Animal Learning & Behavior
1998, 26 (4), 427-432

Observational conditioning of sexual behavior in the domesticated quail

FALIH KÖKSAL
Boğaziçi University, Istanbul, Turkey

and

MICHAEL DOMJAN
University of Texas, Austin, Texas

Three experiments were conducted with male domesticated quail to explore whether sexual responses to a three-dimensional conditioned stimulus (CS) object could be acquired through observation. Observational learning was measured by a savings test in which the observers received exposures to the CS paired with the opportunity to copulate with a female bird (the unconditioned stimulus, or US). In all of the experiments, observing a demonstrator copulate with the CS object and then receive access to the US facilitated the subsequent conditioning of the observers. This facilitation effect was not due to observation of just another male bird (Experiment 1) or observation of a male bird that copulated with the CS object (Experiment 2). Rather, the critical factor was observation of pairings of the CS object with the US. Facilitated sexual conditioning was evident in groups of birds that observed pairings of the CS and US, whether or not they witnessed a demonstrator copulating with the CS object (Experiment 3). The results demonstrate that sexual behavior can be acquired through observational conditioning.

Whether animals can learn by observing another member of their species perform a response has been of interest to psychologists for a long time (Galef, 1988). Studies of imitation and other forms of observational learning identify the conditions under which information is transmitted vicariously and have been used to characterize the cognitive capacities of animals (Zentall, Sutton, & Sherburne, 1996). In addition, some instances of observational learning are of clinical relevance (Mineka & Cook, 1993).

Social learning effects have been studied in a variety of species, including fish, rodents, birds, monkeys, and human infants (Heyes & Galef, 1996). Tasks investigated have included pushing a rod to the left or the right, the conditioning of fear to specific objects, and pecking a ping-pong ball (Heyes, Jaldow, & Dawson, 1994; Hogan, 1988; Mineka & Cook, 1993).

In the typical observational learning experiment, a demonstrator is first trained to perform a target response to obtain a biologically significant event or reinforcer (e.g., food). The demonstrator is then allowed to perform the target response while an observer is set up to watch. Finally, the observer is provided with an opportunity to perform the same response, and either the frequency of the target response or its rate of acquisition is measured. Control subjects receive exposure to an untrained "demonstrator" or a "demonstrator" that gets noncontingent reinforcement. A common result is that exposure to the demonstrator performing the target response facilitates the acquisition of that response by the observer.

A fundamental methodological problem in studies of observational learning is that facilitated acquisition of the target response can occur for a variety of reasons. In fact, many studies lack the control procedures needed to attribute facilitated acquisition in the observer subjects to social learning rather than to socially induced motivational or perceptual processes. The responses of the demonstrator may direct the observer's attention to the target manipulandum or the conditioned stimulus and thereby facilitate the observer's subsequent performance (stimulus enhancement or local enhancement, Zentall, 1996). Alternatively, the observer's behavior may reflect learning about the stimulus–reinforcer contingency that the demonstrator receives rather than learning about the demonstrator's behavior (i.e., observational autoshaping, Hogan, 1988; or observational conditioning, Whiten & Ham, 1992).

True imitation refers to learning to do something as a result of seeing another animal perform the same action (Thorndike, 1898). To be sure that other factors are not involved, the target behavior should not already exist in the repertoire of the observer (Thorpe, 1963). In addition, motivational effects on the observer (social facilitation), effects of witnessing a stimulus–reinforcer contingency (observational conditioning), and effects of the demonstrator drawing the observer's attention to the response manipulandum (stimulus enhancement) should be controlled.

Motivational factors may be ruled out by exposing control groups to an untrained conspecific, a conspecific

The research was supported by NSF Grant INT-9600455 and by NIMH Grant MH39940. Correspondence may be addressed to either author: F. Köksal, Department of Psychology, Boğaziçi University, 80815 Bebek, Istanbul, Turkey (e-mail: koksalfa@hamlin.cc.boun.edu.tr); M. Domjan, Department of Psychology, University of Texas, Austin, TX 78712 (e-mail: domjan@psy.utexas.edu).

 Copyright 1998 Psychonomic Society, Inc.

that receives the reinforcer in the absence of the target response, or a conspecific that receives noncontingent reinforcement. Exposure of observers to paired presentations of a conditioned stimulus (CS) with a reinforcer or unconditioned stimulus (US) in the absence of a demonstrator controls for observational conditioning effects. The development of appropriate controls for stimulus enhancement is more difficult. So far the best procedure has been the *two-action method*, in which each observer is exposed to a demonstrator who manipulates an object in one of two different ways. True imitation rather than stimulus enhancement is said to occur if the observer comes to perform the particular action that it saw its demonstrator perform (e.g., Heyes, 1996).

Previous studies of observational learning have focused on target behaviors related to feeding, fear, and vocalization. The purpose of the present study was to explore possible social learning effects in the sexual behavior system. Domesticated quail (*Coturnix japonica*) served as subjects because procedures for the study of sexual conditioning have been worked out in previous research with this species (e.g., Domjan, 1994). We focused on the acquisition of sexual responses to a terry cloth object that male quail rarely copulate with in the absence of specific conditioning.

Observers were exposed to a demonstrator quail that received pairings of the terry cloth object (the CS) with the release of a live female (the US). In the following phase, the observers were exposed to the same sequence of events as were their demonstrators, and their conditioned sexual responses (i.e., approach, grab, mount, and cloacal contact responses to the CS) were measured. Experiment 1 was conducted to see whether an observational learning effect occurs in the sexual behavior of male Japanese quail. Experiments 2 and 3 were conducted to identify the factors responsible for the observational learning that was identified in Experiment 1.

EXPERIMENT 1

Experiment 1 was conducted with two groups of subjects. During the observation phase, observer males in one group were exposed to a pretrained demonstrator showing sexual responses to a terry cloth object (the CS) and then copulating with a female quail (the US). After 12 observation trials, the demonstrator was removed and the observers received direct pairings of the CS object with a live female. The acquisition of sexual responses in these observers was compared with acquisition in a control group that was exposed to a "demonstrator" during the observation phase without the CS or US.

Method

Subjects. Twelve experimentally naive adult male Japanese quail (*Coturnix japonica*) started as subjects in the experiment. One was lost because of injury, however, and 2 others were dropped from the experiment because of procedural errors. Nine adult females served as copulation partners. The animals were hatched and raised at the University of Texas at Austin. At 30 days of age, the males were removed from mixed-sex brooders and housed individually in metal cages. The females were housed in group cages until they were selected for the experiment. The experimental and colony rooms were set on a 16:8-h light:dark schedule to maintain the birds in reproductive condition. Food and water were available at all times. Male subjects were selected to participate in the experiment on the basis of a pretest for copulatory behavior. The test consisted of placing a sexually receptive female in the male's home cage for 5 min. Only males that copulated during the pretest were included in the experiment.

Two sets of demonstrator males were also used. The demonstrators for the experimental group ($n = 4$) were previously conditioned to copulate with the terry cloth CS. For this conditioning, the terry cloth CS was paired with the opportunity to copulate with a female quail. During the first few trials, the CS object included a taxidermically prepared head and some of the plumage of a female bird. The female plumage was then replaced with terry cloth (see Domjan, Huber-McDonald, & Holloway, 1992). Only birds that consistently copulated with the terry cloth CS were selected to serve as demonstrators for the experimental group. The demonstrators for the control group ($n = 5$) were of similar age and had a similar history of handling.

Apparatus. Twelve experimental chambers, 67 cm high, 122 cm deep, and 122 cm wide, were used. The top, the back, and the right and left sidewalls were made of plywood and painted white. The floor and the front wall were made of wire mesh. A video camera, located about 1 m from the front wall of the chamber, was used to record the behavior of the subjects. A vertically sliding door ($20\ cm^2$) centered along a sidewall provided access to a small compartment in which a female bird was housed when necessary.

Each chamber was divided in half diagonally with a barrier made of two sheets of wire mesh separated by about 2.5 cm. The demonstrator and observer were housed on opposite sides of the divider before the experiment started and during the observation phase. The divider was removed during the subsequent conditioning phase.

The CS object, made of terry cloth, consisted of two parts: a 10.8-cm-tall cylindrical section (3.5 cm in diameter) positioned in front of a horizontal mounting pad (about 6.5 cm wide $\times$ 5 cm high $\times$ 10.5 cm long). While not in use, the CS object was covered by a hood that was made of wood. To provide access to the CS object, the hood was raised to the ceiling of the chamber, using a string passed through an eye hook attached to the ceiling. The CS object was located in the middle of a 45.5 $\times$ 40 cm area marked in front of the door to the female side cage.

Procedure. Each male subject was housed in the observer half of the experimental chamber for the entire duration of the experiment starting 1 week before the observation phase, and its demonstrator partner was housed at all times (except as noted) in the demonstrator compartment. Each observer always received exposure to the same demonstrator, to stabilize observer–demonstrator interactions.

During the observation phase, subjects received one trial per day for 12 days. For the experimental group ($n = 4$), at the start of each trial the hood was raised to expose the terry cloth CS. Thirty seconds later, a female was released into the demonstrator's compartment for 5 min. The demonstrator invariably approached and showed grab, mount, and cloacal contact responses to the terry cloth CS and also copulated with the live female that was released afterward. At the end of the trial, the female was removed and the CS object was covered until the next day's trial. For the control group ($n = 5$), each trial during the observation phase consisted of raising the CS hood for 30 sec. However, the terry cloth CS object was absent and the female was not released. Thus, the control subjects got to see the hood move up and down with another male present in the demonstrator compartment, but they did not get to see the CS object or the demonstrator interacting with the CS.

After the observation phase, the wire mesh barrier that divided each experimental chamber was removed, along with the demonstrator birds. Each subject then received eight CS–US pairings,

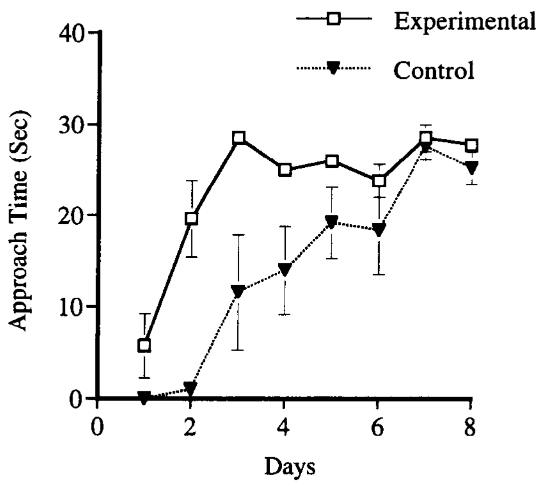

Figure 1. Mean (±*SE*) time spent near the CS object by subjects in Experiment 1. The experimental group previously observed demonstrator males copulate with the CS and then copulate with a female bird (the unconditioned stimulus). The control group previously observed another male bird without the CS or the US.

conducted one per day. For each trial, the hood was raised, revealing the CS object for both the experimental and the control subjects. The female was released from the side cage 30 sec later. The male and female were then permitted to interact for 5 min, during which copulation invariably occurred. The CS was then covered, and the female was removed.

Response Measures

Each conditioning trial was recorded on videotape. Four responses to the terry cloth CS were measured later from the videotapes. A subject was considered to be near the CS if it was in the 45.5 × 40 cm area marked on the floor around the CS. The time accumulated in this area was measured for 30 sec before (pre-CS) and during presentation of the CS on each trial. The pre-CS scores were subtracted from the CS scores to obtain a measure of approach behavior elicited by the CS. We also measured how often each subject grabbed the terry cloth CS, mounted by placing both feet on the CS object, and made a cloacal contact movement by arching its back and thrusting it cloaca against the terry cloth mounting pad. The videotapes were scored by several people uninformed about the group assignment of the subjects.

Results and Discussion

When the demonstrators and the observers were first placed in the experimental chambers, they pecked each other through the wire mesh partition. However, these responses habituated in 2–3 days. Release of the female into the demonstrator compartment during the observation phase elicited approach to the wire mesh partition on the part of the observers. After several trials, the observers in the experimental group also started approaching the partition when the CS was presented.

Approach to the CS during each of the eight trials of the conditioning phase is shown in Figure 1. Subjects in the experimental group spent nearly all available time near the CS by Trial 3. In contrast, subject in the control group did not reach this high level of performance until Trial 7. A repeated measures analysis of variance (ANOVA) showed significant effects of group [$F(1,7) = 10.33, p < .05$] and trials [$F(1,7) = 17.44, p < .001$] and a group × trials interaction [$F(7,49) = 2.59, p < .05$].

The frequencies of grab, mount, and cloacal contact responses directed toward the CS object were analyzed in the same fashion. The experimental subjects showed significantly more grabs [$F(1,7) = 5.75, p < .05$] and more mounts [$F(1,7) = 36.77, p < .001$] than did the control group. However, no significant group differences were observed for the cloacal contact response.

The results of Experiment 1 demonstrate that an observational experience can enhance the subsequent sexual conditioning of male Japanese quail. This effect was not due to mere exposure to another male bird. However, a number of other factors could have been responsible for the faster conditioning evident in the experimental group. For example, the effect may have been caused by observing the demonstrator interact with the CS, observing the CS being paired with the release of a female quail, or observing a demonstrator copulate with the female. Experiments 2 and 3 were conducted to sort out these alternatives.

EXPERIMENT 2

Experiment 2 was conducted to investigate the importance of having the demonstrator approach and copulate with the CS object. Three groups of observers were compared. One group saw a demonstrator copulate with the CS object and then receive access to a female quail, as the experimental group in Experiment 1. A second group saw a demonstrator copulate with the CS object but in this case the demonstrator did not receive access to a female quail. For the third group, the demonstrators were not conditioned to copulate with the CS object.

Method

The methods were similar to those of Experiment 1 in all unspecified respects. Twenty-four male quail served as subjects, along with 24 female copulation partners. In addition, 24 males served as demonstrators. Sixteen of the demonstrators were previously conditioned to approach and copulate with the terry cloth CS. The remaining 8 demonstrators did not show any conditioned responses to the CS.

The subjects were randomly assigned to one of three groups (*ns* = 8) for the observation phase of the experiment. Group D+CS–US received the same observational procedure as did the experimental group in Experiment 1: exposure to a demonstrator male showing conditioned sexual responses to the terry cloth CS, which was paired with the presentation of a female quail. Group D+CS also observed a demonstrator showing conditioned sexual responses to the terry cloth CS. But for Group D+CS, the CS was covered after 30 sec, and the demonstrators did not receive access to a female quail. (Previous work had indicated that extinction of the conditioned sexual responses was unlikely in these demonstrators, given

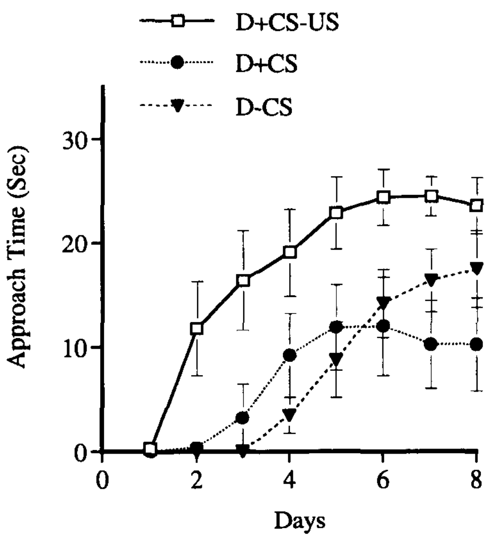

Figure 2. Mean (± *SE*) time spent near the CS object by subjects in Experiment 2. Group D+CS–US previously observed demonstrator males copulate with the CS and then receive exposure to the US. Group D+CS previously observed demonstrator males copulate with the CS without getting the US, and Group D−CS observed demonstrator males that did not copulate with the CS.

the relatively short duration of the observation phase.) Group D−CS received the same procedure as did Group D+CS, except that the demonstrators for Group D−CS did not show conditioned sexual responses to the CS object.

After 12 observation trials conducted 1 per day, each demonstrator was removed from the apparatus, each observer was placed into the demonstrator's compartment, and 8 conditioning trials were conducted (1 per day) for all of the observers. The conditioning trials were conducted as in Experiment 1, but this time the wire partition separating the observer and demonstrator compartments was left in place to minimize changes in context between the observation phase and the subsequent conditioning phase. With the partition in place, the size of the compartment in which the observers were conditioned was smaller than in Experiment 1. Therefore, the criterion for an approach response was made a bit more stringent as well. A subject was considered to have approached the CS if it stepped into an area 22.7 × 22.7 cm marked on the floor around the CS object.

Results and Discussion

Approach to the CS object during each trial of the conditioning phase is shown in Figure 2 for each group. The highest level of responding was evident in Group D+CS–US, which had previously observed CS–US pairings as well as a demonstrator showing conditioned sexual responses to the CS. Group D+CS, which had previously observed only a demonstrator responding to the CS, showed slower acquisition of the conditioned approach response. Similarly low levels of responding were evident in Group D−CS, which had observed a demonstrator that did not approach and copulate with the CS.

A repeated measures ANOVA showed a significant effect of group [$F(2,21) = 6.59, p < .01$], a significant effect of trials [$F(7,147) = 25.13, p < .001$], and a group × trials interaction [$F(14,147) = 2.23, p < .01$]. Subsequent analysis of the group effect with the Newman-Keuls test ($p < .05$) indicated the Group D+CS–US responded more than each of the other two groups, which did not differ from each other.

A similar pattern of group differences was evident with copulatory responses directed toward the CS. Significant main effects of groups were obtained for the grab, mount, and cloacal contact responses [$Fs(2,21) = 3.85, 3.69$, and 5.20, $ps < .05$, respectively]. Analyses of these group differences with the Newman-Keuls test ($p < .05$) indicated that Group D+CS–US made significantly more grab, mount, and cloacal contact responses than did Group D−CS. Group D+CS–US also made more grab, mount, and cloacal contact responses than did Group D+CS, but this difference was significantly only for cloacal contacts. Groups D+CS and D−CS were not significantly different from each other in any copulatory response measure.

The fact that no significant differences were obtained between Groups D+CS and D−CS suggests that seeing a demonstrator perform conditioned sexual responses to the CS was not sufficient to increase the subsequent conditioned responding of the observers. Increased responding was obtained only if the observers also witnessed pairings of the CS with the release of a female bird.

EXPERIMENT 3

The results of Experiment 2 suggest that the facilitation of learning evident in Experiments 1 and 2 did not constitute learning by imitation. Observing a demonstrator copulate with the CS object was not sufficient to produce the facilitation effect. The demonstrators also had to have the CS object paired with the release of a female bird, the US. Observing a demonstrator receive CS–US pairings permits two forms of observational conditioning: instrumental conditioning and classical conditioning. Instrumental observational conditioning is possible because copulation with the CS object on the part of the demonstrator is immediately followed by the US. Classical observational conditioning is possible because the CS object is paired with the US. Experiment 3 was conducted to decide between these alternatives.

Method

The methods were similar to those of Experiment 1 in all unspecified respects. Twenty-four adult male quail served as subjects. An equal number of females served as copulation partners. In addition, 8 previously conditioned males served as demonstrators.

The subjects were randomly assigned to one of three groups (*ns* = 8) for the observation phase. Group D+CS–US was treated the same way as was Group D+CS–US in Experiment 2. On each observation trial, these subjects were exposed to a demonstrator showing conditioned sexual responses to the CS object, which was paired with the release of a female bird. Group CS–US observed the same type of CS–US pairings but in the absence of a demonstrator. Group US/CS was also trained without a demonstrator but received

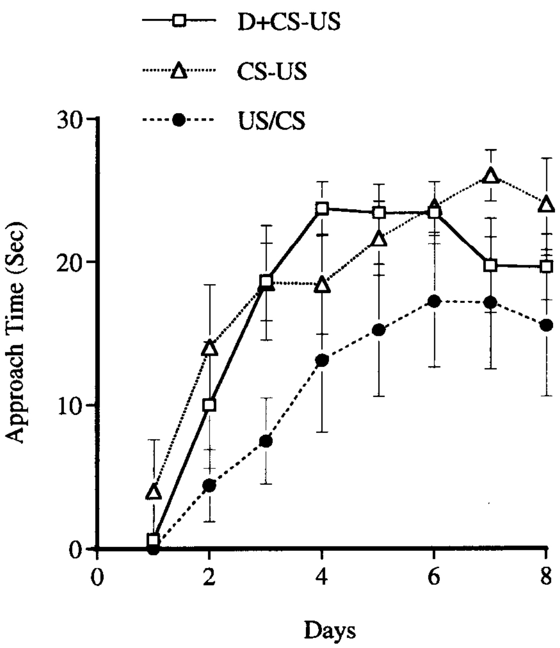

Figure 3. Mean (±*SE*) time spent near the CS object by subjects in Experiment 3. Groups D+CS–US and CS–US previously observed pairings of the CS with the US, whereas Group CS–US previously saw unpaired presentations of the CS and US. Demonstrator males were available only for Group D+CS–US.

unpaired presentations of the CS and US. For Group US/CS, presentation of the US, a live female bird, occurred 30–50 min before presentation of the CS on each of the 12 days of the observation phase.

After 12 observation trials, the demonstrator birds were removed from the experimental chambers for Group D+CS–US. The subjects were then moved to the demonstrator compartments, and 8 conditioning trials were conducted 1 per day, as in the previous experiments. The criterion for an approach response consisted of stepping into an area 22.7 × 22.7 cm around the CS object.

Results and Discussion

Approach to the CS object during the conditioning phase of the experiment is summarized in Figure 3. Groups D+CS–US and CS–US both showed more responding than did Group US/CS unpaired.

Observational instrumental conditioning was possible in Group D+CS–US because the demonstrators in this group received the US after approaching and copulating with the CS object in the observation phase. If observational instrumental conditioning occurred, the subjects in Group D+CS–US should have responded more vigorously than subjects in Group CS–US, which did not see a demonstrator interact with the CS. To evaluate this possibility, we first compared the performance of Groups D+CD–US and CS–US with a repeated measures ANOVA. This analysis showed a significant effect of trials [$F(7,91) = 21.20$, $p < .01$]. However, the main effect of groups and the group × trials interaction were not significant [$F(1,13) = 0.20$, and $F(13,91) = 1.41$, respectively]. These findings indicate that observational instrumental conditioning did not occur.

Because Groups D+CD–US and CS–US responded similarly and both observed CS–US pairings, the data from these two groups were combined and compared with those from Group US/CS unpaired. This comparison allowed us to evaluate the effects of witnessing CS–US pairings on subsequent sexual conditioning. The analysis showed significant effects of groups [$F(1,21) = 4.98, p < .05$] and of trials [$F(7,147) = 22.51$, $p < .01$]. These results indicate that prior observations of the CS paired with the US resulted in greater responding during the conditioning phase than did prior observations of the CS and US presented in an unpaired fashion.

Given the design of Experiment 3, we do not know whether observation of CS–US pairings facilitated the subsequent conditioning of the CS-approach response or observation of unpaired CS/US presentations retarded subsequent conditioning. However, the facilitation interpretation is more compatible with the results of Experiments 1 and 2 and therefore provides a more parsimonious interpretation of the results of the present series of experiments. Whether the facilitation or the inhibition interpretation is favored, the present results indicate the existence of observational conditioning in the sexual learning of male quail.

GENERAL DISCUSSION

The purpose of the present study was to determine whether copulatory behavior is susceptible to observational learning effects, and to identify some of the factors responsible for such effects. In all three experiments, exposure to a demonstrator that copulated with a CS object and then received the opportunity to copulate with a female bird (the US) facilitated the subsequent conditioning of the observers. In Experiment 1, this facilitation effect was evident in comparison with a control group that received exposure to a demonstrator that was not exposed to either the CS or the US. Subsequent experiments showed that seeing a demonstrator copulating with the CS object was neither sufficient (Experiment 2) nor necessary (Experiment 3) to increase subsequent sexual learning in the observers. Rather, the critical factor consisted of witnessing presentations of the CS paired with the release of a female bird (the US). Exposures to the CS paired with the release of a female facilitated subsequent conditioning of the observers whether or not the observers saw a demonstrator copulating with the CS object.

The results of the present experiments suggest that true imitation or copying did not occur in the sexual conditioning of male Japanese quail. However, the subjects were sensitive to observing CS–US pairings, a result indicative of observational conditioning (Zentall, 1996). Zentall has suggested that observational conditioning is usually a form of second-order conditioning, because merely seeing the US during the observation phase is not directly reinforcing. Contrary to this suggestion, the observational conditioning effect documented in the present experiments may have involved first-order conditioning, at least to some extent. First-order conditioning may have occurred because exposure to a female quail on the other side of a wire mesh barrier has been found to be an effective US in the sexual conditioning of males, although such a visual US is less effective than actually copulating with the female (Holloway & Domjan, 1993).

Examples of observational conditioning have been reported previously in the feeding behavior of pigeons (Zentall & Hogan, 1975) and chickens (Johnson, Hamm, & Leahey, 1986). In these studies, observation of a CS–US contingency was found to be sufficient to enhance subsequent conditioning. Zentall (1996) recently suggested that the presence of a demonstrator interacting with the CS and US may enhance observational conditioning effects by drawing additional attention to the conditioned and unconditioned stimuli. Such enhancement did not occur in the present study. We found no effect of the presence of a demonstrator in groups that witnessed CS–US pairings (Experiment 3). This suggests that our results were not due to stimulus or local enhancement.

Our findings are similar to the results of studies (Johnson et al., 1986) in which neither the presence of a demonstrator nor its responses were needed for observational conditioning to take place. In other cases, such as the observational conditioning of fear documented by Mineka and Cook (1993), the responses of the demonstrators (e.g., fear responses) served as a US for the observers. In these cases, the presence of the demonstrators, and their responses, were necessary for learning to occur.

We do not know why the conditioned sexual responses of the demonstrators had no effect on the observers in our experiments. However, the age of our subjects may have been important. Our subjects were tested in adulthood, after they had undergone sexual and filial imprinting. Observation of another adult male quail responding sexually to an unusual object may have little effect at this age. The sensitive period for sexual imprinting starts shortly after hatching and ends around 4–5 weeks of age (Oetting, Pröve, & Bischof, 1995). It may be that the responses of a demonstrator have a greater influence on observers that are closer to the age of sexual imprinting.

The present experiments focused on changes in the behavior of male quail. Recent evidence reported by Galef and White (1998) suggests that observational learning effects may also occur in female quail. In these experiments, female quail increased their preference for a previously nonpreferred male as a result of seeing that male copulate with another female. Further research is required in order to determine whether the mechanisms of this "mate copying" effect in females is similar to the observational conditioning effect documented in the present set of experiments.

REFERENCES

Domjan, M. (1994). Formulation of a behavior system for sexual conditioning. *Psychonomic Bulletin & Review*, **1**, 421-428.

Domjan, M., Huber-McDonald, M., & Holloway, K. S. (1992). Conditioning copulatory behavior to an artificial object: Efficacy of stimulus fading. *Animal Learning & Behavior*, **20**, 350-362.

Galef, B. G., Jr. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In B. G. Galef, Jr. & T. R. Zentall (Eds.), *Social learning: Psychological and biological perspectives* (pp. 3-28). Hillsdale, NJ: Erlbaum.

Galef, B. G., Jr., & White, D. J. (1998). Mate-choice copying in Japanese quail, *Coturnix coturnix japonica*. *Animal Behaviour*, **55**, 545-552.

Heyes, C. M. (1996). Genuine imitation? In C. M. Heyes & B. G. Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 371-389). San Diego: Academic Press.

Heyes, C. M., & Galef, B. G., Jr. (Eds.) (1996). *Social learning in animals: The roots of culture*. San Diego: Academic Press.

Heyes, C. M., Jaldow, E., & Dawson, G. R. (1994). Imitation in rats: Conditions of occurrence in a bi-directional control procedure. *Learning & Motivation*, **25**, 276-287.

Hogan, D. E. (1988). Learned imitation by pigeons. In B. G. Galef, Jr. & T. R. Zentall (Eds.), *Social learning: Psychological and biological perspectives* (pp. 225-238). Hillsdale, NJ: Erlbaum.

Holloway, K. S., & Domjan, M. (1993). Sexual approach conditioning: Unconditioned stimulus factors. *Journal of Experimental Psychology: Animal Behavior Processes*, **19**, 38-46.

Johnson, S. B., Hamm, R. J., & Leahey, T. H. (1986). Observational learning in *Gallus gallus domesticus* with and without a conspecific model. *Bulletin of the Psychonomic Society*, **24**, 237-239.

Mineka, S., & Cook, M. (1993). Mechanisms involved in the observational conditioning of fear. *Journal of Experimental Psychology: General*, **122**, 23-38.

Oetting, S., Pröve, E., & Bischof, H.-J. (1995). Sexual imprinting as a two-stage process: Mechanisms of information storage and stabilization. *Animal Behaviour*, **50**, 393-403.

Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative process in animals. *Psychological Review Monographs*, **2**(4, Whole No. 8).

Thorpe, W. H. (1963). *Learning and instinct in animals* (2nd ed.). London: Methuen.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer, & M. Milinski (Eds.), *Advances in the study of behavior* (Vol. 21, pp. 239-283). San Diego: Academic Press.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In C. M. Heyes & B. G. Galef, Jr. (Eds.), *Social learning in animals: The roots of culture* (pp. 221-243). San Diego: Academic Press.

Zentall, T. R., & Hogan, D. E. (1975). Key pecking in pigeons produced by pairing keylight with inaccessible grain. *Journal of the Experimental Analysis of Behavior*, **23**, 427-430.

Zentall, T. R., Sutton, J. E., & Sherburne, L. M. (1996). True imitative learning in pigeons. *Psychological Science*, **7**, 343-346.

(Manuscript received April 13, 1998;
revision accepted for publication June 15, 1998.)