

Naturalistic Conditioned Stimuli Facilitate Sexual Conditioning Because of their Similarity with the Unconditioned Stimulus

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Previous sexual conditioning studies with male Japanese quail have shown that adding taxidermic female head and neck cues to a conditioned stimulus (CS) facilitates conditioned sexual responding. The present experiment examined CS-US similarity as a possible mechanism for this facilitation. During sexual conditioning trials, artificially colored CSs with or without taxidermic female head cues were paired with copulatory access to artificially colored female quail (the unconditioned stimulus or US) to form similar and dissimilar CS-US combinations. As in previous experiments the presence of taxidermic female cues on the CS enhanced conditioned copulatory responding. Additionally, more conditioned copulatory responding developed when the CS and US colors were similar compared to when they were different. The results indicate that similarity between the CS and US strengthens the sexual conditioning of male quail, and similarity in color is more important than similarity in shape. The results also suggest that CS-US similarity may be one factor responsible for the facilitated conditioned responding that occurs when female cues are added to a CS object. The behavior systems approach is used to interpret the findings.

In traditional Pavlovian conditioning experiments, an arbitrary conditioned stimulus (CS) that is initially ineffective in eliciting a behavioral response is paired with a biologically relevant unconditioned stimulus (US) that elicits behavior unconditionally. Guided by the principle of equipotentiality, early investigators of learning phenomena assumed that theories of associative learning applied equally to any combination of CSs and USs or responses and reinforcers.

Experimental findings that challenged the principle of equipotentiality started appearing in the 1960's (for a review see Domjan, 1983). In particular, it was discovered that "relevant" CSs and USs often form selective associations – they become associated more quickly, and under less optimal conditions, than do unrelated CS-US combinations. Perhaps the most familiar example was Garcia and Koelling's (1966) discovery that rats show a predisposition to associate audio-visual cues with foot shock and taste cues with illness. Later experiments by LoLordo and his associates demonstrated that in pigeons, auditory cues are more effective than visual cues in avoidance conditioning, but visual cues are more effective than auditory cues in conditioning reinforced with food (e.g., Foree & LoLordo, 1973).

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Some have suggested that stimulus relevance relations reflect the ecology of the species (Garcia & Ervin, 1968; Gemberling & Domjan, 1982; Rozin & Kalat, 1971; Seligman, 1970). For an omnivore like the rat, for example, tastes are more likely than audiovisual cues to precede postingestional malaise in the natural environment. Thus, rats predisposed to associate taste cues with subsequent illness were selected for over those that were not so predisposed. That might be why, in present generations, tastes are more easily associated with illness. In the natural environment of pigeons, auditory cues may be more predictive of danger than visual cues, and that may be why auditory cues become more easily conditioned with shock (Foree & LoLordo, 1973).

Examples of stimulus relevance also have been demonstrated in the Pavlovian conditioning of sexual behavior. In this paradigm, a CS is paired with access to a potential sexual partner, which provides the US. After a number of CS-US pairings the CS acquires the ability to elicit sexual anticipatory responses in the absence of the sexual partner. Early investigations of sexual conditioning were conducted with conditioned stimuli such as a light or contextual cues that had no particular relevance to the sexual behavior system (e.g., Domjan, Lyons, North, & Bruell, 1986; Hollis, Cadieux, & Colbert, 1989; Zamble, Hadad, Mitchell, & Cutmore, 1985). More recently, however, interest has shifted to sexually relevant conditioned stimuli.

An example of learning involving a sexually relevant stimulus was provided by Carr, Loeb, and Dissinger (1965). They reported that sexual experience increased the preference of male rats for the odor of estrous females. In this study, the CS was a telereceptive cue (odor) that served to identify the US (an estrous female) at a distance. Learning to use cues that permit identification of a potential sexual partner at a distance no doubt facilitates sexual behavior and has functional utility. Recent studies of sexual conditioning in male Japanese quail have extended the approach pioneered by Carr et al. (1965). However, in these studies the telereceptive sexually relevant CS was a visual rather than an olfactory cue.

Why might visual cues be more important to male Japanese quail than other telereceptive stimuli? Quail are ground birds that live in habitats characterized by tall grasses and other ground vegetation (Schwartz & Schwartz, 1949). In such an environment, a potential telereceptive cue that serves to identify a female at a distance is the sight of a part of the female's body, such as her head. These partial female cues are reliably paired with the presence of the female and hence may serve as sexually relevant stimuli in the quail's natural habitat. Based on these considerations, a number of experiments have examined sexual conditioning in male Japanese quail with a CS object made of terrycloth that included a taxidermically prepared female head and partial neck feathers (see Figure 2 and reviews by Domjan, 1998; Domjan, Cusato, & Krause, 2004).

The visual cues of a female's head and neck feathers, when added to a CS, facilitate male conditioned sexual responding (Cusato & Domjan, 2000). Conditioned stimuli that are unrelated to the male's naturally occurring social behavior (a light, tone, or a plain terrycloth object) usually elicit only conditioned approach behavior (Domjan et al., 1986). In contrast, a CS object that includes cues of a female's head and neck comes to elicit both sexual approach and

copulatory or consummatory responses (Cusato & Domjan, 1998). Adding partial female cues to a CS object also affects a variety of conditioning phenomena. Köksal, Domjan, and Weisman (1994) showed that CSs with female head and neck cues are resistant to the Kamin blocking phenomenon (Kamin, 1969). Other studies have shown that headed CS objects are not susceptible to the response attenuating effects of CS preexposure or increasing the CS-US interval (Akins, 2000; Cusato & Domjan, 1998). Compared to CS objects that lack female head cues, the headed CSs also are more effective in second-order conditioning (Domjan et al., 2004).

Krause, Cusato, and Domjan (2003) demonstrated that CS objects with female head and neck cues are also especially resistant to extinction. During the conditioning phase of this experiment, male quail experienced only five pairings of the headed CS object and a live female (the US). Birds in the control condition experienced the same number of conditioning trials but with a CS object that lacked female cues. During the subsequent extinction phase, all of the birds received 90 nonreinforced presentations of their respective CS object. Males in the no-head CS condition ceased responding to their CS during the extinction phase. However, the headed CS continued to elicit sexual responses at the end of extinction at a rate that did not significantly differ from pre-extinction levels.

Examples like these of learning and behavioral phenomena that seem to contradict general-process conceptions of learning have been referred to as “misbehavior,” “biological constraints,” or “adaptive specializations in learning” (Breland & Breland, 1961; Hinde & Stevenson-Hinde, 1973; Rozin & Kalat, 1971; Seligman & Hager, 1972; Shettleworth, 1972). For instance, adaptive specialization explanations for learning phenomenon were adopted by Garcia and his associates. They theorized that the tendency to associate taste cues with illness probably evolved in omnivorous species as a means to facilitate the avoidance of poisonous food (Garcia & Garcia y Robertson, 1985).

An adaptive specialization account may also be formulated to explain the special efficacy of female head and neck cues in male sexual conditioning. According to this account, the cues of a female’s head and neck may facilitate conditioned responding because male quail are predisposed to associate the cues of a female with sexual opportunity. Such a predisposition may have evolved because female head and neck cues reliably precede and accurately predict copulatory opportunity during naturally occurring sexual interactions.

An alternative approach is to explain the special efficacy of female cues in sexual conditioning in terms of general mechanisms of learning. One such general process mechanism that could account for the facilitating properties of female head and neck cues is CS-US similarity. Males may respond more vigorously toward a CS that includes limited female cues because of the similarity of such a CS to the live female that provides copulatory reinforcement. CS-US similarity has been shown to facilitate the establishment of associations in several different conditioning paradigms (Rescorla & Furrow, 1977; Testa, 1974).

The present experiment was designed to examine the effects of CS-US similarity in sexual conditioning. CS-US similarity was investigated previously in an experiment using taxidermically prepared female cues that were obtained from different strains of Japanese quail (Cusato & Domjan, 2000, Experiment 1). Some

of the taxidermic heads were prepared from normal brown females taken from the same population as the females that provided copulatory opportunity during the conditioning trials. Other taxidermic heads were prepared from a strain of blonde females, making the female cues on the CS object much lighter than the brown females that served as unconditioned stimuli. A third group of subjects received a CS object made entirely of terry cloth.

Cusato and Domjan (2000) found that the brown-headed CS elicited significantly more conditioned responding than the blonde-headed CS. This is suggestive of the importance of CS-US similarity in sexual conditioning, but there was a potential confounding variable in the experiment. The brown cues were more familiar to the males than the blonde cues since the subject males were group housed with brown conspecifics for the first month after hatching, and no effort was made to control their visual exposure to brown conspecifics in adulthood. Thus, the fact that the brown headed CS elicited more conditioned responding than the blonde headed CS may have had less to do with its similarity to the female US, and more to do with its familiarity.

To better assess the role of CS-US similarity in the facilitated responding observed in previous experiments (Akins, 2000; Cusato & Domjan, 1998, 2000; Domjan et al., 2004; Köksal et al., 1994; Krause et al., 2003), the present experiment manipulated CS-US similarity so that each CS-US combination was equally unfamiliar to the male subjects. The taxidermic female head on the CS and the live females that provided copulatory opportunity were both artificially colored to create similar and dissimilar combinations of CSs and USs. This artificial coloring ensured that each CS-US combination was equally novel to the male subjects.

Method

Subjects

The experiment was conducted in two counterbalanced replications. Thirty-two experimentally naïve adult male Japanese quail (*Coturnix japonica*) served as subjects, and 16 naïve adult female quail were used to provide the males with copulatory opportunity. All of the male birds had brown plumage. Brown plumage females were used as well but their head and neck feathers were artificially colored using non-toxic marking pens prior to the start of experimentation. The coloration included the entire head and neck of the female, and extended 5-6 cm down the chest, as measured from the base of the female's head. All of the birds were selected from the breeding colony maintained at the University of Texas at Austin. At one month of age, they were removed from brooders and housed in metal quail cages (G.Q.F. Manufacturing Co., Savannah, GA). While in the metal cages, male birds were housed individually and females were housed in groups. All birds were maintained on a 16:8 light-dark cycle, which provided sufficient photostimulation to maintain them in reproductive condition.

Males were selected for participation in the experiment on the basis of a pretest for copulatory behavior. For the pretest, an artificially colored female quail was placed in the male's home cage for 5 min, which is usually sufficient for sexually active males to initiate copulatory behavior (Schein, Diamond, & Carter, 1972). Only males that made cloacal contact with the female during the 5 min pretest were selected for the experiment. To control for possible color effects, half of the males were pretested with a female whose head, neck, and chest plumage was colored red. The remaining males were pretested with a female that was colored blue. All of the colored females were then used as copulation partners for the males during conditioning. The color of the female used during the pretest was counterbalanced with the color of the female the male was going to have access to during the conditioning trials. Five of the 32 males that passed the pretest failed to copulate in the experimental chambers during conditioning, probably because of the relative novelty of the

experimental chambers and the unusual appearance of the females. The data from these subjects were omitted from the results since they did not experience the copulatory US.

Apparatus

Eight experimental chambers like the one shown in Figure 1 were used in the experiment. Each was 90 cm (wide) x 68.5 cm (high) x 120 cm (deep). The front access door and floor of each chamber were made of wire mesh; the ceiling and remaining walls were made of sealed plywood. A smaller compartment (29.5 cm x 35.5 cm x 60.5 cm) was attached adjacent to the chamber, centered at floor level on a side wall. The side compartment was used to hold a live female bird. A 14 cm x 16.5 cm vertically sliding door (the US door) separated the side compartment from the main experimental chamber. A 40-watt light bulb near the ceiling provided illumination, and food and water were available to the birds all times.

The CS was a terry cloth object filled with soft polyester fiber. It consisted of a 10.8 cm vertical section (3.5 cm in diameter) positioned in front of a 6.5 cm (wide) x 5 cm (high) x 10.5 cm (long) horizontal mounting pad. Two different types of CS objects were used. One lacked female head and neck cues and the other had a taxidermically prepared female head with approximately 3 cm of neck feathers mounted on top of the vertical section. The head and no head versions of the CS object are shown in Figure 2. To manipulate similarity with the colored females, the headed CS objects were made of red terry cloth with a red taxidermic female head. The no-head CS objects were made of blue terry cloth.

While not in use, the CS object was covered by a 19 cm (long) x 19 cm (wide) x 15.8 cm (high) hood made of light wood. When the hood was down, it completely obscured the male's view of the CS. When the hood was raised, the male had full access to the CS object. The CS was secured to the floor approximately 17.5 cm from the door to the female compartment, in the middle of a marked area 45.5 cm x 40 cm.

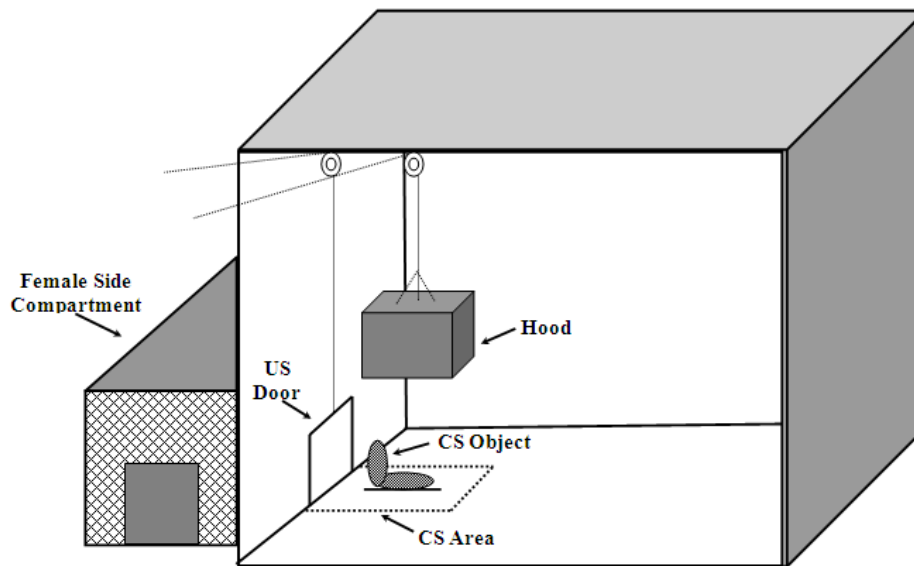


Figure 1. Eight identical testing chambers like the one shown above were used in the present experiment. The hood and US door could be raised and lowered from outside the chamber, and the CS area surrounding the CS object was used to measure conditioned approach responding. The US females were housed in the side compartment and the male subjects were housed in the main testing chamber during alternate 24 hr periods. The hood remained lowered over the CS object for all but the 30 sec CS and 5-min US periods. The no-head version of CS object is shown here. The testing chambers that housed the males in the head CS conditions were identical in all other respects.

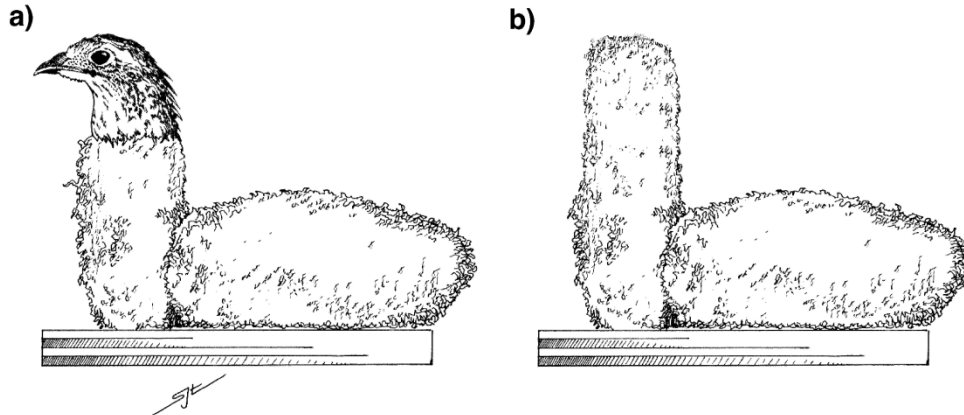


Figure 2. The head (a) and no head (b) CS objects used during the conditioning trials. Both objects were made of terry cloth filled with soft polyester fiber and consisted of a vertical section positioned in front of a horizontal mounting pad. The CS object on the right was made entirely of blue terry cloth. The CS on the left was made of red terry cloth and a red marking pen was used to color the taxidermically prepared female head and partial neck mounted on top of the vertical section.

Procedure

Prior to the start of each replication, the male subjects were randomly assigned to one of two squads. Each squad was housed in the experimental chambers during alternate 24-hr periods. While the subjects of one squad were in the experimental chambers, the other squad was housed in the colony cages. The birds that spent the previous night in the experimental chambers received their daily treatment trial the next morning. The birds were then exchanged so that the second squad could receive its trial that afternoon and remain in the chambers overnight. The alternate housing procedure began eight days prior to the start of the conditioning trials so that the subjects would habituate to the testing environment and to being handled. During the last three days of habituation, the plywood hood in each chamber was raised and lowered two or three times (the CS objects were not yet in place). The hood remained raised for 2-min, and 10-min elapsed between each trial. The females were housed in the side cages adjacent to the experimental chambers during habituation and throughout the entire experiment.

Subjects differed in terms of the type of CS they received and the coloration of the female that provided copulatory reinforcement (the US) during conditioning trials. Independent groups were exposed to a red terry cloth CS with a red female head or a blue terry cloth CS object lacking female head cues. To create similar and dissimilar CS-US combinations within each of the two CS type conditions, some of the males received their CS paired with a female quail that had been colored red while others received their CS paired with a female that had been colored blue. Thus, four groups were included in the experimental design: red head CS paired with a red US (Group Head-Same, $N = 7$), red head CS paired with a blue US (Group Head-Different, $N = 7$), blue no head CS paired with a blue US (Group No Head-Same, $N = 5$), and a blue no head CS paired with a red US (Group No Head-Different, $N = 7$). Unpaired control groups were not included in the present study to reduce the complexity of the experimental design. However, previous experiments investigating the role of female head cues in the sexual conditioning of male quail have included such unpaired controls. In all of these experiments unpaired presentations of the headed CS object elicited negligible responding. For example, Cusato and Domjan (1998, Experiment 1) reported very low levels of CS-elicited grab, mount, and cloacal contact responding (i.e., mean frequencies less than 1) in subjects that received unpaired presentations of a headed CS and the female US across 15 days of conditioning.

Conditioning trials began on the day after habituation and 1 trial a day was conducted for 7 days. A trial began when the hood was raised to reveal the CS object to the male. Thirty seconds later, the US door was opened releasing the live female into the main experimental chamber where copulation invariably occurred. After 5 min, the hood was lowered to cover the CS object, and the

female was removed from the main experimental chamber and placed back into the side cage. To control for differences between individual females, the male-female assignments were rotated daily within each of the two female color groups so that no male had access to the same female on consecutive conditioning days.

Response Measures

The conditioning trials were video taped and scored for the amount of time the males spent near the CS (approach responding) and the number of grab, mount, and cloacal contact responses they made to the CS object during the thirty-second CS presentations (i.e., before the live female was released). A bird was considered to have approached the CS if it entered the 45.5 cm x 40 cm marked area in which the CS was located. A grab response was recorded if the male held a portion of the CS (usually some part of the vertical section) in its beak. As in previous experiments of this nature, a careful distinction was made between peck and grab responses. During the peck response, the male contacts but does not hold a portion of the CS object in its beak. A mount response was recorded if the male got on top of the CS object with both feet and a cloacal contact response was recorded if the bird arched its back bringing its cloaca in contact with the back of the CS object. Inter-observer reliability for these response measures is traditionally very high. For example, Pearson product-moment correlations measuring inter-observer reliability in the Krause et al. (2003) experiment were 0.99, 0.99, 0.95, and 0.97 for the approach, grab, mount, and cloacal contact responses, respectively. Inter-observer reliability was not assessed in the present study, but an observer that coded behaviors in the Krause et al. (2003) experiment also coded the same response measures in the present experiment. The experimenters verified that copulation between the male and the live US-female occurred during the 5 minute US periods each day of conditioning, but these responses were not recorded for analysis.

Results

Results of the conditioning days are summarized in Figure 3. The head and no head CS objects elicited very little responding on the first day of conditioning but responding emerged as a function of the daily trials. All of the groups developed similar levels of approach responding, but the conditioned grab, mount, and cloacal contact responses were differentially enhanced as a function of CS-US similarity and the presence of female species typical cues. The highest level of conditioned copulatory responding occurred among subjects that received a head CS object whose color was similar to that of the US female and the lowest levels of these responses were evident with the no head CS whose color was different from that of the US female. Conditioned grab responding was enhanced by CS-US similarity and conditioned cloacal contact responding was enhanced by the female cues and CS-US similarity. Conditioned mount responding was enhanced only by the presence of female cues on the CS.

The different conditioned responses were analyzed with separate 2 (same vs. different CS-US combinations) x 2 (head vs. no head CS objects) x 7 (conditioning days) mixed analyses of variance (ANOVAs). Analysis of the approach responding revealed a significant main effect for days, $F(6, 132) = 67.81$, $p < 0.05$, but no significant main effects or interactions involving CS-US similarity or CS type.

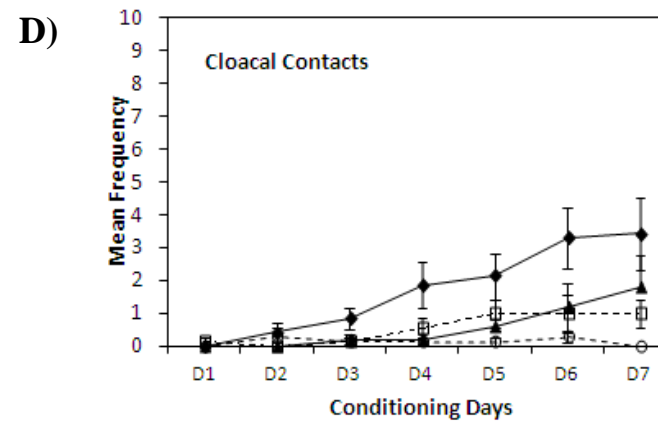
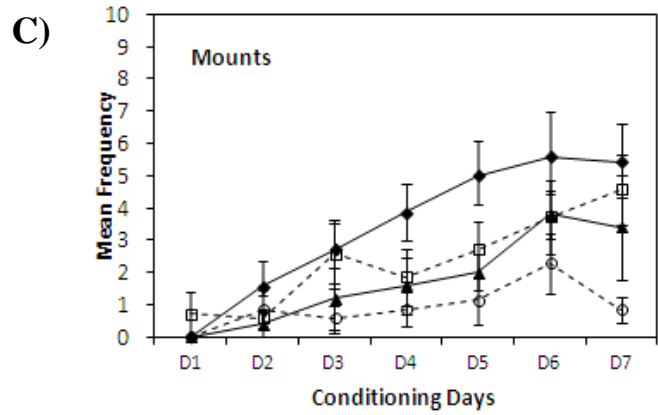
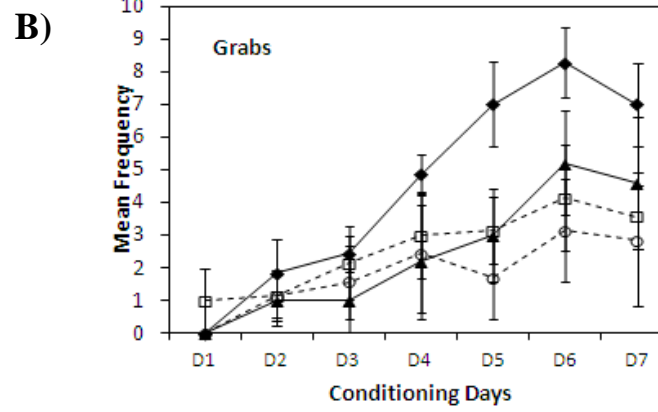
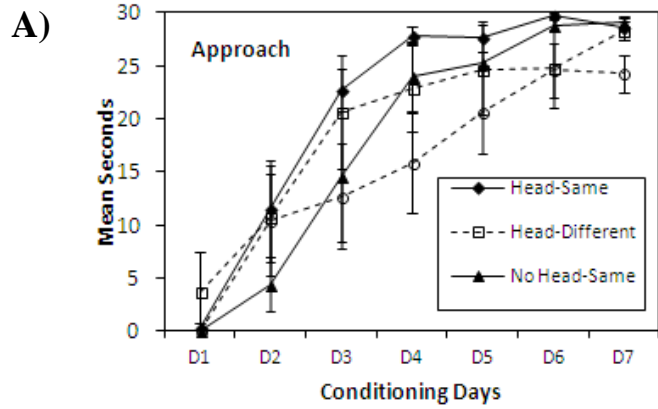


Figure 3. Mean approach (A), grab (B), mount (C), and cloacal contact (D) responding to the CS objects with and without female head cues during the 7 days of conditioning (1 trial per day). The CS and US were either similar or different in color.

Analysis of the grab response revealed a significant days effect, $F(6, 132) = 19.54, p < 0.05$, as well as a significant days x CS-US similarity interaction, $F(6, 132) = 3.29, p < 0.05$, the latter due to very robust responding in the Head-Same condition. But the main effect for CS type was not significant, $F(1, 22) = 1.13, p > .05$, nor was the CS type x days interaction, $F(6, 132) = 1.04, p > 0.05$. These results suggest that conditioned grab responding was enhanced when the headed CS and the US were the same color.

Analysis of the mount response also revealed a main effect for days ($F(6, 132) = 18.95, p < 0.05$). The main effect for CS type also was significant ($F(1, 22) = 5.92, p < 0.05$) indicating that the head CS elicited more responding than the no head CS, but the days x CS type interaction just missed significance, $F(6, 132) = 2.16, p = 0.05$. The main effect of CS-US similarity ($F(1, 22) = 2.17, p > 0.05$) and the CS-US similarity x days interaction ($F(6, 132) = 1.80, p > 0.05$) for the mount response also were not significant.

Analysis of the cloacal contact response revealed a main effect for CS type and CS-US similarity, $F(1, 22) = 5.44$ and 5.73 , respectively, $ps < 0.05$. The main effect for days as well as the days x CS type and days x CS-US similarity interactions also were significant, $F(6, 132) = 11.77, 2.85$, and 5.16 , respectively, $ps < 0.05$. These results indicate more rapid acquisition of the cloacal contact response when the color of the CS matched that of the US female. Cloacal contact responding was also enhanced when the CS included the species typical cues of a female quail. However, the days x CS type x CS-US similarity interaction was not significant ($F < 1$).

Discussion

Contrary to early assumptions of equipotentiality, the rules of learning do not apply equally to all conditioned and unconditioned stimuli. Nearly forty-five years after Garcia and Koelling's (1966) landmark discovery of selective associations, the existence of biological predispositions and their effect on learning are well-established. However, few experiments have examined the specific features of CSs and USs that lead to selective associations. Once identified, selective associations are rarely investigated further to determine either their underlying mechanisms or the extent to which their causal mechanisms fall within or outside the parameters of general-process learning theory.

In a variety of situations, naturalistic conditioned stimuli have been found to promote more rapid and robust learning than arbitrary cues (for a review see Domjan, 2005). This relationship has been extensively documented in sexual conditioning. Studies have shown that female species typical cues are unusually effective in the sexual conditioning of male Japanese quail. Compared to arbitrary CSs, CS objects with female head and neck cues elicit the full range of sexual approach and copulatory responses (Domjan, 1998; Domjan et al., 2004). Other experiments have shown that, unlike arbitrary CSs, headed CS objects are resistant to the Kamin blocking phenomenon (Kamin, 1969; Köksal et al., 1994), extinction (Krause et al., 2003), and the response attenuating effects of CS preexposure and increases in the CS-US interval (Akins, 2000; Cusato & Domjan, 1998).

Cusato and Domjan (2000) tested whether the special efficacy of female cues was the result of a selective association between the species typical cues and

sexual reinforcement by examining appetitive conditioning with food as the US. Somewhat surprisingly, the female head and neck cues were found to facilitate conditioning whether the US was food or sexual reinforcement. These results suggested that the special efficacy of female cues does not reflect an adaptive specialization unique to the sexual behavior system of quail and encouraged the search for a general-process explanation.

The present experiment investigated CS-US similarity as a possible general-process mechanism that might account for the special efficacy of species typical cues in sexual conditioning. Males may respond more vigorously toward a CS object with limited female features because, compared to an arbitrary CS, the headed CS object more closely resembles the live female that provides sexual reinforcement. Unlike an earlier related study (Cusato & Domjan, 2000, Experiment 1), the present experiment manipulated similarity between the CS and the US artificially so that each CS-US combination was equally unfamiliar to the subjects. Both the taxidermic female cues and the live females that provided the US were artificially colored to create similar and dissimilar CS-US combinations.

As in previous studies of this kind (Cusato & Domjan, 1998, 2000; Domjan et al., 2004; Krause et al., 2003) the presence of female cues on the CS object enhanced conditioning. This was seen in the present experiment in the acquisition of cloacal contact responding. Moreover, subjects that were conditioned with the same CS-US color combination developed more conditioned grab and cloacal contact responding than the subjects conditioned with different CS and US colors. However, the lack of unpaired control conditions in the present experiment dictates a degree of caution when drawing conclusions based solely on the present findings. But unpaired controls have been included in all previous studies of this nature (Domjan et al., 2004), and in all of these studies responding in the unpaired conditions has been relative low and significantly different compared to the paired conditions.

Unlike the copulatory responses, approach responding was not enhanced by the presence of female cues on the CS object or CS-US similarity. Such a difference between conditioned approach and copulatory responding has been observed in previous experiments (e.g., Cusato & Domjan, 1998) and is consistent with ethological views that consider appetitive behaviors to be less stimulus bound than consummatory behaviors (Baerends, 1988; Eibl-Eibesfeldt, 1970; Tinbergen, 1951). Why the mount response remained unaffected by CS-US similarity in the present study is less clear. This was surprising since similarity between the CS and US enhanced the conditioning of grab and cloacal contact responding, and in past studies the mount response has been significantly enhanced with the addition of female head cues to the CS object (e.g., Cusato & Domjan, 1998, 2000; Krause et al., 2000). Future investigation is needed to clarify why CS-US similarity facilitates some consummatory responses but not others.

Taken together, the findings from Cusato and Domjan (2000, Experiment 1) and the present experiment strongly suggest that the facilitation of responding to a naturalistic CS documented in previous sexual conditioning experiments (Akins, 2000; Cusato & Domjan, 1998, 2000; Köksal et al., 1994; Krause et al., 2003) occurs at least in part because the addition of female cues to the CS object makes the CS more similar to the live female that provides the US. Similarity between

the CS and the US has been shown to facilitate the formation of associations in more traditional conditioning paradigms (Rescorla & Furrow, 1977; Testa, 1974). Testa (1974) also proposed CS-US similarity as a possible contributing mechanism to the learning that occurs over long CS-US intervals. In light of the present findings, CS-US similarity probably contributed to the acquisition of strong approach responding that Akins (2000) observed with a 20-min CS-US interval. Similarity between the head CS and the live US female also may explain the nontraditional results obtained in the previous extinction (Krause et al., 2003), blocking (Köksal et al., 1994), and second-order conditioning (Domjan et al., 2004) experiments. However, it is unlikely that similarity between the CS and the US is the only underlying cause of the facilitation effect since including female head and neck cues in a CS object also facilitates CS-directed responding when food is used as the US (Cusato & Domjan, 2000, Experiment 2).

The design of the present experiment served to identify color as the critical feature of a head CS that makes it similar to the US female. The CS head cues resembled the live female's head cues in color, shape and size, but the subjects nevertheless showed higher levels of responding only if the CS and US colors matched. The findings from Cusato and Domjan (2000, Experiment 1) regarding the grab response also support the view that color is important. In that experiment, grab responses were facilitated only when a brown headed CS object was paired with a normal brown female. The use of a blonde headed CS object paired with a brown female did not facilitate responding even though the blonde headed CS had the same speckled pattern, size, and shape as the live brown female.

The importance of color similarity between the CS and US in the present experiment is consistent with previous findings showing that Japanese quail have a sophisticated visual system capable of discriminating a wide variety of colors, and the perception of color in this species is dominant over the perception of either shape or form (Fidura & Gray, 1966). Male quail also exhibit the effects of sexual imprinting, showing robust preferences in adulthood for the same color females as those to which they were exposed as chicks (Gallagher, 1976, 1977). But why might color similarity have facilitated the development of conditioned sexual responding in the present experiment when relatively novel colors were used? By definition, increased similarity between two events means that the events have more stimulus elements in common. CS-US similarity may have facilitated conditioning because the shared stimulus elements were present in the live female that served as the US, and this increased temporal contiguity made it easier for those cues to become associated with sexual reinforcement. Such an account also has been suggested to explain how CS-US similarity facilitates other forms of Pavlovian conditioning (Testa, 1974).

Alternatively, an explanation of the present results based on innate color preferences cannot be entirely dismissed since the head CS and no head CS objects were made of different colored terry cloth (red and blue, respectively). In fact, individual quail chicks have been shown to exhibit preferences for one equally unfamiliar color over another (Duecker, 1977; Kovach, 1983, 1990). However, this explanation seems unlikely since responses to the different CS objects on the first day of conditioning were relatively low and not significantly different. Moreover, such low levels of CS-elicited responding on day one followed by

incremental increases due to CS-US pairings is consistent with the results of previous sexual conditioning experiments investigating the facilitating effects of female quail head and neck cues (Domjan et al., 2004). This is especially important given the omission of unpaired control groups in the present design.

Given the growing evidence supporting CS-US similarity as a dominant explanatory mechanism for the special efficacy of female head and neck cues in male sexual conditioning, it may be tempting to dismiss stimulus relevance explanations as relatively less viable. However, the present findings caution against an absolute distinction between general-process and adaptive specialization explanations for such unconventional learning effects. Instead, it may be more accurate to consider to what extent species specific ecological factors influence the manifestation of conventional conditioning mechanisms (Domjan et al., 2004), and in turn, determine what theoretical framework is best able to integrate elements of ethology and animal learning. One such integrating framework is provided by the behavior systems approach (Timberlake, 1994).

Behavior systems have been developed for a variety of behaviors and species including the defensive and feeding behavior of rats (Fanselow, 1994; Timberlake & Lucas, 1989) and the sexual behavior of male Japanese quail (Domjan, 1994). From this perspective, adaptive processes such as natural and sexual selection determine which specific cues in the animal's environment are most important for survival and reproduction. These naturalistic cues then gain privileged access to the behavior system, and in turn, modulate the general process mechanisms that underlie the learning that occurs when they serve as conditioned stimuli. With respect to male quail and sexual behavior, because female head and neck cues reliably preceded and thus, accurately predicted sexual opportunity in the natural ecology and evolutionary history of male quail, they occupy a special place in the male quail sexual behavior system, and thus, are especially effective as CSs in male quail sexual conditioning. In light of the present findings, we may conclude that this special efficacy is achieved at least in part through the general process learning mechanism of CS-US similarity.

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