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Conditioning of sexual proceptivity in female quail: Measures of conditioned place preference

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Abstract

The present experiments were conducted to explore the nature of conditioned sexual proceptivity in female quail. Females exposed to males subsequently approached the area where the males were previously housed (Experiment 1). This increased preference for the male's area reflected an increase in female sexual proceptivity and not an increase in non-directed locomotor activity (Experiment 2). These findings provide the first evidence that female quail show conditioned responses that may be considered to be proceptive responses toward male conspecifics. The proceptive responses are expressed as tonic changes in preference for areas where males have been observed in the past rather than as specific phasic conditioned responses.

Keywords

sexual proceptivity; sexual conditioning; place preference; Japanese quail

1. Introduction

According to Beach (1976), sexual behavior can be expressed in three forms, representing different stages of the reproductive interaction between males and females: attractivity, proceptivity, and receptivity. These three stages are interrelated and are sometimes difficult to discriminate. Attractivity is a measure of an individual's sexual value and is often inferred from the behavior of the sexual partner. Proceptivity refers to behaviors indicating how much an individual is attracted to a sexual partner. Some manifestations of proceptivity are approach, solicitation, and contact responses. Receptivity refers to consummatory behaviors that occur as a response to sexual stimulation by the reproductive partner. Although receptivity is often of interest as a characteristic of female sexual behavior, it also occurs in males interacting with a female sexual partner.

Males and females differ in their expression of these three characteristics. Female attractivity is often determined by female characteristics indicative of the ability to produce and care for offspring. In contrast, male attractivity is determined by male characteristics

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indicative of the ability to provide resources or parental care (Alcock, 2009; Jennions and Kokko, 2010; Kvarnemo, 2010).

Males and females also differ in their expression of proceptivity. For example, in laboratory conditions male Japanese quail approach and remain near a narrow window that provides visual exposure to a female conspecific. Females, however, do not approach or remain near a window that allows visual access to a male quail (Domjan and Hall, 1986a, b). Delville and Balthazart (1987) suggested that females peck at males as a form of solicitation behavior. One of us (G.G.) observed similar responses in a semi-naturalistic setting in coturnix quail and other authors have observed related responses in other bird species (e.g., *Rhea americana*, Fernández and Mermoz, 2003; *Colinus virginianus*, Stokes, 1967). Female quail continuously housed with males may approach, peck at, walk around, and show their backs to males as solicitation behaviors. However, in controlled laboratory conditions the frequency of these behaviors is low and they have been difficult to reproduce and study in a systematic manner.

Receptivity in females may be expressed in either a passive or an active manner. Passive receptivity consists of the female remaining near a male. Active receptivity involves responses such as lordosis in rats and other mammals, and squatting in birds. Lordosis and squatting are generally described as the female lowering her body and raising her posterior toward the male (Barnett, 1975; Noble, 1972). This body position facilitates the mounting and delivery of sperm into the female reproductive tract.

Although attractivity, proceptivity, and receptivity have been described for females of some species, research on sexual behavior in general has focused on males as subjects. Male sexual behavior is often more demonstrative and easier to observe than female behavior. This is particularly true for Japanese quail. A male Japanese quail in reproductive condition will approach, grab, mount, and display cloacal contact with a female. Males of this species also show other sexually related behaviors such as crowing and strutting, which can be easily observed and measured (Mills et al., 1997). In contrast, female sexual behavior is more subtle and difficult to observe. Female Japanese quail do not display strong approach responses to a male quail (Domjan and Hall, 1986b) but are more likely to remain stationary during the copulation sequence if they are sexually receptive (Delville et al., 1986; Noble, 1972; Rutkowska and Adkins-Regan, 2009). In consequence, female sexual receptivity in quail has been defined by the absence of resistance, rather than by the presence of clearly defined pro-active responses. In addition, sexual reward and satiation are less evident in female quail than in males.

Both proceptive and receptive sexual responses have been studied using Pavlovian conditioning procedures. For example, Hollis et al. (1989) examined the conditioning of sexual behavior in male-female pairs of the blue gourami fish, *Trichogaster trichopterus*. One animal of each pair was exposed to a red light (the conditioned stimulus or CS) followed by visual access to its sexual partner (the unconditioned stimulus or US). As a result of this procedure, both males and females acquired a conditioned frontal display response to the CS. The Pavlovian signal also increased the courtship behavior of the males, and decreased their level of aggression during direct interactions with females. However, Pavlovian conditioning did not alter how the females reacted when given access to a male. In a subsequent study, Hollis et al. (1997) found that Pavlovian conditioned males produced far more viable offspring than non-conditioned animals.

Zamble et al. (1985) focused on changes in sexual receptivity as a result of Pavlovian conditioning. They found that male rats were quicker to copulate if they encountered a copulation partner after the presentation of a conditioned stimulus (CS) that was previously

paired with exposure to a female. Analogous findings were subsequently reported in male quail (Domjan et al., 1986; Mahometa and Domjan, 2005). But, such effects have not been reported for female subjects.

Comparison of sexual conditioning in male and female Japanese quail was examined for the first time by Gutiérrez and Domjan (1997). They found that after paired presentations of a CS and access to a copulation partner (US), males increased their proceptive responses toward female quail by approaching the CS and quickly entering the box in which the stimulus female was housed. In contrast, females did not approach the CS or enter the box housing a stimulus male. Although the female quail did not show a significant increase in proceptivity, they evidenced conditioned increases in sexual receptivity. Females that received paired presentations of the CS and US showed longer bouts of squatting when their male sexual partner was present than females in an unpaired control group.

Gutiérrez and Domjan (1997) may have failed to observe conditioned proceptive responses in females because of methodological limitations of the procedures they used. First, sexual behavior was studied in discrete trials with subjects that were socially isolated between the trials. Under these circumstances, males copulated rapidly after being introduced to females, but the females did not show similarly rapid proceptive responses. Second, the females may have had little opportunity to avoid or escape the sexual advances of the male, and they did not have a chance to select their mate.

Naturalistic observations of quail indicate that during the breeding season males form territories and later females come to those territories to nest and pair with the resident male (Moreau, 1951). Recent findings on the European quail have shown that females often switch pairs (Rodríguez-Teijeiro et al., 2003) and may actively seek new pairings. This suggests that an appropriate experimental situation to study proceptive responses should permit females to approach a male's territory and provide the female with the opportunity to approach or avoid the male. The experiments reported in this paper were conducted to explore this possibility using an area preference paradigm. Female Japanese quail were first given the opportunity to learn where a male is housed and were then tested for their tendency to visit that area. Experiment 1 employed a between-subjects design and Experiment 2 employed a within-subject design.

2. Experiment 1

In Experiment 1, independent groups of female quail were first given the opportunity to observe either a stimulus male, a stimulus female, or no bird in a distinctive area and were then tested for their preference for that area. If increased spatial preference reflects conditioned proceptive behavior, it was hypothesized that a female would approach or enter an area in which a male had been previously observed, but would not show the same response if a female or no bird was previously seen in that area.

2.1. Methods

2.1.1. Subjects—Twenty-one sexually naive adult female Japanese quail were selected for the experiment. All subjects were between 4 and 6 months old. They were raised in the colony maintained at the University of Texas at Austin. All subjects were kept in mixed-sex cages until 30 days of age, when they were sexed and separated. Females were kept in group cages until they were selected for the study. During the experiment, they were housed in the test cages. In order to keep the subjects in reproductive condition, the room lights were set to maintain a photoperiod cycle of 16 hours of light and 8 hours of darkness, with the light phase starting at 6 am each day. Subjects were randomly assigned to one of three groups: stimulus-male, stimulus-female, and no-bird.

2.1.2. Apparatus—The experiment was conducted in several rectangular arenas that were 183 cm wide, 122 cm deep, and 107 cm high. The walls and ceiling were made of sealed plywood and the front was wire mesh to permit observation of the subjects. The arena was divided into two equal sized areas, each measuring 91.5 cm × 122 cm. To make the two sides of the arena distinctive, one had a sand floor and tree branches, and the other had a wire-mesh floor and lacked the tree branches.

A female subject lived in one of the areas during the experiment, and the other area housed a male, a female, or no stimulus bird, according to the group assignment of the subject. Whether the subject female was housed in the sand-floor area or the mesh-floor area was counterbalanced across groups.

2.1.3. Procedure—During habituation the subjects were restricted to their own side of the experimental arena and their view of the other side was blocked by a masonite panel. The stimulus side of the arena was empty. After five days of this condition, the subjects were pretested for their preference for the different zones of the experimental chamber. During the pretest sessions, no stimulus birds were present, and the subjects were given access to both sides of the arena. Spatial preference was measured with a time-sampling procedure. Whether the subject was in its home area or on the other side of the arena was recorded every 5 sec (using a computer-generated signal to cue the observations), during three 5-minute observation periods. The first observation period was conducted right after the subjects were given access to both sides of the experimental arena; the second and third observation periods were scheduled 30 min and 60 min after the first observation period. At the end of each pretest session, subjects were again restricted to their own side of the arena. Tests were run between 2 and 5 p.m. every day.

During the three days following the pretest, a wire screen was set up to separate the two halves of the apparatus, and a male (for group stimulus-male), a female (for group stimulus-female), or no bird (for group no-bird) was placed on the opposite side of the female's area. During the following two days the stimulus male or female was removed, and the subjects were tested again for their preference for the different zones of the arena, using the same procedure as in the two pretest days.

The time-sampling observations were aggregated for the pretest and test phases as the percentage of observations in which the subject was in the male's area. These data were then analyzed with a 3 (group) × 2 (phase) mixed design analysis of variance.

2.2. Results

Figure 1 shows the mean percentage of observations in which the female subjects were noted to be in the side opposite their own housing compartment during the pretest and test sessions. When females were allowed to explore the experimental arena during the pretest, they preferred and stayed in their own side. Subjects in all three groups were observed to be in their own area between 65% and 90% of the time. Females showed similar responses in area preference during the pretest, independently of the group to which they were assigned. This is not surprising, since no treatment was performed up to this point.

After three days of visual exposure to males, the spatial preference of subjects in the stimulus-male group changed. The subjects in this group increased their preference for the male's area during the test compared to the pretest. During the pretest, females in this group were observed to be in the male's area about 25% of the time. During the test, however, they were recorded to be in the male's area 60% of the time. An analysis of variance showed that the differential increase in preference for the opposite side among the groups resulted in a significant group by phase interaction, $F(2, 18) = 3.57$, $p < .05$. A post-hoc analysis using

the Tukey test ($p < .05$) revealed that the increase in preference for the opposite area in the stimulus-male group was statistically significant. In contrast, the changes in area preference observed in groups stimulus-female and no-bird during the test sessions were not significant.

2.3. Discussion

The results of Experiment 1 show that female quail exposed to males increased their preference for the area in which the males had been housed, whereas females exposed to another female or no stimulus bird did not significantly change their preference for the opposite side of the arena. The changes observed in group stimulus-male show that females prefer to enter a male's territory, but do not tend to approach areas where females were previously present. This suggests that the change in spatial preference reflects sexual factors and not social factors, which would have resulted in approach directed toward any conspecific's area.

The increased preference for the opposite side of the experimental arena in the stimulus-male group is consistent with our original hypothesis that conditioned proceptive behavior may be observed by measuring the tendency of a female to enter a male's area. However, increased preference for the male's area also may have reflected increased locomotor activity resulting from exposure to male quail. Females that moved about more would have ended up spending more time in the area previously occupied by the male. Consistent with this interpretation, preference for the male area was never much above 50% in group stimulus-male.

The design of Experiment 1 did not permit ruling out increased nondirected activity as an explanation of the results. This possibility was addressed in Experiment 2.

3. Experiment 2

Experiment 2 provided a within-subject assessment of the development of female preference for a distinctive area that was previously occupied by a male. The experimental chambers were reconfigured to provide females with visual access to two equivalent stimulus areas. During the training period, a male was housed in one of the stimulus areas, whereas the other one was empty. It was hypothesized that if the females selectively increased their preference for the area where the male had been housed, this would reflect proceptive behavior and "search" for the male in his territory. Such an outcome could not be produced by increased locomotor activity *per se* because any increase in locomotion would increase time spent in both stimulus areas to the same extent.

Experiment 2 also tested whether exposure to the calls made by males is sufficient to induce an increase in spatial preference. During the first phase of the experiment, visual exposure to the stimulus males was precluded by an opaque barrier that did not block auditory cues.

3.1. Methods

3.1.1. Subjects—Eight sexually naive adult female quail were selected for the experiment. They were bred and raised in the same way as animals in Experiment 1. During the experiment they were housed in the experimental arenas, and all subjects received the same experimental treatment.

3.1.2. Apparatus—A rectangular arena similar to that used in Experiment 1 was divided by two wire screens into three triangle shaped areas (see Figure 2, top panel). One of the areas contained a stimulus male quail; the second area housed a female subject; the third area was empty during the experiment. The female area was twice the size of each of the stimulus areas, which were symmetrically located in the left and right corners of the arena.

As in Experiment 1, half of the experimental arena had a sand floor, and half had a wire floor. The position of the sand was counterbalanced across subjects, so that for half of the subjects the stimulus male was located on the sand-floor side, and for the remaining females, the stimulus male was located on the wire-floor side. Because the female's area straddled the middle of the arena, half of it had the sand-floor and half had the wire-floor.

3.1.3. Procedure—The subjects lived in their test arenas for ten days, for habituation purposes. During this time, a masonite panel separated the female's area from the two stimulus areas, so the females could see neither the area containing the stimulus male nor the empty area. The females, however, were able to hear the stimulus males behind the masonite panel. During the next two days, the subjects were pre-tested for their preference for the different zones of the test arena. During the pre-test sessions no stimulus males were present, and the subjects were given access to both stimulus areas. Spatial preference was evaluated in the same way as in Experiment 1. During each of the three days following the pretest, wire screens were set up dividing the three areas, and a male was placed in one of the stimulus areas. Finally, during the next two days, the subjects were tested again for their preference for the different zones of the arena, following the same procedure as used during the pretest.

3.2. Results

Figure 2 (bottom panel) shows the mean percent of observations during which the subjects were noted to be in the male and the empty stimulus areas during pretest and test phases. During pretest, females were observed to be in the male area (24%) only slightly more often than in the empty area (19%). An analysis of variance revealed that this difference was not significant, $F < 1.0$. During test, however, females were observed to be in the male area much more often (44%) than in the empty area (16%). This change in area preference resulted in a significant area by phase interaction, $F(1, 7) = 9.65$, $p < .05$.

3.3. Discussion

The results of the Experiment 2 confirm the findings of Experiment 1 indicating that females show increased preference for an area where a male conspecific had been observed in the past. This preference was evident in a within-subject design and could not be attributed to increased arousal or increased non-directed exploratory behavior. Females could enter either of the two equivalent stimulus areas, but they preferred the one where a male had been housed. These results suggest that females show approach behavior to a male's territory that can be interpreted as proceptive sexual behavior.

The within-subject design of Experiment 2 also provided an important control for individual differences in baseline preferences. Unlike Experiment 1, Experiment 2 evaluated preference for a male area and an empty area before and after visual exposure to a male conspecific. This eliminated possible effects of baseline differences between subjects.

The results suggest that female quail can control their reproductive opportunities by approaching or avoiding places where a male may be encountered. Thus, they may not only exert mate choice, but also actively search for in areas where a male may be found and thereby increase their chances for sexual interactions with males.

In a study of social proximity behavior, Domjan and Hall (1986b) found that male quail tend to approach and remain near females but females show much less of a tendency to approach and remain near males. The results of the present experiment combined with Domjan and Hall's findings suggest that approaching a male's territory and approaching a male may be controlled by two different processes and may represent different behaviors by the female.

Evidently, females approach a male's territory, but once visual contact has been established, no further approach is initiated by the female (as observed by Domjan and Hall, 1986b). In terms of behavior systems theory (Domjan, 1994, 1997; Timberlake and Lucas, 1989), the female's proceptive behavior may be primarily evident in her general search behavior rather than focal search and approach when a potential mate has been identified.

Experiment 2 also suggests that auditory cues provided by a male may not be sufficient to establish a spatial preference. Exposure to the calls of the male during the 10-day habituation phase did not induce an increase in preference for the male stimulus area. Goodson and Adkins-Regan (1999) previously demonstrated that playback of male calls presented to female quail resulted in approach to the source of the call. Results of the present study suggest that such approach to male calls is not sufficient to induce a spatial preference when the male is absent from that area.

4. General Discussion

The present experiments were designed to investigate how female quail learn to anticipate sexual interactions and opportunities, and how this anticipation is manifest in their behavior. Two experiments were conducted to evaluate whether females show changes in preference for different areas of an experimental arena that could be interpreted as evidence of a change in sexual proceptivity. In this paradigm, female quail were visually exposed to a sexual partner or another female housed in an area with distinct physical characteristics. Then, the stimulus birds were removed, and the female subjects were allowed to explore the male or female area during several test trials. How long the subjects remained in the stimulus area during the test trials was considered indicative of their interest in males or females.

The results of Experiment 1 showed that female quail exposed to males increased their preference for the area in which the males had been seen. In contrast, females exposed to another female or no other bird did not significantly change their preference for the stimulus area.

The increase in time spent in the area where a male was previously seen could have resulted from an increase in preference for that specific area, or from a general increase in exploratory behavior. These alternatives were tested in Experiment 2, which showed that females approach the specific area where a male had been housed, and do not randomly increase their exploratory activity. This suggests that females are able to identify male areas, probably using contextual cues associated with the male.

The results of Experiment 2 also suggested that exposure to auditory cues provided by a male is not sufficient to induce a place preference. For the preference to develop, females had to have visual access to the male in the distinctive area. The greater salience of visual rather than auditory cues provided by a conspecific of the opposite sex was previously observed in male quail. Domjan and Hall (Experiment 6, 1986a) found that males visually exposed to females remained in close proximity to a window separating them, and although further presentation of other cues increased their proximity, it was the visual cues that had the most control over that proceptive behavior. Similarly, Domjan and Nash (1988) evaluated proximity behavior of males to various kinds of stimuli including live female quail, live birds of other species, and several taxidermic models that allowed them to test the relative importance of visual cues versus olfactory, auditory or other behavioral cues provided by live female quail. The results showed that visual cues, especially a combination of head and neck stimuli, were sufficient to elicit and maintain social proximity behavior in male quail.

Overall, the results of Experiments 1 and 2 show that females approach and remain in areas where they have previously observed males. This basic finding suggests that female quail

are more sexually proactive than was previously thought. Previous studies have shown that female quail can learn to predict the presence of a sexual partner and this increases their sexual receptivity, as evidenced by increased squatting behavior (Gutiérrez and Domjan, 1997). The present studies indicate that conditioning can also increase active sexual proceptive responses in female quail. This evidence of female proceptivity is consistent with previous observations. Delville and Balthazart (1987) have suggested that females peck at males as a form of solicitation behavior. Subsequently, Goodson and Adkins-Regan (1997) demonstrated that female quail preferentially approach a speaker that plays sounds of a male crowing as opposed to sounds of the calls played in reverse.

The results of the present experiments are also consistent with information from field studies. These studies suggest that male quail first establish territories during the breeding season. Females then visit these territories, select a nest site, and establish a pair-bond with the resident male (Kawahara, 1967; Moreau, 1951). These observations suggest that females approach a general area deemed to be appropriate for nesting and mating. Once a female is in a male's territory, it is the male who is then primarily involved in maintaining the social proximity of the pair.

It is important to note that in both of the present experiments the female quail approached male areas, but the male was not present at the time of their approach. This suggests that females learned to associate the presence of a male with certain contextual cues. Approach to a male's territory in a natural setting may be also mediated by associative learning. This possibility, however, remains to be examined in detail.

Previous studies have shown the importance of contextual control of sexual behavior in quail. Crawford et al. (1994) showed that sexual experience in a particular context facilitates quail male sexual responding to a taxidermic model in that context; they demonstrated this to be a Pavlovian contextual conditioning effect, rather than an effect of general sexual experience. Hilliard et al. (1997) additionally demonstrated that contextual control of male quail sexual behavior may occur after a single exposure to a female in a particular context. Akins (1998) further explored sexually conditioned changes in place preference as a result of context-US associations and the role of context as an occasion setter for sexual approach behavior. She found that male quail increased their preference for a place in which they had access to a sexually receptive female (Experiment 1). They also responded more readily toward a CS that predicted the presence of a female (Experiment 2), and showed a preference for the area in which that CS was presented (Experiment 3).

Similar effects have been studied in the sexual behavior system of rats. For example, Oldenburger et al. (1992) found that sexually active females presented with copulatory access to a male showed a preference for the area associated with copulation versus an empty area. In a subsequent experiment, however, they found that when a caged male was presented in the alternative area, female rats preferred that area over the area associated with copulating males. Using a similar place preference test, Paredes and Alonso (1997) found that when they allowed female rats to pace their sexual interactions with males, they increased their preference from a previously neutral context to one associated with sexual encounters. Similarly, Coria-Ávila et al. (2005) demonstrated that an odor paired with paced sexual interactions in female rats, induces preference for a partner associated with that odor. Thus, it seems that in rats, proceptive responses are more easily expressed if the experimental situation allows the female to pace their responses. Both of our experiments offered this possibility to the females, by limiting the sexual responses of the males, and by testing changes in female preference in absence of males. Future studies with rats and quail in which females have the opportunity to pace their sexual encounters (e.g., Broekman et al., 1988) may further elucidate the conditions under which females show sexual proceptivity.

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Highlights

- Females exposed to males subsequently approached the area where the males were previously housed.
- Place preference reflected an increase in female proceptivity, not an increase in general activity.
- This is the first evidence that female quail show conditioned proceptive responses toward males.

Figure 1.

Mean (+ S.E.) percentage of observations in which the females were noted to be in the side opposite their own during pretest and test phases of Experiment 1. During the conditioning phase, a male, a female, or no bird was housed on one side of the arena, and the female subject was housed on the other side, with a wire mesh separating the two areas. During testing, the stimulus subjects were removed from the arena.

Figure 2. Floor plan of the test arena (top panel) and mean (+ S.E.) percentage of observations in which the females were noted to be in the male and empty stimulus areas during pretest and test phases of Experiment 2 (bottom panel).