

**DISCRIMINATIVE COURTSHIP
CONDITIONING
IN THE PIGEON, COLUMBA LIVIA***

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ABSTRACT

Fifteen male pigeons were exposed to a Pavlovian discriminative conditioning procedure in which presentations of CS⁺ were followed by brief access to a female conspecific while presentations of CS⁻ were not. The conditioned behavior which emerged to the CS⁺ in this context were found to bear a clear topographical resemblance to various elements of the unconditioned courtship repertoire of this species. Moreover, a substantial number of these conditioned responses were directed at the CS⁺ object, itself. The most noteworthy responses to CS⁻ presentations took the form of an increase in the frequency and intensity of the advertising call vocalization plus a marked tendency to turn away from the CS⁻ object itself when illuminated. These observations were discussed in light of their significance for current theoretical accounts of Pavlovian conditioning.

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INTRODUCTION

Within the last ten to fifteen years, remarkable changes have occurred in the way theorists think about Pavlovian (or classical) conditioning as an adaptive process of behavioral modification. As Rescorla (1988) has pointed out in an article entitled "Pavlovian conditioning: it's not what you think it is", the old, mechanistic, reflex-switching notions of Pavlovian conditioning have given way to the much more sophisticated view of Pavlovian conditioning as a process by which organisms learn about relationships among events in the environment as a result of the "surprise" resulting from the perception of "... a discrepancy between the actual state of the world and the organism's representation of that state." (p. 153). The learning which emerges under such circumstances can then be said to have the adaptive advantage of restoring the validity of the internal representation of the world maintained by the organism.

The earlier assumption that the topography of the conditioned response (CR) usually conforms to that of the unconditioned response (UR) has given way to the realization that a complex array of factors determine not only if a CR will appear but also its form and directional characteristics in a given setting. Moreover, the idea that Pavlovian conditioning is applicable only to the limited domain of autonomic reactions plus a few scattered skeletal responses has had to be discarded in light of the discovery that Pavlovian processes are implicated in the modification of a wide range of behavior in both direct and indirect ways. By focusing on the courtship repertoire of the pigeon, *Columbia livia*, the present study represents one attempt to demonstrate not only that complex, species-typical reaction patterns are susceptible to Pavlovian control but also that the nature of this control is far more complex and subtle than had previously been imagined.

The possibility that complex, species-typical (“instinctive”) reaction patterns might be susceptible to classical conditioning was originally broached by Pavlov (1927). Ethologists such as Lorenz (1965) and Eibl-Eibesfeldt (1967) have long held similar views, but Skinner’s (1938) widely accepted assertion that respondent behavior consists of autonomic responses, plus a few scattered skeletal responses such as the eyeblink and the kneejerk, reduced classical conditioning in the eyes of many to a relatively minor process of behavioral modification, even for species of intermediate phylogenetic level such as the rat and the pigeon.

Similarly, Pavlov’s (1927) original “stimulus substitution” account of classical conditioning fell upon hard times as the observations of such early investigators as Hilgard (1936), Zener (1937), Hilgard and Marquis (1940), and Kimble (1961) indicated that clear differences in topography can exist between the conditioned response (CR) and the unconditioned response (UR). Such differences are obviously incompatible with a literal, orthodox reading of a “stimulus substitution” account of classical conditioning.

Several decades later, the discovery of the auto-shaping phenomenon by Brown and Jenkins (1968) was one of several major developments forcing an extensive reexamination of widely accepted views of both the nature and behavioral domain of classical conditioning. As evidence from a variety of research strategies accumulated pointing to the Pavlovian nature of the auto-shaping phenomenon (See reviews by Hearst and Jenkins, 1974; Schwartz and Gamzu, 1977; Locurto, Terrace and Gibbons, 1981), it became clear that the behavioral domain of Pavlovian conditioning is potentially much greater than many psychologists had previously suspected. Moreover, Mackintosh (1974) was moved to suggest that the dismissal of Pavlov’s “stimulus substitution” account of classical conditioning may have been premature, particularly if the principle is rendered in more liberalized terms.

In a classic set of experiments, Jenkins and Moore (1973) demonstrated

that the pairing of a lighted response key (the conditioned stimulus, or CS) with a food or water reinforcer (the unconditioned stimulus, or US) was sufficient to generate relatively complex, CS directed, species-typical, motor responses appropriate to the reinforcer being signalled. Their observations indicated that pigeons will attempt to “eat” a stimulus object signalling food and “drink” a stimulus object signalling water. As Jenkins and Moore (1973) noted, their findings were in accordance with what might have been expected on the basis of even a strict reading of the “stimulus substitution” principle.

The studies reported here initially represented an attempt to extend the generality of the phenomenon reported by Jenkins and Moore (1973) by employing a reinforcer (US) radically different from either food or water—namely, limited daily access by male pigeons to their mates. The literature contains many reports of the apparent Pavlovian conditioning of courtship behavior and behavior characteristic of other complex “instinctive” reaction patterns in a variety of species (See Hollis, 1982, for a review of such studies). With respect to courtship or reproductive behavior, Farris (1967) was able to bring under Pavlovian control five major components of the courtship ritual of the male Japanese quail, *Coturnix coturnix japonica*, using a buzzer as the CS and exposure to a receptive female conspecific as the US.

In a study with rams by Sokolova (1940, cited by Hafez, Cairns, Hulet and Scott, 1969), the ringing of a high-pitched bell was followed by the presentation of a sexual object. The ringing of a low-pitched bell was followed by no such consequence. Subjects eventually gave clear evidence of having learned to discriminate between the two stimuli, giving a sexual reaction to the high-pitched bell but not to the low-pitched bell.

Breder and Coates (1935) presented male guppies with a glass beaker containing a female guppy for a number of trials and found that later presentations of the empty beaker elicited elements of the species-typical courtship sequence of this species. Verplanck (1955) reported similar findings

with male three-spined sticklebacks, *Gasterosteus aculeatus*.

Also working with the three-spined stickleback, Sevenster (1973) employed an operant conditioning paradigm in which brief exposure to a female conspecific was contingent upon a prior rod biting response. Over the course of conditioning, the rod became the object of species typical courtship behavior, suggesting, from a Pavlovian perspective, that it may have acquired in surrogate form some of the properties of a female conspecific.

The evidence cited above derives from relatively formal experimental procedures and strongly suggests that complex, species-typical reproductive patterns can be brought under Pavlovian control. However, the lack of adequate control procedures in some cases and/or a general lack of interest in the directional properties of the conditioned behavior in others preclude the possibility of directly relating such observations to those of Jenkins and Moore (1973).

A survey of the ethological literature reveals a number of anecdotal reports of seemingly similar phenomena. Craig (1911, 1913, 1914), Whitman (1919) and Levi (1941) all refer to instances of misdirected courtship behavior by pigeons of various species. Ficken and Dilger (1960) described instances of redirected copulatory behavior by individuals of several avian species. Surveys of such periodicals as *Auk*, *Condor* and *Ibis* yield a number of reports by amateur ornithologists of misdirected reproductive behavior (see, for example, Owen, 1897; Kear, 1960; Hetrick and McCaskie, 1965; Mueller, 1970; Potter, 1972).

Other examples of redirected reproductive behavior have come from the observation of domestic (farm) animals. Hafez, Schein and Ewbank (1969) have noted that various stimulus factors in the environment which have borne a consistent relationship to reproductive activity in the past seem to enhance that activity in the future. Specific examples of enhanced and/or redirected

reproductive behavior in cows (Parshutin, 1956, cited by Hafez, Schein and Ewbank, 1969), stallions (Wierzbowski, 1959, cited by Hafez, Williams and Wierzbowski, 1969), and turkeys (Hale, Schleidt and Schein, 1969) encourage speculation that such behavior could have arisen through a process of Pavlovian conditioning.

In a pilot study by Rackham (1971), the brief illumination of a floor-mounted CS object signalled male pigeons that a daily 30 minute reunion with their mates was imminent. Signs of conditioning began with approach reactions to the CS object but these were soon superseded by such major components of the species-typical courtship ritual as nodding, bowing, cooing, strutting, pirouetting and what was taken to be nest calling. Both still and cinematic photography revealed that many of these responses were directed at the CS object, itself.

Allowing for the difference in reinforcers, these results were remarkably similar to those later reported by Jenkins and Moore (1973) with food and water reinforcers. However, the lack of appropriate control procedures for non-associative artifacts meant that it was not possible to preclude alternative interpretations of the outcome. Gerry (1975) and Gilbertson (1975) subsequently replicated these essential findings but in the context of attempting to operantly condition the pigeon's keypeck by using the "opportunity to court" as a reinforcer. Neither employed a control procedure for non-associative artifacts in a Pavlovian context.

By employing appropriate control procedures together with more sophisticated techniques of data acquisition and a blind scoring procedure to minimize the possibility of bias on the experimenter's part in scoring conditioned reactions, the studies reported here were designed to provide a more satisfactory test of the generality of the effect reported by Jenkins and Moore (1973). In particular, it was expected that to the extent Jenkins and Moore's observations with food and water reinforcers were valid, male

pigeons would come not only to exhibit a species typical courtship reaction in the presence of a localizable CS object signalling imminent access to their mates but would also direct certain elements of this conditioned reaction to the CS object itself.

METHOD

The four experiments reported here employed a Pavlovian discriminative conditioning procedure in which presentations of one stimulus light, the CS⁺, were always followed by the US (access to the mate) but presentations of a second stimulus light, the CS⁻, were not. Since these stimuli differed in terms of location, color, brightness, and shape, their use as CS⁺ or CS⁻ was counter-balanced in each experiment. The decision to use a discrimination control procedure rather than Rescorla's (1967) "truly random" procedure was essentially a matter of convenience. With very long inter-trial intervals such as those used in these experiments, a randomly occurring control stimulus would occur within 15 minutes of the US about once in 100 trials. It would thus, in effect, be explicitly unpaired with the US.

Each successive experiment involved slight changes in apparatus and/or procedure in an effort to minimize the effects of extraneous stimuli which could potentially modulate the course and extent of conditioning to the nominal CS objects. Since most features of the apparatus and procedure were common to all experiments, a generalized account of these is offered with details pertinent to particular experiments provided as appropriate.

Subject.— Subjects were fifteen (15) mated pairs of White Carneaux pigeons, *Columbia livia*. Four pairs served in Experiments 1, 2 and 4, respectively, and three pairs served in Experiment 3. Each pair was permanently housed in a conditioning chamber with male and female normally

separated by a partition.

Apparatus.—Four conditioning chambers were constructed for these experiments. From a frontal perspective, the inner dimensions of each chamber were 74 cm (width) by 44 cm (depth) by 41 cm (height from hardware cloth floor to ceiling). A sliding, fiberboard partition divided each chamber into two compartments of equal size. A chain constructed of heavy duty elastic bands was secured to the ceiling of each experimental room and exerted a constant tension on the partition, the upward movement of which was normally prevented by the armature of a heavy duty solenoid. Activation of the solenoid retracted the armature, allowing the partition to move upward almost instantaneously (typically within 300 milliseconds), giving the male and female unrestricted access to one another.

The left compartment housing the male differed from the right compartment housing the female only with respect to the presence of a ceiling-mounted microphone (Fanon MKC-54) and two stimulus lights. One of the stimulus units consisted of a Dialco mounting socket equipped with a #1820 bulb and a blue, hemispheric lens. This was flush-mounted on the rear wall of the male's compartment, 18 cm down from the ceiling and 6 cm to the left of the partition. The second, somewhat smaller unit consisted of a Sylvania 28-SB indicator lamp fitted with a yellow lens cap. For experiments 1 and 2, this unit was mounted in the front of the male's compartment, on the channel supporting the movable partition, at a height of 10 cm above floor level.

For Experiments 3 and 4, the yellow light was mounted on the back wall of the male's compartment, directly beneath the blue stimulus light, at a height of 13 cm above floor level. This step was taken in an effort to counter the tendency in Experiments 1 and 2 for subjects' responsiveness to the front-mounted stimulus light (as CS⁺) to decline in comparison to the rear-mounted blue stimulus light (as CS⁺), possibly as a result of habituation

to the front-mounted light which was more or less constantly in the subjects' field of view. To increase the salience of these lights as stimulus objects, they were caused to flash, when presented, by momentarily interrupting the filament circuit at 1/2 second intervals.

In Experiments 1 and 2, filmed records of behavior were obtained with either a Bolex Super 8 camera (Model 160) or a Nizo Super 8 camera (Model S-180). A Beaulieu 16 mm camera (Model R16B) was used for this purpose in Experiments 3 and 4. A slow motion, frame-by-frame 8 mm or 16 mm projector was used to analyze filmed records of behavior. Pigeon vocalizations were recorded using a Uher four track, reel to reel tape recorder.

Each conditioning chamber was located in one of four experimental rooms giving off a central observation/control room. A standard 24 hour day/night timer provided subjects in each experimental room with an artificial day of 15 hours "daylight" and 9 hours darkness which corresponded roughly to a late spring day in mid-latitudes of the northern hemisphere.

Procedure.— In each experiment, the order in which subjects were run for a given session was randomly determined. A typical conditioning trial was initiated by depressing a hand switch which simultaneously activated the event programming apparatus, camera and Uher tape recorder. Following a pre-CS interval of 4 seconds (for baseline purposes), the subject received either a positive trial (illumination of CS⁺ followed by access to the mate for 20 to 30 minutes) or a negative trial (illumination of CS⁻ only). Upon completion of a trial for the first subject, the apparatus was reset for the next scheduled subject, and so on, until all subjects in a given experiment received a trial for that session.

Subjects received two trials per day—one in the morning and one in the evening—with an inter-trial interval of ten to twelve hours. In each block of ten trials, subjects received five presentations of CS⁺ and five of CS⁻ on

a randomized basis.

In Experiment 1, subjects received a total of 120 trials (60 CS⁺; 60 CS⁻) in combination with a technique of systematic extension of the CS duration over trials in an effort to condition later components of the courtship ritual. In practice, however, a substantial decline was observed both in the number and precision of courtship CRs given to CS⁺ presentations when the CS duration was increased from 13 seconds to 20 seconds. In an effort to recoup these losses, the CS duration was set back to 13 seconds from Trial 41 and this value was maintained for the duration of the experiment. In Experiments 2, 3 and 4, the pre-CS and CS durations were each fixed at 4 seconds. Subjects in Experiment 2 received 120 trials (60 CS⁺; 60 CS⁻) while subjects in Experiments 3 and 4 each received a total of 90 conditioning trials (45 CS⁺ and 45 CS⁻).

To assess the degree to which conditioning had occurred, a set of behavioral categories was established. The categories ultimately adopted were generally similar to those used in the earlier pilot study of Rackham (1971), and, thus, owe their origin in part to Levi (1941), Goodwin (1956) and Fabricius and Jansson (1963).

BEHAVIORAL CATEGORIES

Approach Door.—For this category to be scored, it was necessary for subjects to take at least three steps toward the door (partition) separating male and female or move within 6 cm of it. In the event that other more complex activities occurred which necessarily brought the animal close to the door, this category was not used unless the animal clearly paused at the door for at least one-half second.

Approach CS.—Applicable only in the CS⁻ interval, this category represented

movement toward the CS object involving at least three steps, or, alternatively, movement bringing the animal within 6 cm of the CS site. In the event that other, more complex activities occurred which necessarily brought the animal close to the CS site, this category was not used unless the animal clearly paused at the CS site for at least one-half second.

Bowing.—Movement in which the animal tilted or pivoted forward to bring its back, neck and head into horizontal alignment— i.e., parallel to the floor. This response often occurs in association with such other courtship behavior as rushing or circling.

Bowing Coo.—Levi (1941) labeled this vocalization “crowing” and found it to be an integral component of the bowing display. Goodwin (1956) referred to it as the “display coo” and transcribed it as “Oo-roo-k’too-coo”. Fabricius and Jansson (1963) preferred Heinroth’s (1949) transcription—“wang-wang-rook-ho”.

Circle.—This category involved steady movement around the periphery of the compartment to describe an arc of 360°. In a more spacious environment, such behavior might be better classified as “strutting”.

Tail Response.—A spreading and/or depression of the tail feathers was classified as a tail response.

Rush CS.—Applicable only in the CS interval, this category involved a sudden run, jump or hop toward the CS site, often, but not necessarily, accompanied by bowing and tail responses.

Oscillation-1.—The animal moved around the periphery of its compartment,

describing an arc of less than 360°, then reversed direction to describe another such arc. At least one reversal of direction was required for this category to be scored.

Oscillation-2.—It was to be expected that as conditioning proceeded, certain zones would acquire greater significance for the animals than others. In excitatory conditioning, those zones associated with the CS⁺ site and the partition could both be expected to elicit approach behavior. A simultaneous tendency to approach both areas could lead to oscillation between them. To document such a tendency, a sub-category labelled “Oscillation-2” was established. Applicable only in the CS interval, this sub-category involved oscillation specifically between the partition and the CS site.

Orient.—Applicable only in the CS interval, this category involved any slight movement of the head leading to a momentary (at least one-half second) fixation of the CS by one or both eyes. Use of this category was precluded by the use of any other category except “Face Away”.

Advertising Call.—Goodwin (1956) spoke of a low, moaning vocalization which he transcribed as “Oorh” or “Oh-oo-oor”. Levi (1941) transcribed this call as “Whooo-a, whooo-a, whooo-a” while Fabricius and Jansson (1963) rendered it as “aoo, aoo, aoo ...”. The advertising call, as it was labelled in these experiments, is emitted by isolated males and is indicative, perhaps, of a low level of sexual excitement.

Face Away.—Applicable only in the CS interval, this category was used to document movements of the head and/or body resulting in the animal facing in a direction 180° ($\pm 45^\circ$) away from the CS site for at least one-half second.

SCORING PROCEDURE

The animals' vocalizations were quite unambiguous and could be scored by a straight-forward auditing of the audio tape recordings. The motor reactions, however, were sometimes of borderline intensity or precision, making it advisable to employ blind scoring procedures. Accordingly, the film footage for each experiment was cut into short segments covering the individual subjects and their individual trials. The segments were recombined in a randomized sequence for actual data extraction.

To obtain some indication of the accuracy with which the experimenter was able to categorize the recorded response patterns, both he and another observer used a blind scoring procedure to independently analyze a randomly selected sub-set of 50 trials using the behavioral categories described above. Inter-rater agreement was a reasonably high 87% for the trial set observed with differences between observers emerging largely with respect to the intensity of a given response pattern. The subsequent formal analysis of the entire data set was conducted solely by the experimenter in the manner described above. The data extracted were subsequently decoded and assigned to the appropriate subject and trial for further analysis.

RESULTS

The data from each of the four experiments were pooled for purposes of the analysis presented here. Although subjects in Experiments 1 and 2 were exposed to 120 conditioning trials (60 CS⁺; 60 CS⁻), only the first 90 trials (45 CS⁺; 45 CS⁻) are included here to be consistent with the 90 trials (45 CS⁺; 45 CS⁻) presented to subjects in Experiments 3 and 4.

The results are presented in graphic form in Figures 1 and 2 which compare responsiveness to CS⁺ and CS⁻ presentations for each of the

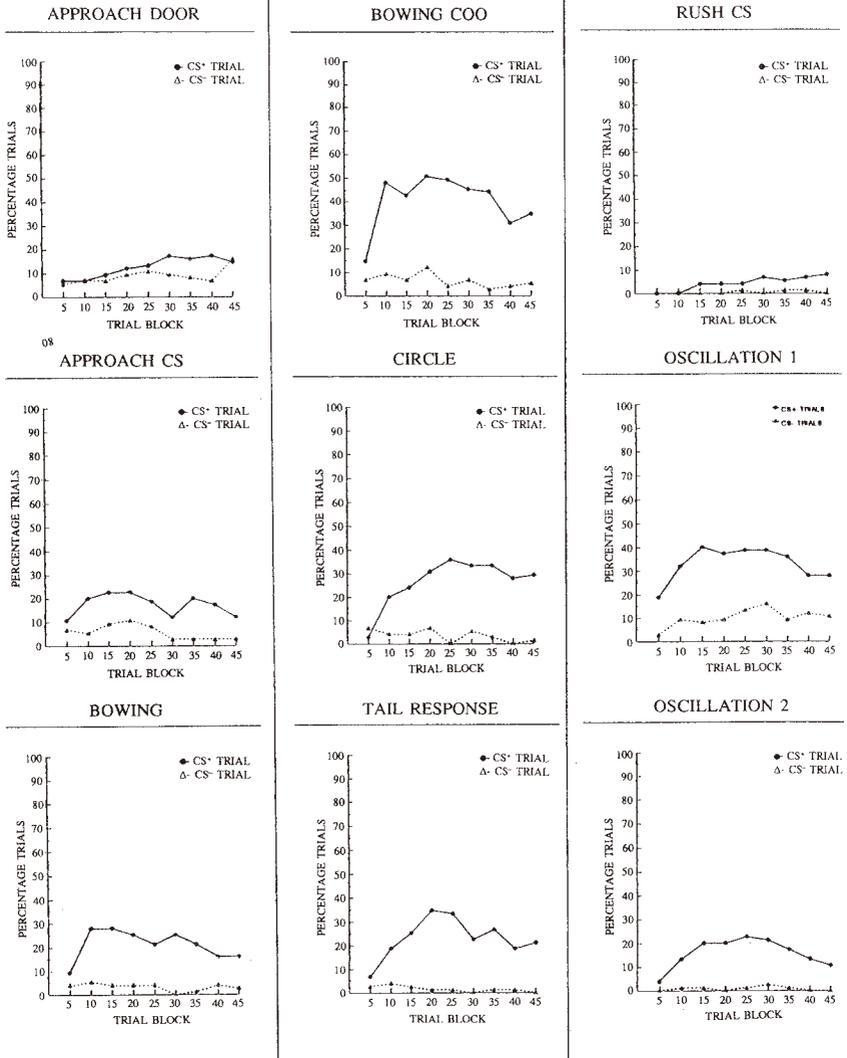


Fig. 1. Percentages (in blocks of 5 trials) of CS+ (●—●) and CS- (Δ---Δ) trials on which the behavioural categories of Approach Door, Approach CS, Bowing, Oscillation-1 and Oscillation-2 were recorded ($N = 15$).

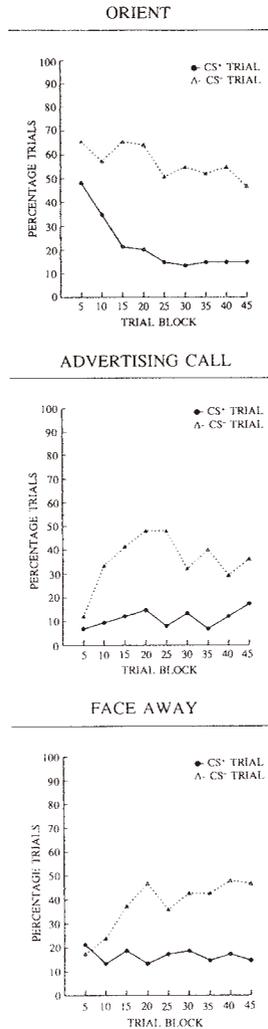


Fig. 2. Percentages (in blocks of 5 trials) of CS+ (●—●) and CS- (Δ---Δ) trials on which the behavioural categories of Orient, Advertising Call, and Face Away were recorded (N = 15).

behavioral categories described above. In addition, the discriminative performance of all 15 subjects over all trials was initially expressed in terms of difference scores (overall responsiveness to CS⁺ minus overall responsiveness to CS⁻) for each behavioral category. These difference scores were subsequently converted to student t-values as statistical tests of differential responsiveness to CS⁺ and CS⁻ presentations for each behavioral category.

It can be seen in Figure 1 that subjects demonstrated a relatively low, but consistent, tendency to approach the partition (Approach Door) on both CS⁺ and CS⁻ trials. While there seemed to be a somewhat greater tendency for this reaction to occur during CS⁺ presentations, the difference between CS⁺ and CS⁻ presentations did not achieve statistical significance.

Although it occurred at a relatively low frequency, the overall tendency to approach the CS site (approach CS) was consistently higher to CS⁺ presentations than to CS⁻ presentations across all trials ($t = 2.81, p < .05$).

It is clear from Figure 1 that the four explicit courtship categories of Bowing, Bowing Coo, Circle, and Tail Response all came under stimulus control, each occurring at a significantly greater frequency to CS⁺ presentations compared to CS⁻ presentations (Bowing: $t = 2.29, p < .05$; Bowing Coo: $t = 3.93, p < .01$; Circle: $t = 2.71, p < .05$; Tail Response: $t = 2.88, p < .05$).

As an aggregate reaction pattern, "Rush CS" was an infrequently used category since it required the appearance of an integrated sequence of behavior consisting of a rapid approach to the CS object itself, the Tail Response, and the Bowing response. Although there seemed to be a slightly greater tendency to use this category during CS⁺ presentations compared to CS⁻ presentations, the difference did not reach statistical significance.

As Figure 1 suggests, Oscillation-1 occurred at a significantly greater frequency to CS⁺ presentations compared to CS⁻ presentations ($t = 3.52, p$

< .01). A major portion of this oscillating behavior was of the Oscillation-2 variety consisting of a back and forth movement between sectors associated with the stimulus site and the partition. Oscillation-2 also occurred at a significantly higher rate to CS⁺ presentations compared to CS⁻ presentations ($t = 3.29, P < .01$).

Turning to Figure 2, it can be seen with respect to CS⁺ presentations that the initial tendency to respond solely with an orienting reaction waned quite rapidly as other response categories began to be used. In contrast, the simple orienting reaction to CS⁻ presentations persisted at a fairly high level across trials, suggesting that little in the way of courtship behavior was occurring during such trials. Overall, the use of this category during CS⁻ presentations was significantly higher than during CS⁺ presentations ($t = -6.59, p < .001$).

With respect to the advertising call, it is apparent from Figure 2 that subjects consistently emitted this vocalization much more frequently to CS⁻ than to CS⁺ presentations ($t = -5.05, P < .001$). The tendency for subjects to “Face Away” from the stimulus site during CS⁺ presentations was consistently lower than the tendency to “Face Away” during CS⁻ presentations ($t = -4.57, p < .001$).

Overall, the results indicate that subjects discriminated between the CS⁺ and CS⁻ stimuli in a number of critical ways. First, a significantly higher incidence of the various elements of the species-typical courtship repertoire occurred during CS⁺ presentations compared to CS⁻ presentations. Second, a significant proportion of this conditioned courtship behavior was directed either toward the nominal CS object or toward objects likely to be associated with the US such as the partition separating the male and female compartments. Third, the significantly greater tendency to emit the Advertising Call during CS⁻ presentations as well as the significantly greater tendencies to simply “Orient” toward or “Face Away” from the stimulus object during

CS⁻ presentations suggest that this stimulus may, in fact, have acquired aversive or inhibitory properties by virtue of signalling that the US would not be available in the near future. This particular finding is strongly reminiscent of the observation by other investigators that pigeons in auto-shaping situations will tend to withdraw from stimuli negatively correlated with the delivery of food (e.g., Hearst and Franklin, 1977; Peden, Browne and Hearst, 1977; Gaffan and Hart, 1981).

DISCUSSION

In demonstrating that the pairing of an approachable, visual, stimulus object with access to the mate will cause male pigeons to perform courtship rituals in response to subsequent presentations of that object, these findings can be taken, for the following reasons, to extend the generality of the phenomenon reported by Jenkins and Moore (1973) with food and water reinforcers. First, the procedure employed was formally Pavlovian, access to the mate (US) having been contingent solely upon prior presentation of the CS. Second, the demonstration of a Pavlovian discrimination in a situation with counter-balanced stimuli and a blind scoring procedure made it possible to rule out such non-associative processes as sensitization or pseudo-conditioning as possible mediators of the phenomenon. Third, as confirmed by still and cinematic photography, courtship CRs which appeared during CS presentations in this context often bore a clear topographical similarity to unconditioned courtship behavior. Fourth, responses normally evoked by, and directed at, the US (female conspecific) began to appear not only in the presence of stimuli associated with the US — e.g., the nominal CS and cues associated with the reinforcement site — but also to be directed at those stimulus objects on a significant number of occasions (Moore, 1973; Mackintosh, 1974). In particular, subjects approached the CS⁺ site, oscillated

between the CS⁺ site and the partition, and even showed some tendency to “rush” the CS⁺ object.

Jenkins and Moore (1973) interpreted their findings with food and water reinforcers in terms of a liberalized version of Pavlov’s (1927) original “stimulus substitution” account of classical conditioning. This liberalized version of “stimulus substitution” theory suggests that, under certain circumstances, conditioned behavior will not only bear a remarkable topographical similarity to unconditioned behavior but may also be directed at the CS object, itself, if the behavior in question has a directional component and the CS object provides the requisite environmental support for such action. The results of the Jenkins and Moore (1973) studies were, in fact, well described by such an account, for pigeons’ attempts to “eat” a stimulus object signalling food and “drink” a stimulus object signalling water were clearly documented by cinematic and other means.

Certain aspects of the present findings with courtship behavior could also be described by such a liberalized account of stimulus substitution theory, for film records of behavior clearly document a striking topographical congruence between conditioned and unconditioned courtship behavior as well as the fact that some of this conditioned behavior was clearly directed at the nominal CS object or at other stimuli associated with imminent access to a female conspecific. However, the present results (and those of Jenkins and Moore) may simply represent special instances of a situation in which the various parameters affecting CR and UR topography and directionality happen to “conspire” to produce a result consistent with even an orthodox version of “stimulus substitution” theory.

As Mackintosh (1985) and Hollis (1982) have argued, the UR (and, by implication, the CR) should be viewed as consisting not simply of a single response but a range of responses, only a subset of which may appear under any particular set of conditions. As Mackintosh (1985) has noted, the

parameters likely to affect the degree of CR/UR topographical overlap and CR directionality include the nature of the CS (including its intensity, sensory properties, localizability, approachability and predictive validity), the nature of the US (including its intensity, sensory and affective properties, and the point in the appetitive/consummatory sequence at which it is introduced to the organism), temporal and spatial relationships between CS and US, and even any instrumental contingencies in effect to which the response system in question may be sensitive.

It follows that the CR and UR might be very similar in form, radically different in form, drawn from the same response system, or from different response systems, in the same direction, or opposite in direction (with the CR serving to compensate to some degree for the effects of the US as in drug tolerance and cardiac conditioning situations). With regard to directionality, a CR with directional characteristics might be directed at the normal CS site, or to other sites associated with the US, or lack any obvious directional characteristics if the CS is diffuse in nature.

As Rescorla (1988) notes, it is now clear that far from forming a single association between a nominal CS object and a US, organisms are capable of forming complex, hierarchical arrays of associations among a wide range of stimuli inherent in a given Pavlovian context.

The present findings with courtship behavior support the observation that a wide range of factors inherent in a given Pavlovian context can produce a diversity of outcomes, all of which are attributable to Pavlovian conditioning. It was clear in the present experiments, for example, that not all subjects came under Pavlovian control, at least in terms of the orthodox criterion of the appearance of conditioned behavior bearing a topographical similarity to the UR. Indeed, some subjects either showed no courtship behavior whatsoever to CS presentations or the frequency or intensity of courtship responses they did exhibit to the CS varied substantially across

trials. Such variability might be explained by differences in reproductive readiness between individuals. Alternatively, the salience of the relationships between the US and stimuli associated with it may have differed between subjects and within subjects over time. Even in those subjects in which conditioned courtship behavior was regularly observed, such behavior was not invariably directed at the nominal conditioned stimulus. Rather, other stimulus objects, such as the partition separating male and female, became regular targets of conditioned courtship behavior. Moreover, although great care was taken to try to eliminate the possibility that extraneous stimuli might be associated with the imminent appearance of the CS or the US, there was a significant number of occasions on which the process of setting up the apparatus for a given trial was observed to trigger anticipatory responses in subjects. Finally, the observation that anticipatory courtship behavior was frequently inhibited by CS⁻ presentations can be taken as further evidence of the variety and richness of associations possible in a Pavlovian context involving a rich species typical repertoire such as the pigeon's courtship behavior. The complexity inherent in such a preparation provides a useful venue for future studies designed to explore what are increasingly recognized as the subtleties of Pavlovian control of behavior.

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