions, the birds were magazine trained. Each bird was placed in the chamber with the food hopper raised and the feeder aperture brightly illuminated. Once the bird approached the raised hopper and consumed grain for approximately 20 s, the hopper was raised and lowered at varying intervals independently of the bird's behavior. This was

repeated until the bird approached and consumed food from the hopper within 3 s for 10 consecutive trials. The feeder light was bright only when the hopper was raised; at all other times during magazine training, it remained dim. The key was covered by an opaque white paper shield during magazine training.

Experimental design. A single subject design with replications across four birds was used. The other two birds served as control subjects. The sequence of phases for the four birds in the experimental series was: (a) baseline, (b) fixed-trial autoshaping with one CS+, (c) discriminated autoshaping (i.e., one CS+ and one CS-), (d) summation test (the CS+ combined with the CS- and with the N), and (e) reacquisition of fixed-trial autoshaping with two CS+s (where one CS+ was the former CS- and the other was the former N). The sequence of phases for the two birds in the control series was: (a) baseline, (b) fixed trial autoshaping with one CS+, (c) random presentations of RS and feeder, (d) summation test (the CS+ combined with the RS and with the N), and (e) reacquisition of fixed-trial autoshaping with two CS+s (where one CS+ was the former RS and the other was the former N).

Baseline. All birds were exposed to three baseline sessions to provide a record of patterns of movement in the chamber after magazine training and prior to autoshaping. During baseline, the white keylight was illuminated continuously, there were no feeder presentations, and the feeder light remained dim. Baseline sessions terminated after 3600 s.

Fixed-trial autoshaping. A 6-mm diameter circle of coloured light (CS+) was projected onto the white keylight for 8 s. At the end of 8 s, the white keylight and coloured circle of light were darkened and the feeder operated for 4 s. The ITI from feeder offset to CS+ onset was variable with a mean of 60 s and a range from 30 s to 90 s. Each pairing of CS+ and feeder operation (US) constituted one trial; sessions terminated after 60 trials. For this and all other phases, key pecks during stimulus presentations, feeder operations, and ITIs were recorded but had no scheduled consequences. Feeder operation time was excluded from calculations of session time and from all data analyses. Autoshaping sessions continued until three criteria were met for three consecutive sessions: (a) at least 95% of key pecks occurred during the CS+, (b) key pecks occurred during at least 90% of CS+ presentations, and (c) mean key pecks per min during the CS+ in any one session differed by no more than 10% from that of any session in the three-day block. Bird 5 did not approach or peck the green circle stimulus during the first three sessions of autoshaping and consequently the entire keylight was transilluminated green for CS+ presentations for two sessions of autoshaping. Bird 5 approached and pecked the CS+ during both of these sessions and the discrete circle stimulus was reintroduced for all subsequent sessions.

Discriminated autoshaping. Paired trials (a feeder operation occurred at every CS+ offset) were randomly alternated with unpaired trials (a feeder operation never occurred at CS- offset). In paired trials, the same CS+ stimulus from the previous Autoshaping phase was projected onto the key for 8 s, at the end of which the white keylight and coloured circle of light were darkened and

the feeder operated for 4 s. In unpaired trials, a different discrete circle of coloured light (CS-) was projected onto the white keylight for 8 s. After 8 s, this circle of light was turned off and the keylight remained white for the duration of the ITI. Food presentations never followed offset of the CS-. ITI duration was variable with a mean of 60 s and a range from 30 s to 90 s. At the end of each ITI, a probability generator set at 0.5 was sampled to determine whether a CS+ or a CS- would be presented on the next trial. Sessions terminated after a total of 60 CS+ and CS- presentations. Criteria for acquisition were the same as for the previous Autoshaping phase.

Random presentations of keylight and feeder operations. In this phase, stimulus presentations and feeder presentations were programmed to occur independently of one another. The keylight was illuminated white throughout this phase except when the key was darkened during a feeder operation. During a stimulus presentation, a circle of coloured light was projected onto the white keylight for 8 s. Stimulus presentations were separated by an ITI with a mean of 60 s and a range from 30 s to 90 s, which was the same as the ITI during Autoshaping and Discriminated Autoshaping. Feeder presentations were scheduled independently of stimulus presentations by sampling from a probability table every 4 s, except during feeder presentations when no sampling occurred. It was possibleThe 4-s sampling rate was determined by limitations in computer memory which precluded more frequent sampling. The probability value was set at 0.15, which approximated the rate of food presentations and, therefore, the mean interfood interval in all other phases. Using the scheduling procedures described, it was possible for pairings

(forward, backward, and simultaneous) of the RS and US to occur, and this did, in fact, happen. Sessions terminated after 34 stimulus presentations, which was determined by limitations in computer memory. Each bird in the control series was given 374 stimulus presentations over 11 sessions, which was equivalent to the mean number of CS- presentations during Discriminated Autoshaping for the four birds in the experimental series.

Summation test. Summation tests were conducted without reinforcement. There were two sessions for each bird. The ITI stimulus and duration remained the same as for all autoshaping sessions. Four stimuli (including two combined stimuli) were presented during each session. For the four birds in the experimental series, the stimuli were: (a) CS+ alone, (b) CS- alone, (c) combined CS+ and CS-, and (d) combined CS+ and N. For the two birds in the control series, the stimuli were: (a) CS+ alone, (b) RS alone, (c) combined CS+ and RS, and (d) combined CS+ and N. Stimuli were presented randomly with the constraint that five presentations of each stimulus type occurred in each of three blocks of twenty stimulus presentations. Sessions terminated after 15 presentations of each stimulus type.

Reacquisition of autoshaping. This phase was similar to the first phase of autoshaping in that all trials were paired trials (i.e., CS+ offset was immediately followed by a feeder operation). CS+ and ITI durations were the same as for previous autoshaping sessions. However, this phase differed in that two CS+s were randomly alternated. One CS+ was the former CS- from the Discriminated Autoshaping phase for the four birds in the experimental

TABLE 1

Key Stimuli and Number of Sessions — Experimental Series

	Bird1	Bird2	Bird4	Bird5
<b>Autoshaping</b>				
CS+	Yellow	Yellow	Green	Green
Sessions	17	11	10	12
<b>Discriminated Autoshaping</b>				
CS+	Yellow	Yellow	Green	Green
CS-	Green	Green	Yellow	Yellow
Sessions	15	12	12	10
<b>Summation Test</b>				
CS+	Yellow	Yellow	Green	Green
CS-	Green	Green	Yellow	Yellow
CS+/CS-	Y/G	Y/G	G/Y	G/Y
CS+/N	Y/R	Y/R	G/R	G/R
Sessions	2	2	2	2
<b>Reacquisition of Autoshaping</b>				
CS+1	Green	Green	Yellow	Yellow
CS+2	Red	Red	Red	Red
Sessions	5	12	14	18 <sup>a</sup>

<sup>a</sup>Five sessions of sixty trials followed by thirteen sessions of thirty trials.

TABLE 2

Key Stimuli and Number of Sessions — Control Series

	Bird7	Bird8
<b>Autoshaping</b>		
CS+ Sessions	Yellow 13 <sup>a</sup>	Green 14
<b>Random Stimulus Presentations</b>		
RS Sessions	Green 11 <sup>b</sup>	Yellow 11 <sup>b</sup>
<b>Summation Test</b>		
CS+ RS CS+/RS CS+/N Sessions	Yellow Green Y/G Y/R 2	Green Yellow G/Y G/R 2
<b>Reacquisition of Autoshaping</b>		
CS+1 CS+2 Sessions	Green Red 5 <sup>c</sup>	Yellow Red 5

<sup>a</sup>Nine sessions of sixty trials; four sessions of fifty trials.

<sup>b</sup>Sessions were 34 stimulus presentations in length.

<sup>c</sup>All sessions were fifty trials.

series or the former RS from the Random Presentation phase for the two birds in the control series. The other CS+ was the former N introduced for all birds during the Summation Test. At the end of each ITI, a probability generator set at 0.5 was sampled to determine which CS+ would be presented on the next trial. Sessions terminated after 60 trials, except for Bird 5 where, due to scheduling difficulties, session length was reduced from 60 trials per day to 30 trials per day after five sessions of Reacquisition. Criteria for acquisition were the same as for the first phase of Autoshaping.

Dependent variables. There are two major classes of dependent variables: numerical variables and topographical variables. The numerical variables include (a) Percent stimulus presentations with a keypeck, (b) Mean keypecks per min, and (c) Mean distance from the response key. All measures are calculated for each type of stimulus presentation within sessions. The first two measures are commonly used in studies of autoshaping and inhibition. The third measure is made possible by the automated tracking equipment used in this study and represents the mean absolute distance of a hypothetical point on the top of the bird's head from the response key in three-dimensional space. Topographical variables are X vs. Y or overhead plots of the bird's movements around the experimental chamber.

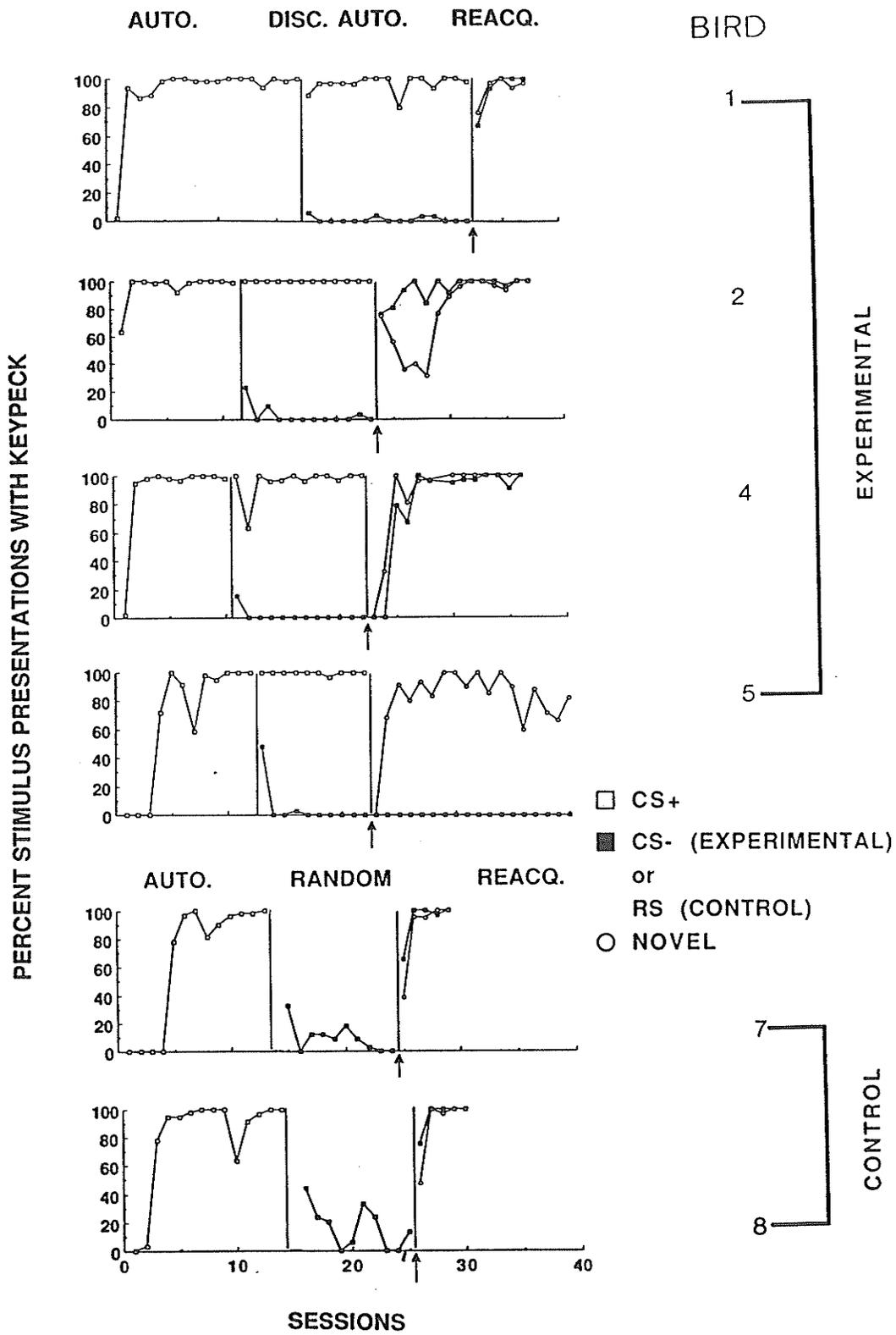
## Results

Data are presented to address four major questions: (1) Was there evidence from traditional indirect tests of conditioned inhibition for inhibitory

control by the CS-? (2) How did spatiotemporal measures of withdrawal from the CS- relate to traditional indirect measures of inhibitory control? (3) What was the relationship between spatiotemporal measures of behaviour during the CS- and the ITI? and (4) How did patterns of approach toward and withdrawal from keylight stimuli during the Random Presentation phase compare with patterns of approach and withdrawal during Autoshaping phases? To address these questions, first I will present summary data across all sessions of all phases except for Summation Tests. Then I will present summary data from Summation Tests. This will be followed by topographical data from Summation Tests for the four birds in the experimental series. Finally, I will present topographical data from all phases except Summation Tests for the two birds in the control series. No consistent movement patterns were observed during Baseline sessions; therefore, Baseline data are not shown.

Summary Data Across Sessions. The first two measures considered are measures which are commonly used in studies of autoshaping and inhibition: (a) Percent stimulus presentations with a keypeck, and (b) Mean keypecks per min. The third measure considered – mean distance from the key – has been used in previous studies of autoshaping from our lab and is made possible by the automated tracking equipment used in this study.

Figure 2. Percent stimulus presentations with a keypeck. For the four birds in the experimental series (Birds 1, 2, 4, and 5), the phases shown are: Autoshaping (Auto.), Discriminated Autoshaping (Disc. Auto.) and Reacquisition of Autoshaping (Reacq.). For the two birds in the control series (Birds 7 and 8), the phases shown are: Autoshaping (Auto.), Random Stimulus Presentations (Random), and Reacquisition of Autoshaping (Reacq.). The arrow beneath the horizontal axis indicates the point at which the Summation Test occurred. Summation Test data are not shown on this figure.



As shown in Figure 2, all four birds in the experimental series rapidly acquired the keypeck response during the first phase of Autoshaping. All birds reached criteria for acquisition. During the first session of Discriminated Autoshaping, all four birds approached and pecked the CS- as well as the CS+. For all other sessions of Discriminated Autoshaping, the percent of CS- trials with a keypeck was at or near 0% and the percent of CS+ trials with a keypeck remained at or near 100%, indicating rapid acquisition of the discrimination between CS+ and CS- trials.

Following the Summation Test, Reacquisition was introduced with randomly alternating CS+ presentations. For the four birds in the experimental series, one CS+ was the former CS- (CS+/-) from Discriminated Autoshaping and the other CS+ was the novel stimulus (CS+/N) introduced during the Summation Test. Birds 1, 2, and 4 acquired keypecking to both the CS+/- and the CS+/N; Bird 5 pecked the CS+/N but never pecked the CS+/- . All three birds who acquired pecking to both stimuli pecked the CS+/N first. Bird 1 pecked the N on trial 7 after 3 exposures to the CS- and 3 exposures to the N; it pecked the CS+ on trial 16. Bird 2 pecked the N on trial 3 after 0 exposures to the CS- and 2 exposures to the N; it pecked the CS- on trial 12. Bird 4 pecked the N on trial 66 in session 2 after 37 exposures to the CS- and 28 exposures to the N; it pecked the CS- on trial 140 in session 3. Bird 5 pecked the N on trial 70 in session 2, after 30 exposures to the CS- and 41 exposures to the N; it never pecked the CS-.

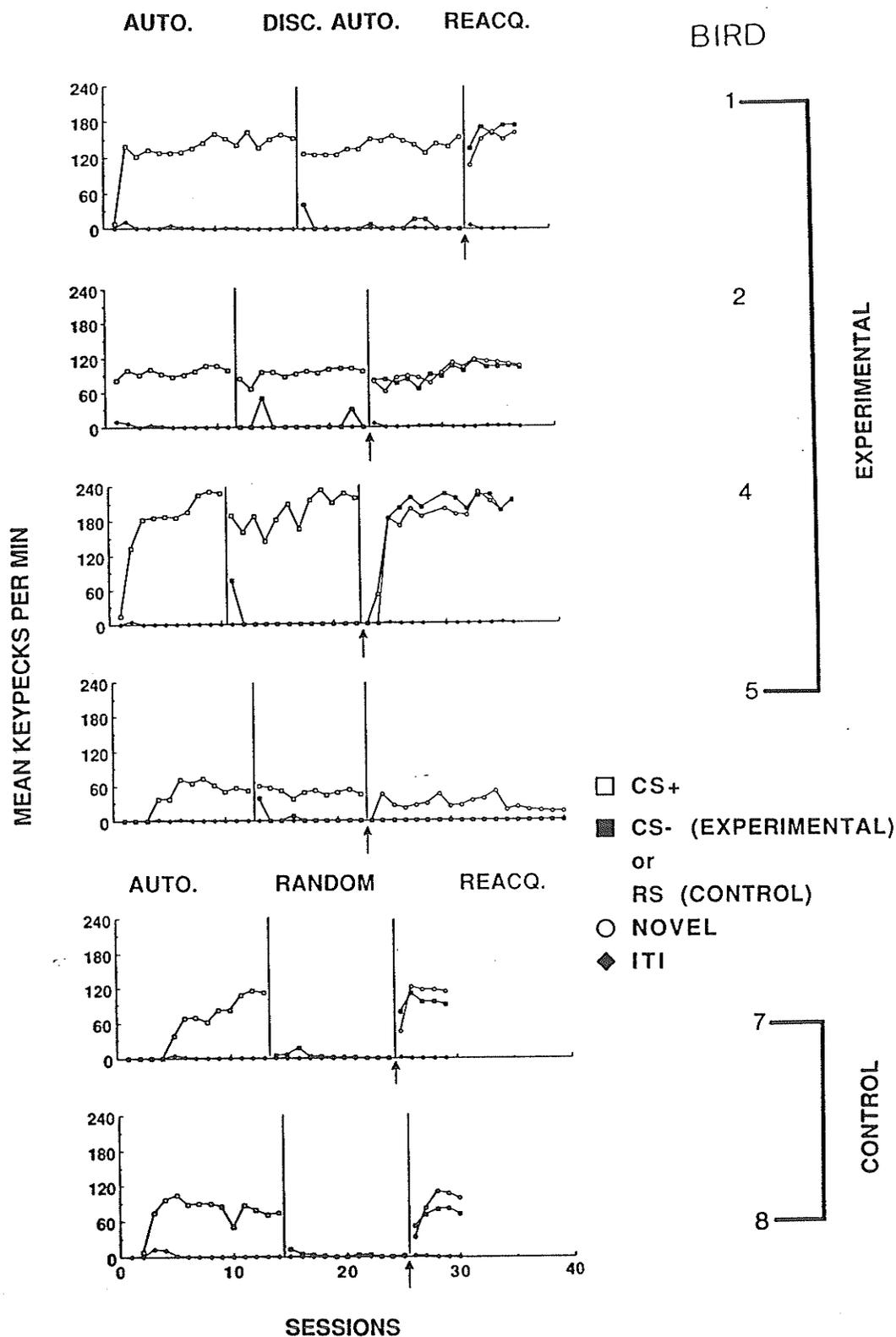
In session 1, Bird 1 pecked on more CS+/N presentations than on CS+/- presentations. After session 1, there was a steady increase in trials with a keypeck for both the CS+/N and the CS+/- until criterion was reached in session 5. In contrast, for Bird 2 there was no difference in the number of CS+/- and CS+/N trials with a keypeck in session 1. For sessions 2 to 5, there was a marked decrease in the percent of CS+/N trials with a keypeck and a marked increase in the percent of CS+/- trials with a keypeck. Percent CS+/N and CS+/- trials with a keypeck equalized in session 7 and stabilized at criterion in session 10. For Bird 4, percent CS+/- trials with a keypeck was lower than percent CS+/N trials with a keypeck for sessions 1 to 4 but stabilized at approximately equal levels by session 8. Bird 5 pecked only the CS+/N and never reached the stability criteria for that stimulus.

In summary, all birds in the experimental series rapidly acquired keypecking to the CS+ during Autoshaping and rapidly showed discrimination between the CS+ and the CS- during Discriminated Autoshaping. During Reacquisition, each of the four birds made its first keypeck to the CS+/N. For all three birds who acquired keypecking to both the CS+/- and the CS+/N, CS+/- and CS+/N trials with a keypeck stabilized at approximately equal levels. Bird 5 did not reach stability on CS+/N trials with a keypeck and never pecked the CS+/. Overall, these data indicate that (1) during Discriminated Autoshaping, all birds rapidly acquired a discrimination between CS+ and CS- trials, and (2) during Reacquisition, all birds acquired a keypeck response more rapidly to the CS+/N than to the CS+/-, which is suggestive of inhibitory stimulus control by the CS-.

The two birds in the control series (Birds 7 and 8) were similar to the four birds in the experimental series in their acquisition of keypecking to the CS+ during Autoshaping. Following Autoshaping, the Random Presentation phase was introduced in which the keylight stimulus was presented randomly with respect to feeder operations. Both birds pecked the RS during this phase; however, percent of RS trials with a keypeck was low and variable compared to percent of CS+ trials with a keypeck in the previous Autoshaping phase. During Reacquisition, both birds made their first keypecks to the former RS (CS+/RS) and pecked during a greater number of CS+/RS trials than CS+/N trials during the first session. For both birds, percent CS+/RS and CS+/N trials with a keypeck increased and stabilized at approximately equal levels after the first session.

There was one major similarity in the pattern of responding for the birds in the control series and in the experimental series. In both series, percent CS- trials with a keypeck and percent RS trials with a keypeck were highest in the early sessions of Discriminated Autoshaping and Random Presentation, suggesting generalization of keypecking from the CS+ in the previous phase of Autoshaping. For birds in the experimental series, keypecking to the CS- decreased following continued exposure to the negative correlation between CS- and food presentation in Discriminated Autoshaping. For birds in the control series, keypecking to the RS decreased following continued exposure to the independent presentation of the RS and food in Random Presentation. In addition to this similarity in performance between birds in the experimental and control series, there were two major differences in performance between them.

Figure 3. Mean keypecks per min during all stimulus presentations. Details are the same as for Figure 2.



First, percent RS trials with a keypeck during Random Presentation was markedly higher than percent CS- trials with a keypeck during Discriminated Autoshaping. This may have been due to occasional forward pairings of the RS and feeder operations during Random Presentation. Second, in Reacquisition, keypecking to the CS+/RS was acquired first for birds in the control series whereas keypecking to the CS+/N was acquired first for birds in the experimental series. For all birds in both series, the N stimulus was red. If all birds in both series had pecked the CS+/N first in Reacquisition, there may have been some question whether this was due to a red preference in autoshaping. However, both birds in the control series pecked the CS+/RS (which was green for one bird and yellow for the other bird) first, suggesting that more rapid acquisition of pecking to the red stimulus (CS+/N) in the experimental series was not due to a preference for red.

Figure 3 shows Mean keypecks per min during all stimulus presentations and ITIs. All four birds in the experimental series pecked the intertrial stimulus (ITS) as well as the CS+ during the early sessions of Autoshaping. However, by the end of this phase all four birds showed stable rates of keypecking to the CS+ and no pecking to the ITS. With the introduction of Discriminated Autoshaping, mean response rate during the CS+ did not change appreciably for Birds 1, 2, and 5, but initially decreased and became more variable for Bird 4. All birds in the experimental series pecked the CS- during Discriminated Autoshaping, although mean response rate during the CS- was low and variable compared to mean response rate during the CS+. Response rate during the ITI remained at zero for all four birds.

Birds 1, 2, and 4 pecked both the CS+/- and the CS+/N during Reacquisition. For Birds 1 and 4, mean response rate during the CS+/- tended to be somewhat higher than mean response rate during the CS+/N. For Bird 2, rates during the CS+/N and CS+/- were nearly equal. By the end of Reacquisition, mean response rates for Birds 1, 2, and 4 during the CS+/- and the CS+/N were approximately equal to mean response rates during the CS+ in Autoshaping and Discriminated Autoshaping. By the end of Reacquisition for Bird 5, mean response rate to the CS+/N stabilized at a level slightly below mean response rates to the CS+ during Autoshaping and Discriminated Autoshaping.

A comparison of Percent trials with a keypeck (Figure 2) with Mean keypecks per min (Figure 3) for the four birds in the experimental series shows that these measures do not always correspond. Specifically, response rate on trials with a keypeck often differs from mean response rate across the session. For example, for Bird 1 in session 1 of Reacquisition, percent CS+/- trials with a keypeck was lower than percent CS+/N trials with a keypeck; however, mean CS+/- response rate across the session was higher than mean CS+/N rate. In other words, Bird 1 keypecked on fewer CS+/- trials but keypecked at a higher rate on those trials. Similarly, for Bird 4 in sessions 4 to 8 of Reacquisition, percent CS+/- trials with a keypeck was lower than or equal to percent CS+/N trials, but mean response rate during CS+/- trials was higher than mean rate during CS+/N trials. In contrast, for Bird 2 in sessions 2 to 6 of Reacquisition, percent CS+/- trials with a keypeck was higher than percent CS+/N trials with a keypeck, but mean response rates during the two stimuli were virtually identical.

In this instance, Bird 2 keypecked on fewer CS+/N trials but response rate on those trials was higher than response rate on CS+/- trials. The most consistent effect of the CS- in Reacquisition was that all four birds in the experimental series pecked the CS+/N first. There was no consistently clear effect on mean response rate. In some sessions of Reacquisition, Birds 1 and 4 pecked on more CS+/N trials than on CS+/- trials, but response rates on CS+/- trials with a keypeck were higher than on CS+/N trials with a keypeck. Conversely, in some sessions of Reacquisition, Bird 2 pecked on more CS+/- trials than CS+/N trials, but response rates on CS+/N trials with a keypeck were higher.

Returning to Figure 3, the two birds in the control series (Birds 7 and 8) acquired stable rates of keypecking to the CS+ by the end of Autoshaping and showed some keypecking to the ITS early in Autoshaping. Mean response rate to the RS in Random Presentation was much lower than mean response rate to the CS+ in Autoshaping for both birds. Comparing Figure 3 with Figure 2 (Percent trials with a keypeck) indicates that while both birds pecked the RS on as many as 40% of presentations in a session, they seldom if ever made more than one keypeck on a trial. This differed markedly from Autoshaping where rapid keypecking throughout the CS+ was the norm. During the first session of Reacquisition, both birds in the control series pecked the CS+/RS first, keypecked on more CS+/RS trials than CS+/N trials (see Figure 2), and had a higher mean response rate to the CS+/RS than to the CS+/N, suggesting that the slower reacquisition of keypecking to the former CS- stimulus for birds in the experimental series was not due solely to a preference to peck red stimuli (the CS+/N). However, for all other sessions of Reacquisition, percent CS+/RS

and CS+/N trials with a keypeck were nearly equal, but CS+/N response rate was higher than CS+/RS response rate. This shows that these two measures (Percent trials with a keypeck and Mean keypecks per min) do not always correspond.

Figure 4 shows the mean distance from the key across sessions. For the four birds in the experimental series, a clear differentiation between mean distance from the key during the CS+ and the ITI developed early in Autoshaping. In early sessions, mean distance from the key was virtually the same during the CS+ and the ITI until a pattern of approaching and pecking the key immediately at CS+ onset and moving away from the area of the key and feeder at feeder offset developed. This pattern resulted in smaller mean distances from the key during the CS+ than during the ITI. When the percent of CS+ trials with a keypeck stabilized (see Figure 2), mean distance from the key during the CS+ stabilized. Mean distance from the key during the ITI appeared more variable than mean distance from the CS+, particularly for Birds 1 and 2, even though ITI durations were longer than CS+ durations. (Note that, like larger sample sizes, longer time periods should produce less variability than shorter time periods.)

With the introduction of the CS- during Discriminated Autoshaping, there was little change in mean distance from the key during the CS+ for Birds 1, 2, and 5. For Bird 4, mean distance from the key during the CS+ increased and became more variable for several sessions, but eventually restabilized at the level of the previous phase of Autoshaping. Although all birds approached and

Figure 4. Mean distance from the key in cm across all sessions. Details are the same as for Figure 2.



pecked the CS- during the first session of Discriminated Autoshaping (see Figure 2), mean distance from the key during the CS- was greater than mean distance during the CS+ for all sessions. In addition, mean distance from the key during the CS- appeared more variable than mean distance during the CS+, despite the fact that the two stimulus durations were equal. As was the case with Autoshaping, mean distance from the key during the ITI was more variable than mean distance from the key during the CS+. The most striking effect of Discriminated Autoshaping was the marked similarity between mean distance from the key during the CS- and the ITI. These measures were virtually identical, both in absolute value and in variability across sessions. As will be illustrated later in topographical figures, the birds reliably approached and pecked the CS+ immediately at CS+ onset and moved away from the area of the key and feeder at feeder offset, but did not move further away from the CS- at CS- onset. Instead, they merely continued the ongoing ITI behavior when the CS- was illuminated.

For all birds in the experimental series during Reacquisition, mean distance from the key during the ITI was greater than mean distance during the CS+/- and CS+/N. In each case, differentiation between ITI distance and CS+ distance occurred only after the reacquisition of keypecking to the CS+ (compare Figure 4 with Figure 2). Distance data from the first eight sessions of Reacquisition are unavailable for Bird 5 due to a disk error. However, this bird never pecked the CS+/- during Reacquisition and the data which are available for the last ten sessions of Reacquisition show that mean distance from the key

during the CS+/- remained virtually identical to mean distance from the key during the ITI.

For the two control birds (Birds 7 and 8), mean distance from the key during Autoshaping was similar to that of the four experimental birds - a clear differentiation between distance from the CS+ and the ITS which developed after the acquisition of keypecking to the CS+. For both birds, mean distance from the key during the ITI was greater than mean distance during the CS+. Introduction of the Random Presentation phase produced no differentiation between mean distance during the RS and the ITI. Mean ITI distance in the Random Presentation phase was lower than that in the previous Autoshaping phase for both birds and was less variable for Bird 7. In addition, mean distance from the RS was greater than mean distance from the CS+ in the previous phase. During the first session of Reacquisition for both birds, mean distance from the key was virtually the same for the ITI and both CS+s. Once keypecking to the CS+s developed for both birds, mean distance from the key during the CS+s decreased and mean distance during the ITI increased to the level seen during the first phase of Autoshaping. Mean distances from the key during the CS+/RS and the CS+/N were virtually identical throughout all sessions of Reacquisition and approximately equal to the mean distance from the key during the CS+ in Autoshaping.

In summary, all birds in both the experimental and control series showed a marked differentiation between mean distance from the key during the CS+ and the ITI in all phases of Autoshaping. In all cases, this differentiation

occurred early in Autoshaping after keypecking ceased during the ITI. Mean distance during the CS+ was smaller and less variable across sessions than mean distance during the ITI. For the birds in the experimental series, the most striking feature of Discriminated Autoshaping was the marked similarity between mean distance from the key during the CS- and the ITI. Both were larger and more variable across sessions than mean distance during the CS+. Indeed, the similarity between CS- and ITI distances across sessions suggests that the birds did not actively withdraw from the CS- but simply did not change their ongoing ITI behavior during the CS-.

The most notable feature of the Random Presentation phase for the control birds was the narrowing of the range of distance from the key compared to the previous Autoshaping phase. For both birds, mean distance during the ITI decreased with the introduction of the Random Presentation phase and mean distance during the RS increased relative to mean distance from the CS+ during Autoshaping. Mean distances during the ITI and the RS were virtually identical throughout the Random Presentation phase, suggesting that the Autoshaping pattern of approaching one type of stimulus (i.e., the CS+) and retreating from the other (i.e., the ITS) was altered by the introduction of randomly presented keylight stimuli and feeder presentations. The differentiation between mean distance during the CS+ and the ITS was reacquired with the pairing of keylight and feeder stimuli during Reacquisition.

Overall, these data suggest that pairing the keylight stimulus and feeder presentations produced two distinct movement patterns: (1) a highly

stereotyped pattern of approach and contact with the CS+ at CS+ onset, and (2) a more variable pattern of movement away from the area of the key and feeder which started at feeder offset. During Discriminated Autoshaping, all birds maintained their pattern of approaching and pecking the CS+ and moving away from the area of the key and feeder at feeder offset. Early in the first session of Discriminated Autoshaping, they approached and pecked the CS- as well as the CS+; however, this was rapidly replaced by a CS- pattern which did not differ from the ongoing ITI pattern. The birds could not be said to actively withdraw from the CS-; they simply did not alter their behavior during the CS- from that which was already occurring during the ITI. In contrast to this clear differentiation of behavior which occurred during paired presentations of keylight stimuli and feeder presentations, random presentations of keylight stimuli and feeder presentations were correlated with a loss of differentiation. Mean distance from the key was virtually identical during the RS and the ITS. Clearly differentiated patterns seen in Autoshaping were replaced by a nearly constant pattern of movement during both the RS and the ITS. In summary, it appears that while all birds actively approached and contacted the CS+ at CS+ onset, birds in the experimental series did not actively withdraw from the CS- in Discriminated Autoshaping. Instead, at CS- onset, birds in the experimental series simply did not change their ongoing ITI pattern of movement around the chamber. Birds in the control series showed a consistent, largely undifferentiated pattern of behavior in the presence of both the RS and the ITS in Random Presentation. These points will be illustrated in later topographical figures.

Summary Data on Summation Tests. Table 3 shows suppression ratios for (1) total keypecks, (2) stimulus presentations with a keypeck, and (3) distance from the stimulus. Ratios are shown for individual birds and as means across all birds in each series (experimental and control). Suppression ratios were calculated by the formula  $a/(a+b)$ . For keypecks, "a" is total keypecks during the (1) CS+ and N, (2) CS+ and CS-, or (3) CS+ and RS; "b" is total keypecks during the CS+. For stimulus presentations with a keypeck, "a" is total (1) CS+ and N presentations with a keypeck, (2) CS+ and CS- presentations with a keypeck, or (3) CS+ and RS presentations with a keypeck; "b" is total CS+ presentations with a keypeck. Although "suppression of distances" is an unusual concept and has little, if any, intuitive meaning, it was computed in a manner similar to the computation of the traditional measures of suppression for comparison purposes. For distances, "a" is mean distance during the (1) CS+ and N, (2) CS+ and CS-, or (3) CS+ and RS; "b" is mean distance during the CS+. For the birds in the experimental series, the combined stimuli were (1) CS+ and CS-, and (2) CS+ and N. For the birds in the control series, the combined stimuli were (1) CS+ and RS, and (2) CS+ and N. For keypecks and number of stimulus presentations with a keypeck, ratios less than 0.5 indicate suppression of responding during the combined stimulus relative to responding during the CS+ alone; ratios greater than 0.5 indicate facilitation of responding; and ratios of 0.5 indicate no change. For distance, ratios less than 0.5 indicate that mean distance from the key was less during the combined stimulus than during the CS+ alone; ratios greater than 0.5 indicate that mean distance was greater during the combined stimulus than during the CS+; ratios of 0.5 indicate no change.

Table 3

Total Keypecks	Stimulus Presentations With Keypeck				Mean Distance From Key	
Experimental Series						
	CS+ & CS-	CS+ & N	CS+ & CS-	CS+ & N	CS+ & CS-	CS+ & N
Bird 1	0.37	0.43	0.46	0.47	0.55	0.55
Bird 2	0.33	0.31	0.38	0.43	0.62	0.55
Bird 4	0.33	0.38	0.35	0.41	0.55	0.54
Bird 5	0.29	0.55	0.32	0.54	0.52	0.45
Mean	0.33	0.42	0.38	0.46	0.56	0.52
Control Series						
	CS+ & RS	CS+ & N	CS+ & RS	CS+ & N	CS+ & RS	CS+ & N
Bird 7	0.22	0.32	0.34	0.46	0.57	0.53
Bird 8	0.52	0.63	0.48	0.50	0.47	0.47
Mean	0.37	0.48	0.41	0.48	0.52	0.50

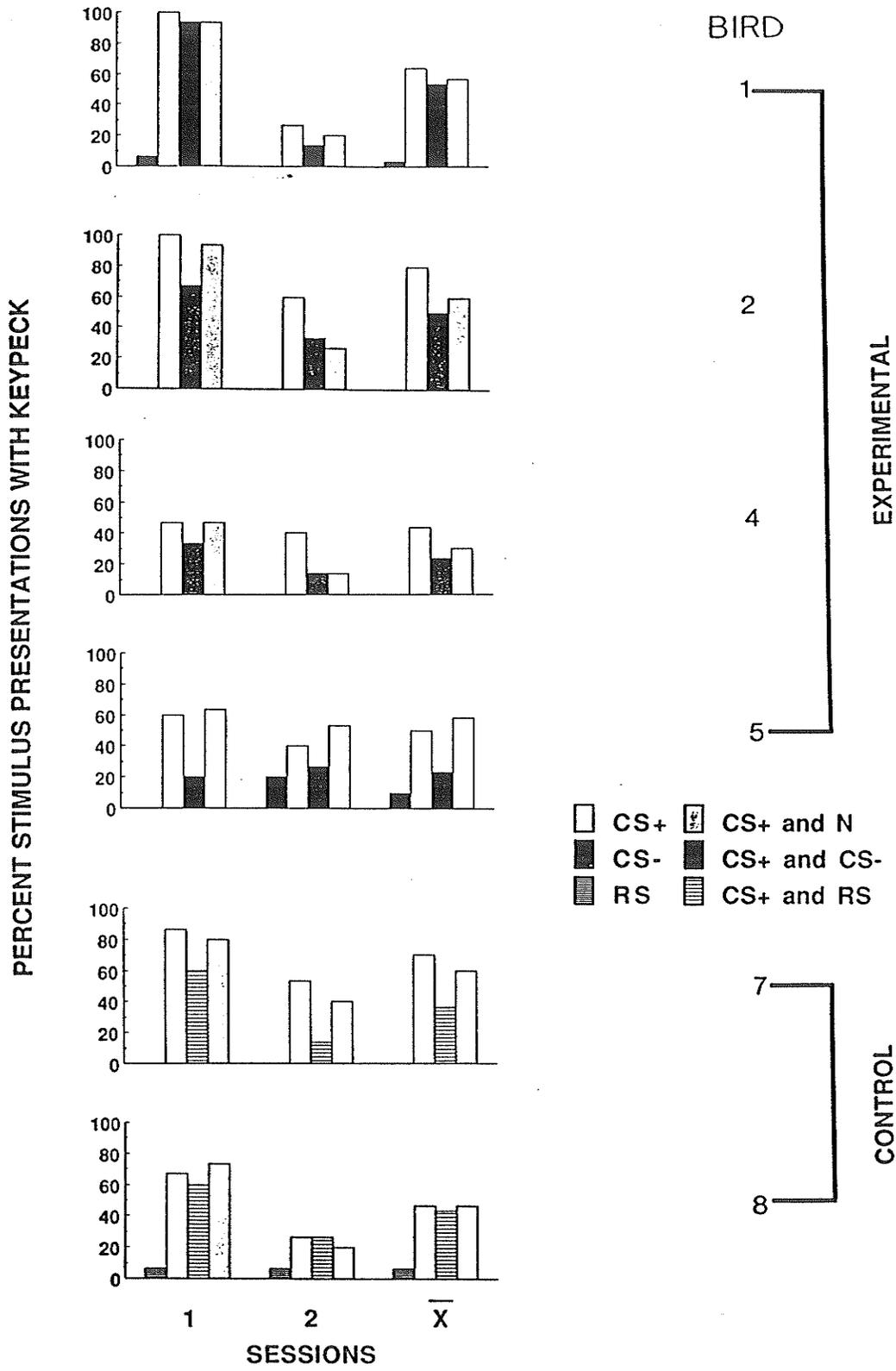
Mean suppression ratios for the experimental series show that keypecks and number of stimulus presentations with a keypeck were suppressed more by the CS- than by the N, when each was combined with the CS+. This pattern was apparent in all but two individual suppression ratios and is strongly suggestive of inhibitory control by the CS-. Mean suppression ratios for distance indicate that mean distance from the key was increased when the CS- or the N was combined with the CS+ and that this increase was greatest for the CS-. However, the effect on distance was not as clear as the effect on either total keypecks or stimulus presentations with a keypeck. For two of the four birds, there was no difference between the increase in distance when the CS- or the N was combined with the CS+. One effect of presenting an inhibitory stimulus in combination with an excitatory stimulus may be an increase in mean distance from the stimulus; however, this effect can also be seen when a novel stimulus is combined with the excitatory stimulus.

Interpretation of these data is further complicated by a comparison with data from birds in the control series. Mean suppression ratios for the control series also show more suppression of keypecks and number of stimulus presentations with a keypeck for the RS than for the N, when each is combined with the CS+. However, individual data from the control birds reveal marked inconsistencies. For example, whereas Bird 7 showed greater suppression of total keypecks than did birds in the experimental series, Bird 8 showed increased keypecking. Suppression of distance was similarly inconsistent. The overall means suggest a modest increase in distance when the RS was

combined with the CS+ and no change for the N. However, Bird 7 showed a marked increase in mean distance for the RS and a smaller increase for the N. In contrast, Bird 8 showed a decrease in mean distance for both stimulus combinations. These variations between the two birds in the control series may be reflective of the fact that stimulus presentations and feeder operations occurred independently during the Random Presentation phase, meaning that each bird received some pairings of stimulus presentations and feeder operations. Data on the temporal distribution of stimulus presentations and feeder operations during Random Presentation are not available for session 1 for either bird due to a disk error. However, for sessions 2 to 11, Bird 7 received a total of 19 simultaneous pairings of keylight stimulus and feeder, 5 forward pairings where feeder onset occurred within 1 s of keylight offset, and 5 backward pairings where keylight onset occurred within 1 s of feeder offset. For sessions 2 to 11, Bird 8 received a total of 7 simultaneous pairings, 2 forward pairings, and 2 backward pairings.

Overall, for birds in the experimental series, suppression ratios for total keypecks and stimulus presentations with a keypeck showed consistency between individual and group data. Suppression of distance was more variable; all birds showed increased distance during combined stimulus presentations, but only two of the four birds showed greater distance from the key during the CS- relative to the N. This suggests that the CS- is functioning as an inhibitory stimulus in terms of suppression of keypecks; however, it is less clear whether one attribute of an inhibitory stimulus is increased mean distance from the key. The lesser effect on mean distance from the key when the CS- is

Figure 5. Percent stimulus presentations with a keypeck for all stimulus presentations during Summation Testing. Data for sessions 1 and 2 and the mean of these two sessions are shown for each bird.



combined with the CS+ may be reflective of the powerful effect of the excitatory stimulus in producing approach to the key. The effect of the CS- may be seen most clearly in what the bird does after it has approached the key — a consistent reduction of keypecks reflected in suppression ratios for stimulus presentations with a keypeck and for total keypecks.

In contrast to the consistency between individual and group data for birds in the experimental series, individual and group data from birds in the control series are inconsistent. One bird (Bird 7) showed a profile consistent with the birds in the experimental series, suggesting, in that case, that the RS may be operating as an inhibitory stimulus. In contrast, the other bird (Bird 8) showed a mixed profile which may be more suggestive of associative neutrality. It is interesting that Bird 7, whose response pattern is suggestive of inhibitory control by the RS, received the greater number of pairings of all kinds (simultaneous, forward, and backward) during the Random Presentation phase.

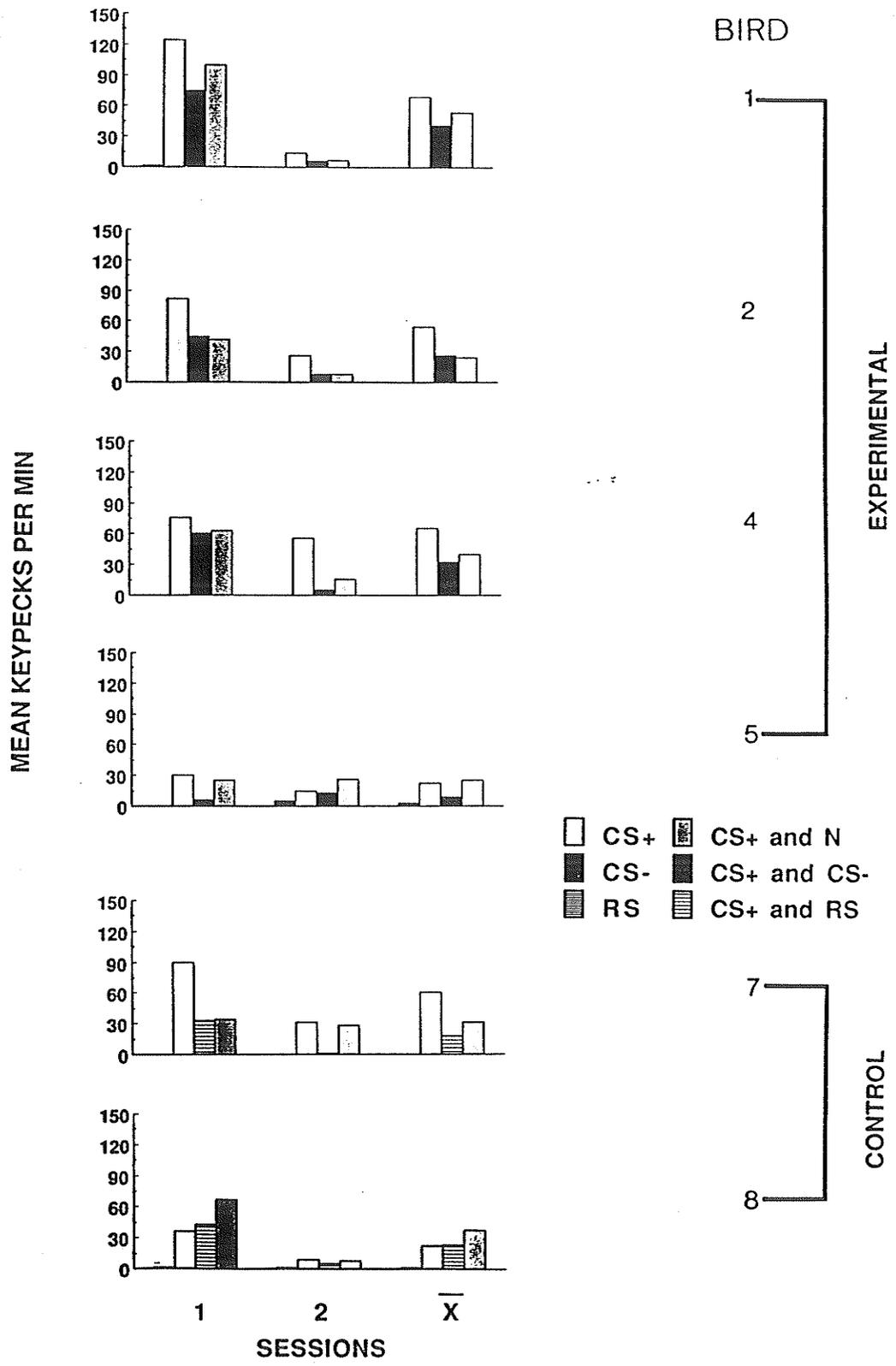
Figure 5 shows the percent of stimulus presentations with a keypeck during the two sessions of Summation Testing. For all birds, this figure shows the effect of testing without reinforcement - a decrease across sessions in the percent of trials with a keypeck. However, for the birds in the experimental series, the decrease in the percent of trials with a keypeck was smallest when the CS+ was presented alone and greatest when the CS+ was combined with the CS-. A similar pattern was apparent for one of the birds in the control series (Bird 7) — the decrease in percent of trials with a keypeck was smallest when the CS+ was presented alone and greatest when the CS+ was combined with

the RS — suggesting that the RS may have been functioning as an inhibitory stimulus for this bird. The pattern differed somewhat for the other bird in the control series. For this bird (Bird 8), there was a more nearly equal decrease across all stimulus presentations, suggesting that the decreases may have been solely due to the effects of extinction combined with a change in stimulus control when stimuli were presented in combination.

Figure 6 shows mean keypecks per min during Summation Testing for all birds. For the birds in the experimental series, mean keypecks per min was greater during CS+ alone presentations than during CS- presentations. Keypeck rate was lower when the CS- was combined with the CS+ than when the N was combined with the CS+ for all but Bird 2. For this bird, rates during both combined stimuli were approximately equal. The two birds in the control series differed markedly from one another in response rate patterns. Bird 7 was similar to the birds in the experimental series in that response rate was highest during the CS+ alone and lowest when the RS was combined with the CS+. For Bird 8, the highest response rate occurred when the CS+ was combined with the N and there was little difference in rate when the CS+ was presented alone and when it was combined with the RS. For both birds, response rate during the RS alone was at or near zero.

Figure 7 shows the mean distance from the key for all stimulus presentations during both sessions of Summation Testing for each bird. For the birds in the experimental series, mean distance from the key was smallest during the CS+ alone and greatest during the CS- alone and the ITS alone.

Figure 6. Mean keypecks per min for all stimulus presentations during Summation Testing. Details are the same as for Figure 5.



Mean distances during the CS- and the ITS were approximately equal. Mean distance from the key was greater for the CS- than for the N when each stimulus was combined with the CS+. This is particularly interesting in the case of Bird 2, which showed no difference between the CS- and the N in the suppression ratio for keypecks (see Table 3). However, this bird showed greater suppression in the percent of trials with a keypeck (see Table 3 and Figure 5) and greater mean distance from the key (see Table 3 and Figure 7) when the CS- was combined with the CS+, relative to when the N was combined with the CS+. This indicates that different measures of conditioned inhibition do not always correspond.

For Bird 7 in the control series, mean distance from the key was similar to that of the birds in the experimental series. Mean distance tended to be greatest during the RS alone and the ITS alone and smallest for the CS+ alone. Mean distance was greater when the RS was combined with the CS+ than when the N was combined with the CS+. For Bird 8, mean distance was greatest during the RS alone and the ITS alone in session 1, but combining the RS or the N with the CS+ actually decreased the mean distance compared to the CS+ alone. In session 2, there was virtually no difference in mean distance from any of the stimuli presented. These response patterns are consistent with the interpretation that the RS may have been functioning as an inhibitory stimulus for Bird 7 and as an associatively neutral stimulus for Bird 8.

Topographical data. Figure 8 shows sample topographical data (mean distance from the key) from the first five CS+ presentations and portions of

Figure 7. Mean distance from the key for all stimulus presentations during Summation Testing. Details are the same as for Figure 5.

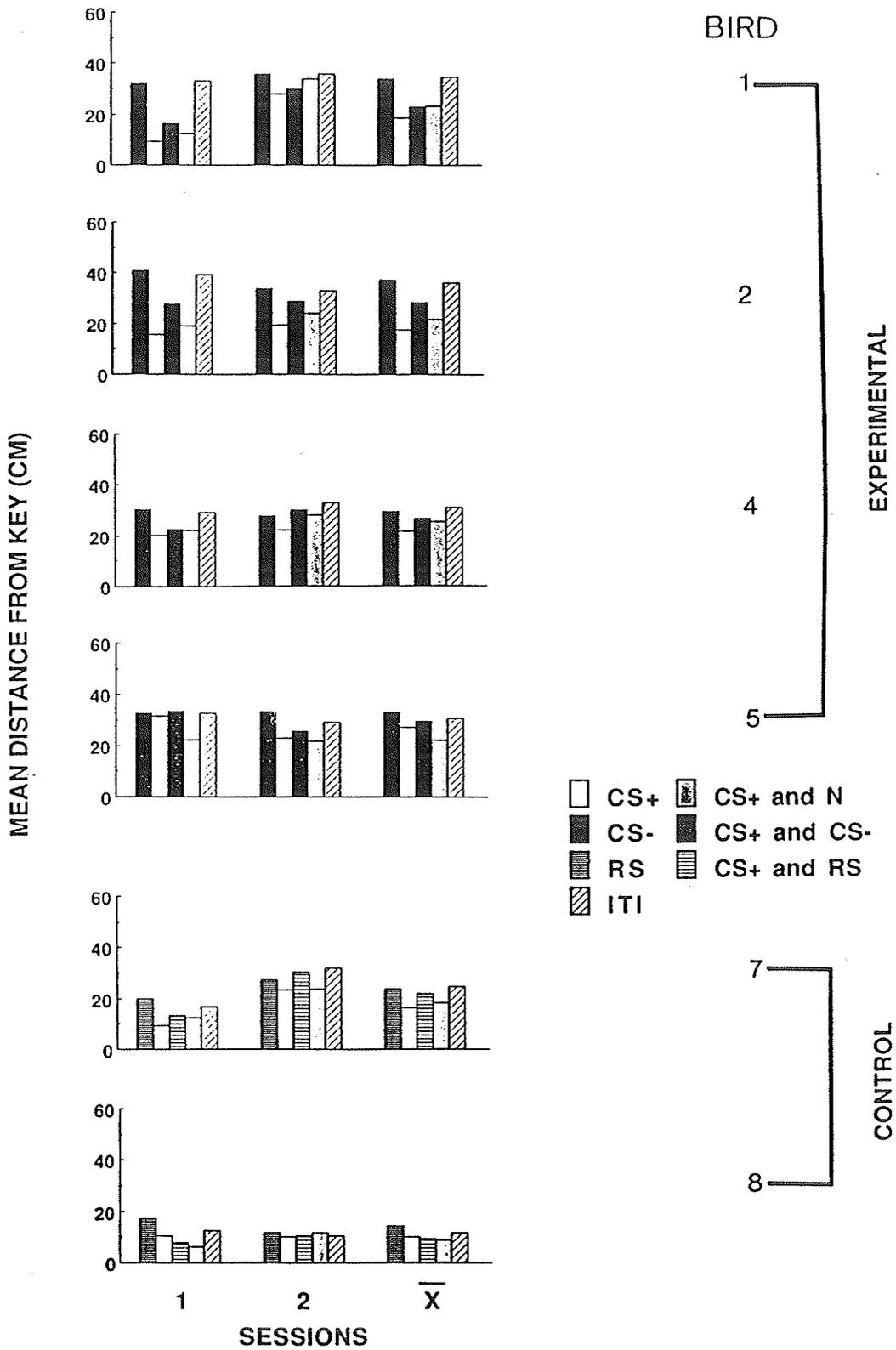
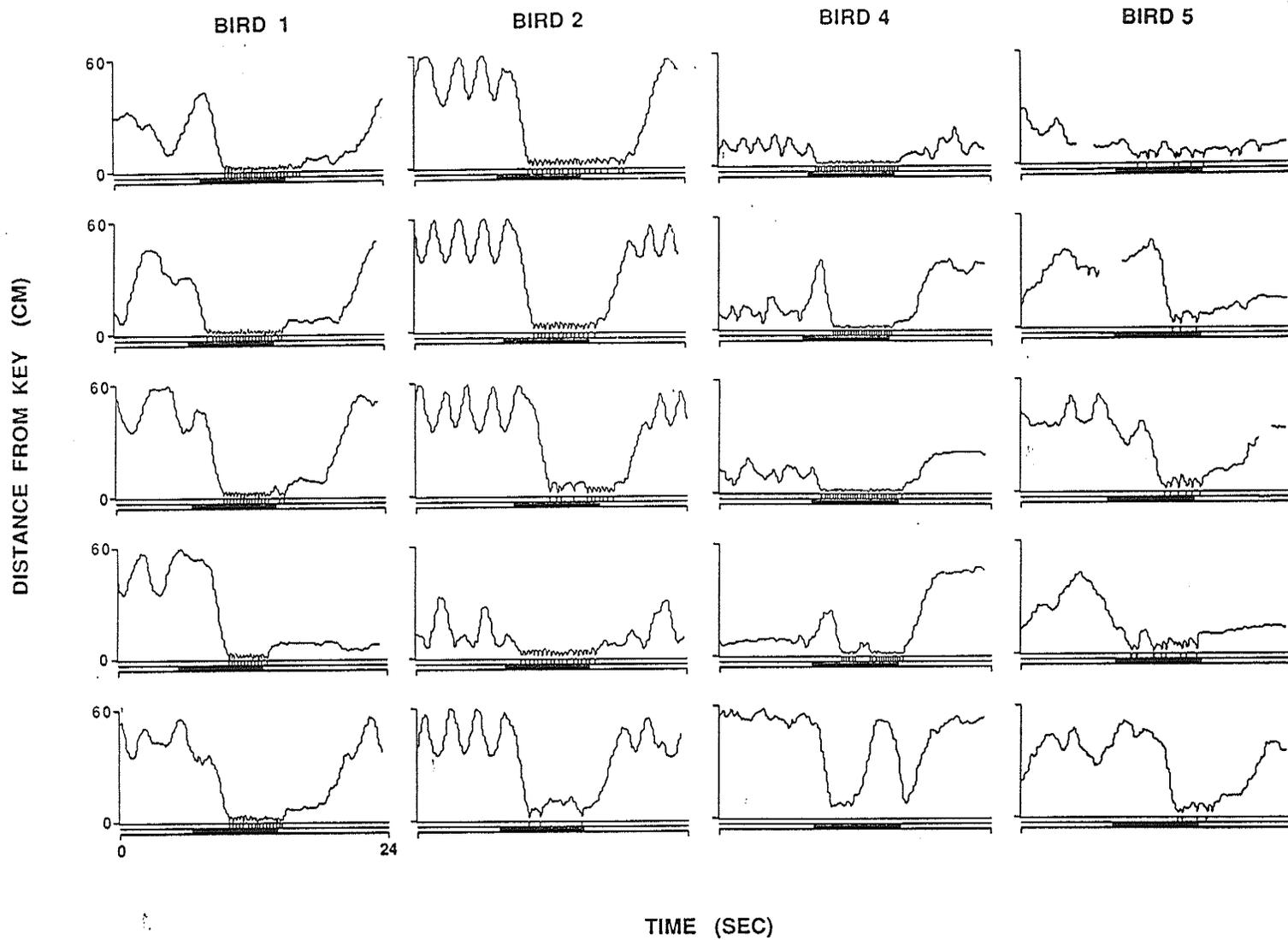


Figure 8. Absolute distance from the key during 24-s intervals in the first session of Summation Testing for birds in the experimental series. The first five CS+ presentations from the first block of trials are shown in consecutive order with portions of the ITIs immediately preceding and following each CS+ presentation. Absolute mean distance from the key in cm is indicated on the vertical axis and session time is indicated on the horizontal axis. Keypecks are shown by vertical marks in the upper band beneath each graph and the 8-s CS+ is indicated by the horizontal bar in the lower band.



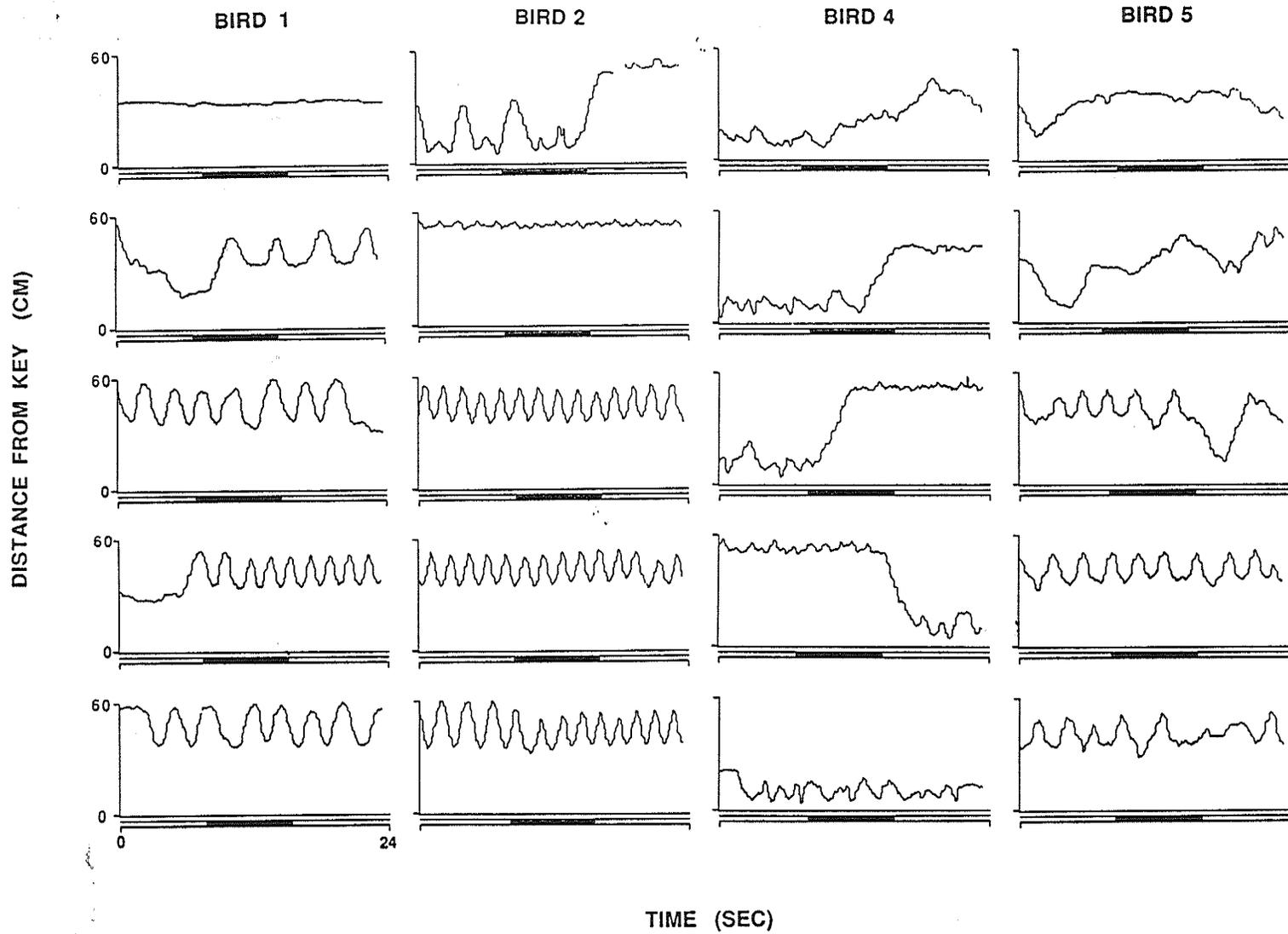
surrounding ITIs in the first session of Summation Testing for the birds in the experimental series. The patterns shown in the top three rows are typical of CS+ and ITI patterns during all phases of Autoshaping, Discriminated Autoshaping, and Reacquisition of autoshaping. The patterns shown in the bottom two rows are less typical because of the effects of extinction. Typical autoshaped patterns consisted of immediate approach to the key at CS+ onset, keypecking throughout the CS+, and immediate movement away from the area of the key and the feeder following offset of the feeder and onset of the ITS. Recall that no feeder operations followed the CS+ during Summation Testing; therefore, movement away from the area of the key and the feeder as shown in Figure 8 is not as immediate as typically seen when a feeder operation follows the CS+. In addition, keypecking during the ITI is not typical of stable state autoshaped responding, but is seen in these graphs because there is no feeder operation to interrupt keypecks at CS+ offset. The other portions of the ITI preceding and following each CS+ are typical of the irregular movement patterns seen during the ITI in all phases of autoshaping. The consistent aspects of these patterns both within and across birds are (1) movement away from the area of the key and feeder at feeder offset, and (2) irregular pacing movements around the chamber during the ITI but no contact with the ITS. (For detailed examples of movement patterns in autoshaping, see Figures 2, 3, and 4 in Eldridge and Pear, 1987, pp. 324-327).

Figure 9 shows sample topographical data (mean distance from the key) during the first five CS- presentations and portions of surrounding ITIs during

These patterns are typical of movement patterns during the CS- and ITI in Discriminated Autoshaping. Recall that the CS- was never followed by feeder operations; therefore, there is no difference between CS- offset during Discriminated Autoshaping and Summation Testing. Typical patterns during Discriminated Autoshaping consisted of moving away from the area of the key and the feeder at feeder offset with irregular movements around the chamber throughout the ITI. What is most striking about the data in Figure 9 is the lack of differentiation between patterns during the ITI and the CS-. In virtually all cases, the movement pattern during the ITI continued without interruption throughout the CS-. After the first session of Discriminated Autoshaping, where all birds approached and pecked the CS- early in the session, there is no consistent evidence that the birds moved further away from the key at CS- onset, that they moved closer to the key at CS- offset, or that they behaved in any way differently during the CS- than they did during the ITI.

Figure 10 shows topographical graphs for the last sessions of Autoshaping, Random Presentation, and Reacquisition for Birds 7 and 8 in the control series. In each row, the large graphs show mean distance from the key across the entire session and the smaller graphs show the top view of the path of the bird as it moved about the chamber during the same session. The graphs in the top row show the last session of Autoshaping for both birds; the graphs in the middle row show the last session of the Random Presentation phase; and the graphs in the bottom row show the last session of Reacquisition. The duration of the CS+ is indicated by the horizontal mark in the lower band

Figure 9. Absolute distance from the key during the first five CS- presentations from the first block of trials in the first day of Summation Testing for birds in the experimental series. Details are the same as for Figure 8.



beneath the figure; pecks are shown by horizontal marks in the upper band. By the last session of Autoshaping (shown in the top row), both birds in the control series developed movement patterns typical of stable state autoshaping: immediate approach to the key at CS+ onset, keypecking throughout the CS+, and movement away from the area of the key and feeder at feeder offset. Throughout the ITI, both birds made irregular movements about the chamber, including pacing movements along the front wall of the chamber. The density of the dark areas in the top view plots gives an indication of the proportion of time spent in various parts of the chamber. The high density areas indicate that Bird 7 spent most of the session time pacing along the front and left chamber walls, with occasional complete circuits of the chamber. Bird 8 spent most of the session time pacing along the front wall with occasional movements to the rear of the chamber. For both birds, these pacing movements occurred during the ITI, as shown in the distance graphs to the left of the top view graphs. These distance graphs show that both birds reliably approached the key during the CS+ and did not approach the key during the ITI.

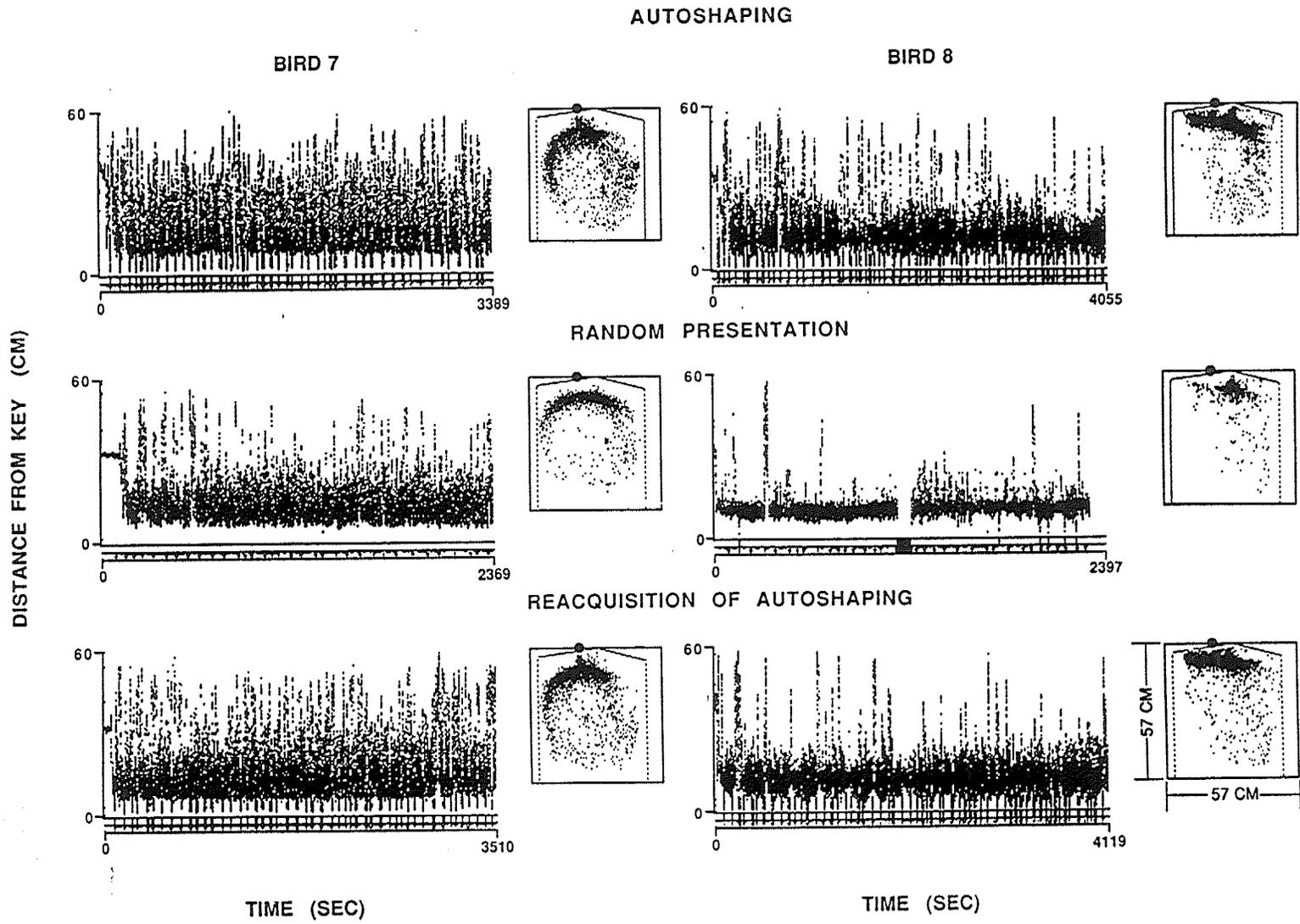
The Random Presentation phase is shown in the middle row of the figure; note that the dark band below the distance graph for Bird 8 indicates a portion of the session where data were unavailable due to a disk error. The introduction of Random Presentation produced marked changes in movement patterns. Approaches and pecks to the RS became infrequent compared to approaches and pecks to the CS+ in Autoshaping. Note that Bird 7 did not approach or peck the RS during the final session of Random Presentation, whereas Bird 8 approached and pecked the RS on six trials. During the

Random Presentation phase, the ITI pattern also changed for both birds. Bird 7 paced back and forth across the front wall of the chamber, with infrequent movements to the rear of the chamber, and Bird 8 virtually ceased pacing movements and positioned itself near the feeder throughout the ITI. These patterns persisted throughout the RS for both birds. The most striking effect of presenting key stimuli and feeder operations independently of one another was the lack of differentiation between RS and ITI patterns, in contrast to the marked differentiation between CS+ and ITI patterns during Autoshaping.

During Reacquisition (shown in the bottom row of this figure), the differentiation between approach and keypecking during the CS+s and pacing movements about the chamber during the ITI was reestablished. For both birds, patterns seen in the first phase of Autoshaping were largely recovered.

To compare movement patterns of the control birds during Random Presentation and of the experimental birds during Discriminated Autoshaping, it is necessary to compare Figure 10 with Figures 8 and 9. It is apparent that behavior differs markedly in the presence of the CS+, the CS-, the RS, and the ITS. During autoshaping, all birds in both series approached the key immediately at CS+ onset and keypecked throughout the duration of the CS+. Although not shown in these figures, all experimental birds approached and pecked the CS- early in the first session of Discriminated Autoshaping. However, after that session there was no observable change in behaviour during the CS- compared to the ITI. All birds continued their ongoing ITI behaviour throughout the CS- and there was no topographical evidence of

Figure 10. Movement topography for the last sessions of Autoshaping, Random Presentation, and Reacquisition of autoshaping for the birds in the control series. The large graphs in each row show absolute distance from the key over the entire session. Details are the same as for Figure 8. The small graphs in each row show the top view of the path of the bird during the same session as shown on the left. The circle at the top of each of these graphs indicates the position of the key, the dotted lines indicate regions of the chamber which were not visible to the videocameras, and each point on the graph represents 1 s of session time.



moving further away from the CS- or moving closer to the ITS at CS- offset. During the Random Presentation phase, both control birds occasionally approached and pecked the key during the RS (perhaps due to occasional pairings of the RS and feeder operations). However, after the first session of Random Presentation, at most one peck occurred on each RS trial and the most typical movement pattern during the RS was the same as that seen during the ITI - irregular movements along the front wall of the chamber and close to the feeder. The differentiated movement patterns seen in Autoshaping were replaced by largely homogeneous feeder-directed movements throughout both the RS and the ITI. The ITI pattern showed no change as long as the CS+ continued to be presented, but changed dramatically when the CS+ was removed. The ITI pattern remained the same when a stimulus negatively correlated with food (the CS-) was added in Discriminated Autoshaping, but changed dramatically when a stimulus positively correlated with food (the CS+) was removed and replaced by a stimulus presented randomly with respect to food (the RS) in the Random Presentation phase.

In summary, data from this study provide some evidence for inhibitory control by the CS-, both in suppressed responding during the Summation Test and retarded acquisition of excitatory conditioning to the previous CS- relative to the N. There are several critical features of these data. First, different measures of the strength of responding did not always correspond (e.g., changes in percent trials with a keypeck were not always consistent with changes in response rate or mean distance from the key). Second, during all phases of Autoshaping, birds in the experimental series showed consistent

patterns of approaching and pecking the CS+ and moving away from the area of the key at feeder offset and ITS onset. Mean distance from the key during the ITI was greater and more variable both within and across sessions than mean distance from the key during the CS+. Topographical data showed irregular movements about the chamber during the ITI and no approaches to or contacts with the ITS. Third, during Discriminated Autoshaping mean distance from the key was virtually identical during the ITI and the CS-. Topographical data indicated that the birds did not actively withdraw from the CS- but simply did not change their ongoing ITI pattern at CS- onset. Actual movement away from the area of the key and feeder occurred at feeder offset and ITS onset. Fourth, when keylight stimuli and feeder operations were presented independently of one another, a pattern of feeder-directed behavior developed which replaced the differentiated behavior seen when keylight stimuli and feeder operations were positively correlated. The feeder-directed responding observed during the Random Presentation phase was similar to that observed in studies of fixed-time schedules of reinforcement where the feeder operates after a fixed duration of time and there is no RS (see Eldridge, Pear, Torgrud, & Evers, 1989; Matthews, Bordi, & Depollo, 1990).

### Discussion

The data from this study address four major questions: (1) Was there evidence from summation and reacquisition tests for inhibitory control by the CS- under the conditions of this study? (2) How did a direct spatiotemporal measure of withdrawal from the CS- relate to traditional indirect measures of

inhibitory control? (3) What was the relationship between behaviour during the CS- and the ITI? and (4) How did patterns of approach toward and withdrawal from keylight stimuli during the Random Presentation phase compare with patterns of approach and withdrawal during Autoshaping phases? In this section, I will discuss each of these questions and then speculate on the contribution of a direct measure of withdrawal from the CS- to our understanding of inhibitory control.

#### Evidence for inhibitory control.

Comparing traditional measures of inhibitory control (i.e., summation and reacquisition) across birds from the experimental and the control series, there is a strong suggestion of inhibitory control by the CS-. In the Summation test, birds in the experimental series showed strong and consistent suppression of responding (both in total keypecks and in percent stimulus presentations with a keypeck) to the compound CS+ and CS- relative to the compound CS+ and N (see Table 3). Greater response suppression to the compound containing the CS- relative to that containing the N indicates that response suppression was not due merely to a decrement in stimulus control occasioned by presenting stimuli in a novel combination. The degree of response suppression is noteworthy in that all birds in the experimental series had an extensive history of Autoshaping prior to the introduction of Discriminated Autoshaping. This history might be assumed to lead to stronger excitatory conditioning to the CS+ (which had more conditioning trials) and weaker inhibitory conditioning to the CS-. Combining a weaker inhibitory stimulus with a more powerful excitatory

stimulus in the Summation Test might be presumed to lead to less response suppression; however, there was clear evidence of suppression to the CS+ and CS- compound.

In the Reacquisition test, all birds in the experimental group showed retarded acquisition to the CS- relative to the N. For all four birds, the first keypeck occurred to the former N rather than to the former CS-. For three of the four birds, acquisition of keypecking to both the N and the former CS- occurred rapidly. The fourth bird acquired keypecking to the N in the second session of Reacquisition, but never pecked the former CS-. The extensive history of excitatory conditioning in Autoshaping prior to Discriminated Autoshaping may have contributed to the speed of reacquisition for both stimuli. The most striking difference which emerged in Reacquisition was that all birds pecked the N before they pecked the former CS-. In combination with the pattern of response suppression observed in Summation tests, this suggests that the CS- was inhibitory.

In contrast to the birds in the experimental series, the two birds in the control series were inconsistent in their pattern of responding on Summation and Reacquisition tests. Bird 7 in the control series showed a pattern of response suppression in the Summation Test similar to that of the birds in the experimental series, which might suggest that the RS was not associatively neutral for that bird. In contrast, Bird 8 in the control series showed no response suppression to either of the compound stimuli in the Summation Test. For this second bird, not only was the RS apparently neutral, but there was no

decrement in responding due to a change in stimulus control when novel stimulus compounds were presented. For both birds in the control series during Reacquisition, the first keypeck was to the former RS, rather than to the N. Similar to the experimental birds, however, reacquisition to both the RS and the N occurred rapidly and nearly equally after the first keypeck. For Bird 7, suppression to the CS+ and RS compound in Summation and more rapid acquisition of pecking to the RS in Reacquisition is consistent with a pattern of increased attention to the RS following the Random Presentation phase, as described by Rescorla (1969). For Bird 8, no suppression to either stimulus compound in the Summation test and more rapid acquisition to the RS in Reacquisition is closer to a pattern of indifference to the stimulus (Hearst, 1972). Neither pattern is consistent with excitation or inhibition accruing to the stimulus following Random Presentation.

It should be noted that the N was novel for all birds in both series during the Summation Test, but was not novel during Reacquisition. The same N stimulus was used during Summation and Reacquisition because of equipment limitations. Therefore, in the Summation test prior to Reacquisition, each bird had already received 30 unreinforced trials of the compound CS+ and N and 30 unreinforced trials of the compound CS+ and CS- (for birds in the experimental series) or 30 unreinforced trials of the compound CS+ and RS (for birds in the control series). For all birds, this prior history may have had some effect on the speed of Reacquisition.

Relationship among measures of inhibitory control.

If one accepts that the pattern of results described above is consistent with inhibitory control by the CS-, the question arises as to the relationship between traditional measures of inhibitory control (i.e., summation and reacquisition) and a direct measure of withdrawal from the CS-. Unlike a number of previous studies (e.g., Hearst & Franklin, 1977; Kaplan, 1984; Wasserman, Franklin, & Hearst, 1974) which relied on a largely temporal measure of withdrawal (i.e., the proportion of time spent on the side of the chamber near the CS+ or CS-), the present study used a largely spatial measure of withdrawal — the mean distance of the bird's head from the response key.

Similar to previous studies of autoshaping from our lab (e.g., Eldridge & Pear, 1987), birds in both the experimental and control series showed a clear differentiation in mean distance from the key during the CS+ and the ITI in Autoshaping. Mean distance from the key was virtually identical during the CS+ and ITI for all birds until percent stimulus presentations with a keypeck stabilized after acquisition (see Figures 2 and 4). Mean distance from the key during the CS+ was smaller and more stable than mean distance from the key during the ITI, which reflected a stable pattern of approaching and pecking the key at CS+ onset and moving away from the area of the key and feeder at feeder offset. Figure 4 shows that variability in mean distance across sessions is greater for the ITI than for the CS+, despite the fact that ITI durations were

longer. (Like larger sample sizes, longer time periods should produce less variability than shorter time periods.)

Figure 8, which shows mean distance from the key during the first five CS+ presentations in Day 1 of the Summation test for the birds in the experimental series illustrates clearly the contrast between the stable and relatively invariable patterns during the CS+ and the more variable patterns during the ITI. In less detail, Figure 10 illustrates these same autoshaping patterns for the birds in the control series. These figures, in addition to Figures 2 to 6 from Eldridge and Pear (1987, pp. 324-329) show three consistent movement patterns during autoshaping: (1) immediate approach to the key at CS+ onset and keypecking throughout the CS+, (2) movement away from the area of the key and feeder at feeder offset, and (3) irregular pacing movements around the chamber throughout the duration of the ITI. These observations are consistent with those of Matthews and Lerer (1987) and Matthews, Bordi, and Depollo (1990), who reported consistent patterns of retreat to the rear of the test chamber after removal of the food hopper, pacing (often along the wall containing the response key and food hopper) in the mid portion of the inter-feeder interval (IFI), and keypecking prior to food delivery. Their procedure, which they called a "ramp" procedure, differed from the standard autoshaping procedure in that the keylight increased steadily in intensity throughout the IFI, peaking at feeder onset. Despite this difference, however, there is a marked consistency between their observations and observations of IFI behavior by Pear and his colleagues (e.g., Eldridge & Pear, 1987), who used a standard autoshaping procedure.

In summary, it can be seen that precise measurement of distance from the key within sessions has added significantly to our understanding of the sequence of behavior during the CS+ and the ITI in autoshaping. Within session measures of distance from the key show clearly the source of the differences in variability in mean distance across sessions for the CS+ and the ITI. Behavior during the CS+ is highly regular and stereotyped and consists of two patterns: (1) approach to the key, and (2) keypecking. Behavior during the ITI is also stereotyped and consists of two general classes of behavior: (1) retreat or movement away from the area of the key and feeder, and (2) pacing throughout the duration of the ITI. However, the topography of both retreat and pacing appear less regular than the topography of approach and keypecking, which may account for the greater variability in the mean distance across sessions for the ITI compared to the CS+. For example, Figure 8 shows that although the birds reliably withdrew from the area of the key and feeder at the start of the ITI, the location of pacing during the ITI varied markedly within sessions. Matthews, Bordi, and Depollo (1990) suggest that keypecking and retreat may be examples of taxic movements (i.e., movement responses which have directedness in response to a stimulus), whereas pacing may be an example of kinesic movement (i.e., increases in general activity or movement in response to a stimulus). Directed movements in response to a stimulus may display less variability in topography and location than nondirected movements.

It should be noted that Matthews, Bordi, and Depollo (1990) use a definition of taxic and kinesic movements which differs from that found in the ethological literature. Matthews, Bordi, and Depollo provide a functional

distinction between taxic and kinesis movements: taxic movements are those which have directedness with respect to a stimulus and kinesis movements show only the quality of a general increase in activity. In contrast, Thorpe (1979) provides an anatomical distinction between taxic and kinesis movements. Taxic movements occur in organisms that have a perceptual apparatus that enables them to make directed movements; kinesis movements occur in organisms that do not have a perceptual apparatus that enables them to make directed movements. Pigeons possess a perceptual apparatus which enables them to make directed movements; Thorpe, therefore, would define all movements of a pigeon as taxic movements. However, Mathews, Bordi, and Depollo (1990) describe the pigeon's movements as taxic or kinesis depending on the environmental variables controlling the movements.

In the first session of Discriminated Autoshaping for the birds in the experimental series, mean distance from the key remained virtually unchanged during the CS+ and the ITI, with mean distance during the CS- greater than during the CS+ for all birds, and slightly less than during the ITI for three of the four birds. Once percent CS- presentations with a keypeck stabilized at or near zero for all birds, mean distances from the CS+, the CS-, and the ITS developed a pattern similar to that seen during Autoshaping — mean distance during the CS+ was small and stable across sessions and mean distance during the CS- and the ITI was larger and more variable. What is most striking, however, is that mean distances from the key during the CS- and ITI were virtually identical, both in absolute level and variability, across all but the first session of Discriminated Autoshaping. Figure 9, which shows mean distance from the key during the first

five CS- presentations in the first session of the Summation test, illustrates clearly the reason for this marked similarity in mean distance during the ITI and CS-. In virtually all cases, the ongoing ITI behavior did not change with the onset of the CS-. There is no reliable indication of active withdrawal or retreat from the CS-; the birds simply continued to do what they were already doing during the immediately preceding ITI. Mean distances from the key during Reacquisition followed the same pattern as during the initial phase of Autoshaping — a clear differentiation of mean distance between the CS+s and the ITI after acquisition, with greater variability in mean distance during the ITI.

If one accepts from the Summation and Reacquisition test data that the CS- in this study was actually inhibitory, then mean distance from the CS- adds to our understanding of (1) "withdrawal" from the CS- as a measure of inhibition, and (2) the relationship between the CS- and the ITI. It is clear from Figure 4 that there is a marked difference in mean distance from the key during the CS+ and the CS-; mean distance for all birds was "close" during the CS+ and "far" during the CS-. This appears to corroborate previous observations that birds approach the CS+ and withdraw from the CS- (Hearst & Franklin, 1977; Kaplan, 1984; Wasserman, Franklin, & Hearst, 1974). However, Figure 4 also shows that the mean distance from the CS- was virtually identical across sessions to the mean distance from the ITS. Figure 9 shows that the birds did not change their behavior during the CS-, but merely continued to do what they were already doing during the preceding ITI. Comparing behavior during the CS- to the ITS, rather than to the CS+, raises the question whether the birds can actually be said to "withdraw" from the CS-.

In most previous studies of withdrawal from the CS- (e.g., Hearst & Franklin, 1977; Kaplan, 1984; Wasserman, Franklin, & Hearst, 1974), the experimental apparatus was a chamber with a tilt floor and two response keys, one on either side of the centre line of the chamber. Weight on one side or the other of this centre line closed a series of microswitches under the floor. CS+ and CS- stimulus presentations occurred randomly on one or the other of the two response keys. Approach to or withdrawal from the stimulus was calculated by recording the amount of time the bird spent on the side of the chamber where the stimulus was presented. An approach-withdrawal ratio greater than 0.5 indicated that the bird spent over half the stimulus time on the same side as the stimulus; values in this range were assumed to reflect approach to the stimulus. An approach-withdrawal ratio less than 0.5 indicated that the bird spent less than half the stimulus time on the same side of the chamber as the stimulus; these values were presumed to reflect withdrawal from the stimulus. Although both the procedure just described and the procedure used in the present study measure approach and withdrawal, the procedures differ in major ways.

While the tilt-floor procedure provides an accurate temporal measure, it provides only a gross spatial estimation of the bird's position relative to the response key. Specifically, the procedure indicates only whether the majority of the bird's weight rests anywhere on the same side of the chamber as the key displaying the CS+ or CS-. The assumption appears to be that since the stimulus varies randomly from side to side, the bird does not develop specific position preferences, but moves actively to approach the CS+ or withdraw from the CS-. When the CS+ is presented, the bird moves toward that stimulus and

closes the micro-switches on the CS+ side of the chamber. When the CS- is presented, the bird moves away from that stimulus and closes the microswitches on the opposite side of the chamber. The data presented by Hearst and Franklin (1977), Kaplan (1984), and Wasserman, Franklin, and Hearst (1974) are consistent with that interpretation: with conditioning, approach ratios increase above 0.5 for presumed excitatory stimuli and withdrawal ratios decrease below 0.5 for presumed inhibitory stimuli.

The present study used a one-key procedure in which all stimuli were projected sequentially on a single key in a fixed position in the chamber. This may have allowed the development of position preferences within in the chamber. For example, overhead plots of the movements of the birds in the control series during Autoshaping (see Figure 10) suggest that pacing during the ITI was variable within and across ITIs; however, individual birds appeared to frequent particular areas of the chamber. These ITI pacing patterns may have had an effect on the patterns of approach to and withdrawal from the CS+ and CS-, respectively. In addition, there are other procedural differences between the present study and previous studies. In particular, the present study included a phase of autoshaping prior to discriminated autoshaping. This was not the case with Kaplan (1984) and Wasserman, Franklin, and Hearst (1974), who introduced discriminated autoshaping without a prior phase of autoshaping. However, despite these equipment, procedure, and measurement differences, the data from the present study raise some questions about the interpretation of data from previous studies of withdrawal.

Distance data from the present study are consistent with observations (e.g., Hearst & Franklin, 1977; Kaplan, 1984; Wasserman, Franklin, & Hearst, 1974) of a differentiation in position from the CS+ and CS- as conditioning occurs. As data from the present study show, early in Autoshaping, there is no differentiation in position; however, as approach and keypecking occur to the CS+, there is a decrease in the mean distance from the key during the CS+, and a concomitant increase in mean distance from the ITS. With the introduction of Discriminated Autoshaping in the present study, there was a brief early phase of approach and pecking to both the CS+ and the CS-, followed by a rapid loss of approach and pecking to the CS-. By the end of the first session of Discriminated Autoshaping, there was marked differentiation in mean distance between the CS+, CS-, and ITS: mean distance from the CS+ was smaller than mean distance from the CS- or the ITS. Observed differences in distance between the CS+ and CS- are consistent with earlier studies.

However, questions arise when we consider the relationship between behavior during the CS- and the ITI. Data from the present study suggest that understanding behaviour during the ITI may be critical to understanding behavior during the CS-. Previous studies (e.g., Kaplan, 1984; Hearst & Franklin, 1977) compared behavior during the CS+ to behavior during the CS- and concluded that the pigeons approached the CS+ and withdrew from the CS-. Data from the present study suggest that the birds did not actively withdraw from the CS- but simply continued to do what they were doing during the preceding ITI. This suggests that perhaps the pigeons in earlier studies did not actively withdraw from the CS- either, but simply continued pacing or other

movements around the chamber already occurring during the ITI. Unfortunately for this hypothesis, Wasserman, Franklin, & Hearst (1974) reported one experiment where they compared approach/withdrawal ratios on trials initiated when the subject happened to be standing on the same side of the chamber as the CS and trials initiated when the subject happened to be standing on the opposite side of the chamber. In essence, they compared approach and withdrawal during the CS+ or CS- to ongoing behavior during the ITI. During the CS+, birds which were on the same side of the chamber at CS+ onset stayed on the same side, and birds which were on the opposite side moved to the CS+ side. Conversely, birds which were on the same side of the chamber at CS- onset moved to the other side, and birds which were on the opposite side stayed on that side. This suggests that birds approached and withdrew from the CS+ and CS- stimuli, respectively, relative to their positions at stimulus onset. Clearly, this differs from the results of the present study, which showed no consistent evidence of movement away from the CS-, relative to the bird's position at the end of the preceding ITI. In the present study, active withdrawal or retreat occurred consistently at feeder offset and was followed by irregular pacing movements around the chamber during the ITI. These pacing movements were not altered by the onset of the CS-. Perhaps the two-key procedure, which requires movement in different areas of the chamber to contact the CS+, engenders more active withdrawal from the CS- than seen in the present study. In other words, it is not clear whether the animals in the two-key procedure are withdrawing from the current position of the CS- or approaching an alternate location of the CS+ on the other side. It would be

interesting to use fine-grained topographical and distance from the key measures of behaviour during the CS- in a two-key procedure.

In a related study, Silva, Silva, and Pear (in press) varied the position of the CS-, while keeping the position of the CS+ constant. In the first phase, the CS+ and CS- were presented in close proximity while patterns of behavior during the ITI were recorded and examined for consistency. The area of the chamber that the bird most frequently occupied during the ITI and the CS- was identified. In the second phase, the CS- (a lighted circle projected onto the white wall of the chamber) was moved from its initial position near the CS+ and presented in the area of the chamber most commonly frequented during the ITI. Had the birds actively moved away from the CS-, the pattern of pacing during the CS- and ITI would have been expected to change. However, there was no consistent evidence of a change in pattern reflecting movement away from area of the chamber where the CS- was presented. This appears inconsistent with the two-key data from Hearst and Franklin (1977), Kaplan (1984) and Wasserman, Franklin, and Hearst (1974). One way of reconciling these different results is perhaps by postulating that the animals in the two-key procedure were approaching the alternate position of the CS+ rather than withdrawing from the current position of the CS-.

During the Summation Test in the present study, mean distance from the key showed predictable relationships with stimulus presentations. As shown in Figure 7, mean distance from the key was greatest during the CS- and ITI and smallest during the CS+. Mean distance increased when the CS+ was

combined with the N, which might indicate the effect of a change in stimulus control, and increased further when the CS+ was combined with the CS-. Therefore, mean distance from the key increased when an inhibitory stimulus was combined with an excitatory stimulus which normally produced close approach to the key.

This is also illustrated in "suppression of distance" ratios in Table 3. Three of four birds in the experimental series showed increased distance from the CS+ and N compound, and all four showed increased distance from the CS+ and CS- compound, relative to the CS+ alone. However, "suppression of distance" ratios showed less difference between the CS+ and CS- compound and the CS+ and N compound than was apparent in suppression ratios for total keypecks or stimulus presentations with a keypeck. Recall that the putative inhibitor and the novel stimulus were combined in the Summation Test with a CS+ which had an extensive history of prior autoshaping. It is probable that the strong approach tendencies engendered by a powerful excitatory stimulus overwhelmed any tendencies not to approach the response key engendered by a weaker inhibitor or by a novel stimulus. Consequently, approach to the compound stimulus was affected less than behavior which occurred after approach — keypecking. This is consistent with data from omission training in pigeons which indicates that approach to the key remains unchanged during omission, but that the location of pecking changes markedly after approach has occurred (Eldridge & Pear, 1987). Consequently, relatively less suppression of distance may reflect the strength of approach to the key during the Summation Test and not simply insensitivity of the distance measure.

Although the data are not shown here, visual examination of topographical data comparing presentations of the CS+ and CS- compound and the CS+ and N compound in the Summation Test revealed no consistent topographical changes which could distinguish between behavior during these compounds. It was not possible to detect any clear patterns of increased latency to approach the stimulus compound, vacillating movements during the approach to the key, or movement away from the key between pecks which might account for the differences in suppression of total keypecks and stimulus presentations with a keypeck to the CS+ and CS- compound and the CS+ and N compound. It is possible that the greater number of excitatory conditioning trials described earlier may have resulted in more powerful excitatory conditioning compared to inhibitory conditioning. Consequently, clear topographical or distance changes related to the effect of the inhibitory stimulus may have been overwhelmed by the more powerful control by the excitatory stimulus. In addition, topographical differences may have been too subtle to be detected by visual analysis at the degree of resolution possible with the existing equipment and computer graphing program. Future analysis with computerized pattern analysis techniques may be able to detect differences between behavior during the CS+ and CS- and the CS+ and N compounds.

#### Relationship between behaviour during the CS- and the ITI.

The most notable contribution in the present study to understanding approach to and withdrawal from excitatory and inhibitory stimuli appears to be in describing the relationship between behavior during the CS- and the ITI. As

described earlier, birds in this study did not actively "withdraw" from the CS-, although mean distance from the CS- was larger and more variable than mean distance from the CS+. Instead, during the CS-, birds simply continued to do what they were already doing during the ITI. In all cases, this consisted of irregular pacing movements around the chamber. There did not appear to be a parallel process of "pull" toward the CS+ and "push" away from the CS-, which is implied by the approach-withdrawal index used in previous studies (e.g., Kaplan, 1984). In fact, in the present study, if there were a "push" process parallel to that of the "pull" toward the CS+, the "push" seemed to occur at feeder offset.

Examination of Figure 8 from the present study and Figures 2 and 5 from Eldridge and Pear (1987, pp. 324 & 328) suggests that the birds approached the CS+ at CS+ onset and moved away from the area of the key and feeder at feeder offset. After that initial movement away from the area of the key and feeder, behavior during the ITI (and the CS-) was relatively variable and consisted of pacing movements around the chamber until the next CS+ occurred. As Figure 9 in the present study indicates, onset of the CS- did not disrupt ongoing ITI pacing behavior. There was no evidence in the present study to suggest that birds withdrew further from the key during the CS- than during the immediately preceding ITI. Therefore, in this situation, it would be misleading to suggest that the birds actively "withdrew" from the CS-; they simply continued to do what they were already doing. Active "withdrawal" appeared to occur at feeder offset. This observation raises two related issues.

First, given that the most active withdrawal appears to occur at the offset of the feeder and onset of the ITS, one might question whether the ITS itself is inhibitory. A study by Silva, Eldridge, and Pear (in preparation) suggests that this may be the case. Summation and Reacquisition Tests were conducted after Discriminated Autoshaping, comparing compounds of the CS+ and CS-, the CS+ and the ITS, and the CS+ and a novel stimulus. The outcome of both tests suggests that the ITS, as well as the CS-, is inhibitory. If the ITS were inhibitory in the present study, then withdrawal from the area of the key and feeder at feeder offset and ITS onset might represent active withdrawal from the inhibitory ITS. Perhaps if the bird has already moved away from the area of one inhibitory stimulus, the CS- might not be considered to make the situation any more inhibitory, and hence, create any additional movement changes or withdrawal. That is an interesting prospect and one which warrants further study. It would be possible, using the tracking apparatus described in this study, to do a novel form of the Summation Test, introducing either the CS- or the ITS only after approach to the CS+ has started. This might provide an opportunity for comparing the amount of disruption in approach produced by the CS- or the ITS. This might indicate whether the bird would actively withdraw from the CS- as well as from the ITS.

From the perspective of the Comparator Hypothesis (Miller & Schachtman, 1985), it is not necessary to suggest that the ITS is inhibitory. Rather, in Discriminated Autoshaping where the CS+ is a strong predictor of the US, the context (including both the ITS and the CS-) would be viewed simply as less predictive than the CS+ and hence, as less excitatory. From that

perspective, there is no clear reason to suspect that behavior during the CS- would differ markedly from behavior during the ITI.

Second, the pattern of movement observed in the present study is consistent with patterns observed by Matthews and Lerer (1987) and Matthews, Bordi, and Depollo (1990), using their "ramp" procedure: (1) retreat from the area of the key and feeder at feeder offset; (2) pacing during the IFI; and (3) keypecking prior to feeder operation. Matthews, Bordi, and Depollo (1990) argue that the minimum requirement for retreat is predictability of the reinforcer. They suggest that retreat is not a postreinforcer event in the sense that it is not elicited by the termination of the current reinforcer. Rather, it appears to be a response to the remoteness of the coming reinforcer. In other words, retreat is a response to a low current probability of reinforcement in a situation where the next reinforcer is predictable, that is, signalled either by a temporal (e.g., fixed-time schedule of reinforcement) or stimulus (e.g., autoshaping) discrimination. In the present study, the reinforcer was entirely predictable; it occurred reliably at and only at CS+ offset. Similarly, keypecking is a response to a marked increase in the current probability of reinforcement, but occurs only when there is a localized signal for reinforcement (Matthews, Bordi, & Depollo, 1990; Tomie, Brooks, & Zito, 1989). This suggests that it may not be necessary to postulate the "push" and "pull" processes of inhibition and excitation to account for approach and pecking and retreat from the key and feeder. Approach and retreat may simply represent directed (taxic) movements related to signals associated with increases or decreases in the momentary probability of the coming reinforcer.

Unlike retreat and keypecking, which are related to changes in the momentary probability of the coming reinforcer, the minimal condition for the occurrence of pacing is simply the repeated presentation of food. Pacing "does not seem to be sensitive to variations in the location of food in time but is a response to the general availability of food" (Matthews, Bordi, & Depollo, 1990, p. 343). In other words, once a bird had retreated from the area of the key and feeder at feeder offset, presentation of the CS- during the period of pacing behavior in the ITI would not necessarily be expected to engender any additional retreat. In that situation, the CS- does not convey additional information about increases or decreases in the momentary probability of the coming reinforcer. Therefore, neither approach nor retreat would be expected to occur in such a way as to change the ongoing pacing pattern.

#### Patterns of approach and withdrawal during Random Presentation.

Turning from an examination of response patterns during Autoshaping and Discriminated Autoshaping to an examination of response patterns during the Random Presentation condition, it is apparent that presenting a keylight stimulus randomly and independently of feeder operations has a marked effect on (1) approach to the key and keypecking, (2) withdrawal from the area of the key and feeder at feeder offset, and (3) the topography of behavior during the ITI. Figure 10, which shows topographical data from the last session of each phase for birds in the control series, illustrates the regular Autoshaping pattern of (1) approach and pecking the CS+ at CS+ onset, (2) moving away from the area of the key and feeder at feeder offset, and (3) pacing movements around

the chamber during the ITI. Approach and keypecking was maintained to the RS for several trials in the first session of the Random Presentation phase, but rapidly decreased and occurred only intermittently by the last session of the phase, as shown in the second row of Figure 10. The clearly differentiated Autoshaping pattern of approach toward and movement away from the key was replaced for both birds by a less differentiated pattern which included few approaches to the RS and less movement in areas away from the key and feeder. Both birds developed an ITI pattern of pacing along the front wall of the chamber, with Bird 8 showed a particularly restricted pattern of near motionless "hanging around" the feeder throughout the entire session. For both birds, (1) differentiation between approach and withdrawal, and (2) more wide-ranging pacing during the ITI were reestablished during Reacquisition.

In contrast to the approach and pecking engendered by a highly predictive, localized signal for reinforcement in Autoshaping, the keylight stimulus in the Random Presentation phase is no longer predictive of feeder operations and, hence, is not consistently approached or pecked (Rescorla, 1967; Tomie, Hayden, & Biehl, 1980; Tomie, Murphy, & Fath, 1980; Wasserman, Deich, Hunter, & Nagamatsu, 1977; Wasserman, Hunter, Gutowski, & Bader, 1974; Wasserman & Molina, 1975). But, as apparent from the present study, it is not only approach and keypecking which are disrupted by the random presentation of keylight and feeder. Both retreat from the area of the key and feeder after feeder offset and wide-ranging pacing movements during the ITI were markedly reduced. Pacing during the ITI continued but tended to be restricted to the immediate area of the feeder. Recall that Matthews, Bordi, and

Depollo (1990) indicate that the minimal requirement for pacing in the IFI is periodic food presentations, but that the necessary and sufficient conditions for keypecking and retreat include predictability of the reinforcer. In the Random Presentation condition in the present study, periodic food presentations remain, but the predictability of the reinforcer has been lost. Thus, Matthews, Bordi, and Depollo (1990) would predict the changes seen during Random Presentation in the present study — maintenance of pacing but the loss of both approach and retreat.

It is interesting, however, that the location of the pacing was also altered by the introduction of Random Presentation. It could be argued that since the keylight was no longer predictive of feeder operations, the most predictive element in the chamber became the context, and perhaps specifically the feeder itself. Certainly in terms of maximum access to the feeder when it operated (now unsignalled), being closer to the area of the feeder was likely to be reinforced by the greatest access time to the feeder. This is consistent with behavior during variable time (VT) schedules of reinforcement where the feeder operates randomly and there are no variable keylight stimuli. Unpublished data from Pear and his colleagues and from Matthews, Bordi, and Depollo (1990) suggest that during VT schedules, birds show patterns of pacing close to the area of the feeder. This pattern of close-to-the-feeder pacing is also characteristic of performance on fixed time schedules of reinforcement (Eldridge, Pear, Torgrud, & Evers, 1988; Matthews, Bordi, & Depollo, 1990).

Summary.

In summary, the current study presented data which suggested that the CS- in Discriminated Autoshaping was, in fact, inhibitory according to traditional tests for inhibitory control (i.e., Summation and Reacquisition). A continuous, spatiotemporal measure of distance from the key provided additional information about withdrawal as an attribute (and hence, appropriate measure) of an inhibitory stimulus. Comparing mean distance from the key during the CS+ and the CS- suggested that, indeed, birds were consistently further from the response key during the CS- than during the CS+. This might be taken to corroborate previous studies (e.g., Hearst & Franklin, 1977; Kaplan, 1984; Wasserman, Franklin, & Hearst, 1974) which indicated that birds consistently approached a stimulus positively correlated with reinforcement and consistently withdrew from a stimulus negatively correlated with reinforcement. However, comparing mean distance from the key during the CS- and the preceding ITI indicated that birds did not actively withdraw from the CS-. Rather, they merely continued their ongoing behavior during the preceding portion of the ITI. Active withdrawal from the area of the key and feeder occurred at feeder offset. Presentation of the CS- tended to occur during pacing in the ITI and did not alter the location or topography of pacing.

These data are inconsistent with previous findings (e.g., Wasserman, Franklin, & Hearst, 1974) which indicated that, even taking position at the end of ITI into account, birds actively withdrew from the area of the CS-. Procedural differences between previous studies and the current study may account for

greater sensitivity to withdrawal in earlier studies; however, the reason for the discrepancy remains unresolved. One possible point of resolution is to consider that the ITS is inhibitory, or at the least, less excitatory than the highly predictive CS+ in this situation. If the bird has already withdrawn from an inhibitory (or less excitatory) stimulus - the ITS - then additional withdrawal would not necessarily be expected during the CS-. Another possibility, as mentioned earlier, is that birds in the two-key procedure may be approaching the position of a previous CS+ rather than withdrawing from the current position of the CS-.

The data from the present study are consistent with data from Matthews and Lerer (1987) and Matthews, Bordi, and Depollo (1990) who observed similar patterns of approach and keypecking, retreat, and pacing using their "ramp" procedure in which periodic food presentations follow a keylight which continuously increases in intensity throughout the IFI. Matthews and his colleagues suggest that retreat and keypecking (including approach) are examples of taxic or directed movements which are related to changes in the momentary probability of signalled reinforcers. Retreat is associated with a decrease in the momentary probability of the next reinforcer (and is not elicited by termination of the current reinforcer) and keypecking is associated with an increase in the momentary probability of the next reinforcer. Retreat and keypecking both require that the reinforcer be predictable, as is the case in discriminated autoshaping.

This suggests that it may not be necessary to appeal to inhibitory processes to account for the regular patterns of movement away from the area of the key and the feeder at feeder offset. A decrease in the momentary probability of the next signalled reinforcer may account for this movement away from the key and feeder. Pacing, which requires only the periodic delivery of food, occurs in the mid portion of the IFI and may be an example of a kinesic movement, perhaps related to foraging patterns (Matthews, Bordi, & Depollo, 1990). Given the temporal arrangements in the present study, most of the CS-s were presented during the pacing portion of the ITI. Consequently, in the present study, being away from the area of the key and feeder during the CS- may have less to do with the CS- being inhibitory than with (a) the fact that the CS- does not signal any changes in the momentary probability of reinforcement, compared to the ITS, and (b) the bird is already engaged in an interim behavior, pacing, which is related to periodic food presentation. This suggests that, despite the fact that the present study showed a greater mean distance from the CS- relative to the CS+ in Discriminated Autoshaping, this difference in distance is not necessarily related to inhibitory control by the CS-. Perhaps, as LoLordo and Fairless (1985) suggest, additional research is required before wholeheartedly embracing the notion that withdrawal from the CS- is an appropriate measure of inhibitory control. Research should be directed specifically toward explicating the variables controlling patterns of movement observed in the presence of putative inhibitory stimuli.

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