One-trial appetitive conditioning in the sexual behavior system

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One-trial Pavlovian conditioning has been demonstrated with aversive reinforcers such as electric shock and lithium chloride. The present experiments using male Japanese quail were conducted to determine if an appetitive unconditioned stimulus (US), the opportunity to copulate with a female quail, can also generate one-trial learning. In Experiment 1, subjects were exposed to a contextual conditioned stimulus (CS) for 35 sec and then given copulatory opportunity. In Experiment 2, male birds were given 0, 2, or 4 min of exposure to the contextual CS before presentation of a female. In both cases, control groups received comparable exposure to both the contextual CS and the sexual US, but in an unpaired fashion. Subjects were tested for sexual learning by reintroducing them to the experimental context in the presence of a test object that incorporated the taxidermically prepared head of a female quail. In both Experiments 1 and 2, subjects for whom the contextual CS and sexual US had been paired displayed significantly more approach to the test object than did unpaired subjects.

One-trial learning is comparatively uncommon in Pavlovian conditioning, being confined to procedures involving noxious or aversive stimuli. For instance, a rat that experiences gastrointestinal illness once after tasting a distinctively flavored fluid will subsequently avoid that fluid (Smith & Roll, 1967). In contrast, Pavlovian conditioning procedures employing appetitive unconditioned stimuli have not yielded evidence of such rapid learning.

In making comparisons across motivational systems, it is necessary to consider classes of responses and stimuli that are roughly comparable. With this in mind, one might compare the learning of aversions and preferences for various substances in chicks. Day-old chicks can learn, in a single conditioning trial, not to peck a brightly colored bead that is coated with bitter-tasting methyl anthranilate (Lowndes & Stewart, 1994; Roper & Redston, 1987). In contrast, more extensive training is required before chicks will show a preference for pecking nutritive food instead of nonnutritive sand (Hogan, 1977). More extensive training is also required to condition pigeons to peck at visual signals for food. Terrace, Gibbon, Farrell, and Baldock (1975), for example, reported that, even under optimal procedural parameters, their fastest learners required about 10 trials to acquire autoshaped keypecking (see also Locurto, Travers, Terrace, & Gibbon, 1980).

In another commonly observed example of rapid conditioning by aversive stimuli, a single pairing of contextual cues with electric footshock is sufficient to induce conditioned freezing in rats (Fanselow, 1990; Kiernan & Westbrook, 1993). In contrast, one-trial learning has not

been reported in the corresponding appetitive conditioning paradigm, in which increased activity and locomotion are conditioned by pairing contextual cues with food presentation (Balsam, 1984; see also Balsam & Schwartz, 1981).

Differences in the speed of appetitive and aversive conditioning may reflect the relative costs and benefits of each type of learning. An animal that fails to avoid a taste associated with severe gastrointestinal distress risks loss of life, whereas an animal that fails to approach a signal for food risks loss of a meal. These considerations suggest that appetitive conditioning may occur quickly in the case of a response that has a greater and more immediate impact on adaptive fitness than does procuring a single meal.

Sexual behavior is the vehicle by which vertebrate species most directly gain genetic representation in future generations. Furthermore, in some organisms, sexual opportunities are few and far between—for instance, in short-lived species that experience only one or two breeding seasons, species in which a minority of males monopolize the majority of the reproductive opportunities, and, perhaps, species in which the density of conspecifics is low and the difficulty of finding them is high. In these circumstances, an animal might accrue significant gains in reproductive fitness through the capacity to learn very quickly about sexual opportunity and suffer penalties in fitness for failing to do so. Thus, we may find rapid learning effects in the sexual behavior system.

Sexual learning has been reported in a variety of species (see Domjan & Holloway, *in press*, for a review) and has resulted in conditioned social displays in fish (Hollis, Cadieux, & Colbert, 1989), conditioned ultrasound vocalizations in mice (Nyby, Whitney, Schmitz, & Dizinno, 1978), and approach and conditioned copulatory responses in male quail (Domjan, O'Vary, & Greene, 1988). Notwithstanding the diversity of these sexually condi-

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Figure 1. The test object.

tioned responses, sexual learning procedures often result in a common outcome: Exposure to a sexually conditioned stimulus increases the responsiveness of males to species-typical cues provided by a female. For example, exposure to a sexually conditioned stimulus decreases the latency of rats to ejaculate when they engage in copulatory behavior in response to a sexually receptive female (Zamble, Hadad, Mitchell, & Cutmore, 1985). Conditioned facilitation of responding to female cues has also been observed in studies with male fish (Hollis et al., 1989) and quail (Domjan, Greene, & North, 1989).

The present experiments were conducted to determine whether sexual reinforcement can produce one-trial learning. Male quail served as subjects, and the conditioned stimulus (CS) was provided by contextual cues experienced when the birds were placed in a distinctive environment. After exposure to the contextual stimuli, the subjects were allowed to copulate with a female, which served as the unconditioned stimulus (US). The consequences of the single conditioning trial were measured using a test of conditioned facilitation of responding to female cues. The test object consisted of a taxidermically prepared female head attached to a model made of terry cloth (see Figure 1). Males rarely approach or copulate with such a test object in the absence of sexual conditioning (e.g., Köksal, Domjan, & Weisman, 1994). We were interested in whether a single context conditioning trial would produce approach and copulatory behavior.

EXPERIMENT 1

Two groups of subjects were compared in Experiment 1. One group received exposure to the contextual CS paired with copulatory opportunity. For the other group, exposure to the CS and copulatory opportunity were unpaired. After a single exposure to the contextual CS, both groups were tested for their response to the test object.

Method

Subjects. Twenty male Japanese quail were hatched in the colony at the University of Texas and then moved to individual cages at 30 days of age. The birds were selected for the experiment when they were 4–8 months old on the basis of a pretest for sexual competence. The pretest consisted of exposure to a sexually receptive female quail in their home cages for 5 min. This period is usually sufficient to distinguish be-

tween copulators and noncopulators (Schein, Diamond, & Carter, 1972). Sexually receptive female Japanese quail of at least 4 months of age served as "US birds."

Apparatus. The experimental chamber (91 × 122 × 107 cm) was light-tight and had plywood walls and ceiling and a wire-mesh floor. Three of the walls were painted white, and the fourth was painted black. Two 35-W light bulbs secured to the ceiling of the chamber (in the right front corner and the back left corner) provided illumination. Male subjects and US females were introduced into the chamber through a port in the ceiling. Another opening in the ceiling provided access for a video camera that had a field of view encompassing the entire floor of the chamber.

Context conditioning was assessed by placing a test object in the experimental chamber. The object (see Figure 1) consisted of two dark-green terry-cloth ovoids stuffed with Poly-fil, a vertical section about 8 cm long and 13 cm in circumference and a horizontal section about 10 cm long and 20 cm in circumference. A taxidermically prepared female quail head, along with about 2.5 cm of neck, was mounted atop the vertical section.

A habituation cage was also used that provided contextual cues distinctly different from the experimental apparatus. The habituation cage was much smaller in area (79 × 51 cm) and had a much lower ceiling (23 cm high). Three walls were painted dark brown. The fourth wall was made of wire mesh and admitted ambient light from the room. The floor was covered with sand, and a 35-W light bulb was mounted on the back wall.

Procedure. Prior to conditioning, all subjects were habituated to handling and placement in a novel chamber. Once a day for 6 days, the subjects were placed in the habituation cage. After 1 min, the house-light was switched on, and, 4 min later, the subjects were removed. In addition, each subject was allowed one daily 5-min exposure to a sexually receptive female quail introduced into the subject's home cage. This treatment was designed to furnish the birds with sexual practice to increase the likelihood that they would copulate in the experimental chamber. Two subjects did not copulate during these 5-min female exposures and were therefore not included in subsequent phases of the experiment.

Following pretraining, the 18 remaining birds were randomly assigned to Group Paired ($n = 9$) and Group Unpaired ($n = 9$). During the conditioning trial, each subject in Group Paired was placed in the completely dark experimental chamber. After a delay of 4 min, the houselights were turned on, allowing the subject to see its surroundings. After a further 35 sec (the context exposure period), a female quail (the US) was released into the chamber. The subject was allowed 5 min to interact with the female, and then both birds were removed. The 5-min US period was videotaped for later analysis.

The subjects in Group Unpaired experienced exactly the same procedure as those in Group Paired, except they did not receive the US in the experimental context. Instead, the experimenter merely opened the ceiling port and inserted his hand into the chamber as if introducing a female bird. To equate sexual experience, Group Unpaired subjects were allowed a 5-min period with a female quail in their home cages about 4 h after exposure to the experimental context.

The next day, the effect of conditioning was assessed by exposing the subjects to the test object. The object was placed in a 29.0 × 40.5 cm test zone delineated with pink string in the middle of the experimental chamber. Each subject was placed in the chamber and left in the dark for 4 min, just as during conditioning. The houselights were then turned on, and the subject's behavior toward the test object was videotaped for 2 min.

After the main experiment was completed, the conditioning procedure was replicated with the subjects in Group Unpaired to see whether they would also show evidence of context conditioning after just one paired trial. One day after the end of the main experiment, the birds in Group Unpaired received the same context-US pairing that had been administered to Group Paired. They were then tested for context conditioning the following day.

Observations. Individual male Japanese quail vary in their readiness to copulate with females, especially in a novel environment (Crawford, Akins, & Domjan, 1994). Videotape of the subjects' interactions with US females during the acquisition trial was used to assess sexual performance.

The copulatory behavior of male Japanese quail is highly stereotyped. The male first seizes the female by the feathers at the back of the neck (the "grab") and then climbs onto the female's back (the "mount"). Finally, opening its wings, the male bird rocks backward, bringing its cloacal opening down and in contact with the female's cloaca (the "cloacal contact movement").

The videotape of the subjects' sexual behavior during the US periods was scored for latency to grab and total number of cloacal contact movements (CCMs). The scores of only one observer were employed in statistical analyses, but a second observer also scored half of the trials. Pearson product-moment correlations of .99 and .92 for latency to grab and number of CCMs, respectively, revealed a high degree of interobserver reliability in these measures.

The videotape of the test trial was scored for approach to the test object and for the number of mounts of the object. Approach was defined in terms of how much of the 2-min test period the subject spent in the marked area in which the test object was located. A mount was scored when the subject placed one or both feet on the test object. An additional mount was scored if the subject placed one foot on the floor of the cage and then replaced that foot on the object. Again, Pearson product-moment correlations revealed a high degree of interobserver reliability (1.00 and .99 for approach and mounts, respectively).

Results

Because we were interested only in learning motivated by sexual reinforcement, the subjects that failed to copulate during the conditioning trial were excluded from the study. Four of the birds in Group Paired failed to copulate with the US female during the conditioning trial (in fact, they did not approach the female at all). Two of the subjects in Group Unpaired also failed to display any sexual behavior during their context-US pairing following the main experiment. The remaining subjects in Group Paired ($n = 5$) and Group Unpaired ($n = 7$) showed comparable unconditioned responses to female quail. The mean latencies to grab the US female for Group Paired and Group Unpaired (106.76 and 39.95 sec, respectively) were not significantly different [$F(1,10) = 1.60$, $p > .05$]. Nor did the mean numbers of CCMs differ between paired versus unpaired birds (6.00 and 7.29, respectively) ($F < 1.0$).

The results of the main experiment are depicted by the first two bars in the left panel of Figure 2. Following the single context-US pairing, the subjects in Group Paired spent an average of 60.70 sec in the test zone, whereas the animals in Group Unpaired spent only an average of 3.37 sec near the test object during the 2-min test period. An analysis of variance (ANOVA) showed that these means were significantly different [$F(1,10) = 7.41$, $p < .05$]. The paired birds also mounted the test object more frequently than did the unpaired birds ($M_s = 3.00$ and 0 mounts, respectively) [$F(1,10) = 4.86$, $p < .05$].

The failure of the subjects in Group Unpaired to respond vigorously during the test session was not due to a general lack of sexual motivation on the part of these birds. The results of the supplemental context-US pairing administered to Group Unpaired are shown by the bar in the right panel of Figure 2. After receiving a single context-US pairing, the subjects in Group Unpaired responded strongly to the test object, spending significantly more time near the object (39.17 sec) than they

Figure 2. Test results of Experiment 1. Left panel: Seconds of approach to the test object after one reinforced (Group Paired) or one unreinforced (Group Unpaired) context exposure. Right panel: Seconds spent near the test object by Group Unpaired after one reinforced context exposure.

had during the main experiment (3.37 sec) [$F(1,6) = 6.90$, $p < .05$]. (They also mounted the object significantly more often [1.71 vs. 0 mounts] [$F(1,6) = 7.08$, $p < .05$].) Furthermore, after their supplemental context-US pairing, the subjects in Group Unpaired approached the test object as much as the subjects in Group Paired had during the main experiment [$F(1,10) = 0.62$, $p > .05$]. (They also mounted the test object as often [$F(1,10) = 0.68$, $p > .05$].)

EXPERIMENT 2

In contextual fear conditioning, learning is directly related to the duration of context exposure prior to presentation of the US (Fanselow, 1990; Westbrook, Good, & Kiernan, 1994). Experiment 2 was conducted to see whether or not a similar relationship exists in sexual conditioning. Independent groups were exposed to the contextual CS for 0, 2, or 4 min before access to a female; a fourth group received CS and US exposures in an unpaired fashion.

Method

The methods were identical to those of Experiment 1 in all unspecified respects. On the conditioning day, the subjects were released into the dark experimental chamber and were left in darkness for 4 min. The lights were then turned on, and a female quail became accessible either immediately (Group 0, $n = 10$) or after 2 min (Group 2, $n = 5$) or 4 min (Group 4, $n = 11$) of context exposure.¹ The US female remained in the experimental chamber for 4 min. The subjects in Group Unpaired ($n = 11$) received the same context exposure as did the subjects in Group 4, but they received access to the US female in their home cages rather than in the experimental chamber (at least 1 h before or after the conditioning trial). Context conditioning was tested as in Experiment 1. After the main experiment was completed, Group Unpaired received a supplemental context-US pairing (4 min of context exposure followed by 4 min of access to a female) followed by a test trial the next day.

Figure 3. Test results of Experiment 2. Seconds spent near the test object after one context exposure reinforced immediately (Group 0), after 2 min (Group 2), after 4 min (Group 4), or not at all (Group Unpaired).

Results

As in Experiment 1, only data from subjects that copulated during their context-US pairing were used. Ten of the original 37 subjects failed to copulate with the US female in the experimental chamber (2 in Group 0, 1 in Group 2, 4 in Group 4, and 3 in Group Unpaired) and were dropped from the experiment. Comparing the sexual behavior scores of the remaining subjects in Groups 0 ($n = 8$), 2 ($n = 4$), and 4 ($n = 7$) during the main experiment with those of Group Unpaired ($n = 8$) during the supplemental procedure revealed no differences in latency to grab the US female ($M_s = 69.43, 22.45, 21.21$, and 44.22 sec, respectively) [$F(3,23) = 1.87, p > .05$] or in the number of CCMs emitted ($M_s = 6.0, 6.5, 5.57$, and 6.0 , respectively) ($F < 1.0$).

The results of the main experiment are summarized in Figure 3. Groups 0, 2, and 4 displayed strong approach to the test object, spending an average of 70.96, 86.06, and 85.44 sec, respectively, in the test zone during the 2-min test. In contrast, Group Unpaired spent only 14.99 sec in the test zone. A one-way ANOVA revealed that the groups differed significantly during the test session [$F(3,23) = 5.92, p < .01$]. Post hoc comparisons using the Newman-Keuls test ($p < .05$) showed that, whereas the approach scores for Groups 0, 2, and 4 did not differ from each other, the approach scores for Group Unpaired were significantly less than the scores of each of the paired groups.

As in Experiment 1, the failure of the subjects in Group Unpaired to approach the test object during the main experiment was not a function of low sexual motivation in this group. Following their single context-US pairing, Group Unpaired birds approached the test object much more than they had during the main experiment, spending an average of 86.20 sec in the test zone during the supple-

mental test trial [$F(1,14) = 15.40, p < .05$]. In addition, the approach scores of Group Unpaired in the supplemental test trial were not significantly different from the scores of Groups 0, 2, and 4 in the main experiment ($F < 1.0$).

DISCUSSION

Experiments 1 and 2 provide clear evidence for one-trial sexual conditioning. Paired subjects, which copulated with a female quail after exposure to the distinctive cues provided by the experimental context, interacted significantly more with the test object than did unpaired subjects, which copulated with a female in their home cage.

Although inclusion in the study was selective, based on the subjects' copulatory performance, three lines of evidence support the idea that our results did not reflect simple differences in sexual motivation. First, the paired and unpaired groups in Experiments 1 and 2 did not differ with respect to either their latency to grab US females or the total number of CCMs directed toward these females, implying that they did not differ in general sexual motivation or competence. Second, when subsequently given the benefit of one context-US pairing, the subjects in the unpaired groups increased test-object-directed sexual behavior to levels that were indistinguishable from those of the paired groups. Third, in Experiment 2, there was no relationship between the latency to copulate with US females exhibited by the subjects in Groups 0, 2, and 4 and the period of time they spent near the test object (Pearson $r = .005$). These findings indicate that the strength of the paired subjects' sexual response to the CS object was related to their conditioning history rather than to individual differences in sexual motivation (as measured by latency to copulate with the US female).

To our knowledge, the present results constitute the first clear demonstration of one-trial Pavlovian conditioning using an appetitive US. Furthermore, the effect is procedurally robust, occurring with intervals ranging from 0 sec to 4 min between the onset of the contextual CS and introduction of the US female.

At this writing, fear conditioning in rats using a shock US is the only thoroughly investigated example of one-trial contextual conditioning. In this paradigm, a critical parameter is how long subjects spend in the presence of the contextual CS before the onset of the US (Fanselow, 1986; Westbrook et al., 1994). If shock occurs simultaneously with exposure to the CS context, acquisition of the conditioned freezing response is disrupted (Blanchard, Fukunaga, & Blanchard, 1976; Fanselow, 1986). In Experiment 2 of the present study, there was no evidence of a sexual learning analog to this "immediate shock deficit." Subjects given the opportunity to copulate with a female quail immediately upon exposure to the CS context responded as vigorously during the test trial as did subjects that received the female quail 2 or 4 min after contextual CS onset.

The presence of the immediate-US deficit in fear conditioning but not sexual conditioning may be related to differences between sexual and aversive USs. Electric shock is an event that happens "to" a subject; it demands neither the animal's participation nor its cooperation, and the functional onset of the shock US is virtually instantaneous with the flick of the experimenter's switch. Sexual reinforcement, on the other hand, occurs only if the subject takes note of a female and interacts with her. It is difficult to specify exactly which elements of the presentation of a female quail were critical in the present experiments. Visual access to female quail (without physical contact) is sufficient under some circumstances to condition sexual approach to arbitrary cues (Crawford & Domjan, 1993). However, stimuli experienced during the act of copulation exert much more powerful US effects (Hollway & Domjan, 1993). For the subjects in Group 0 of Experiment 2, copulation-related stimuli were not instantaneous with the onset of the contextual CS. Instead, latencies to copulate with the US female in Group 0 ranged from 6.59 to 118.64 sec ($M = 69.43$ sec). Therefore, there was probably a significant "functional" delay from the onset of the contextual CS to sexual reinforcement, making this experiment inadequate to evaluate the immediate-US deficit in Japanese quail sexual learning.

In both Experiments 1 and 2, copulatory opportunity in the home cage rather than in the experimental apparatus did not induce responding to the test object. Therefore, some aspect of being placed in the experimental apparatus prior to sexual reinforcement produced the conditioning effect. However, we do not know what aspects of placement in the contextual CS were critical. In the course of the procedure, paired subjects experienced a number of cues that may have entered into association with the sexual US, including physical handling, darkness, an abrupt change to bright lighting, and contextual cues afforded by the experimental apparatus. Further experiments will be required to determine which of these factors mediated the one-trial sexual learning effect that we observed.

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NOTE

1. For Group 0, the US female was confined to a small wooden box in the experimental chamber during the 4 min of darkness that preceded the conditioning trial. Just before illumination of the chamber, the box was raised to the ceiling of the chamber by means of a system of strings and pulleys, releasing the female. This procedure ensured that interaction with the US female would coincide with exposure to the contextual stimuli.

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