Dissociation of conditioned appetitive and consummatory sexual behavior: Satiation and extinction tests

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Sexual responses were conditioned in male Japanese quail using the opportunity to copulate with a female as the unconditioned stimulus (US). The conditioned stimulus (CS) was a 3-D object made of a taxidermically prepared female quail head mounted on a terry-cloth body. Both appetitive conditioned responses (approach and proximity to the CS) and consummatory conditioned responses (mount and cloacal contact directed toward the CS) developed when 2-min presentations of the CS were followed immediately by the US, but not when the CS and US were separated by trace intervals of 10 or 20 min (Experiment 1). Postconditioning sexual satiation suppressed conditioned cloacal contact responses more than conditioned approach to the CS (Experiment 2), and "acute" extinction suppressed both conditioned mounting and conditioned cloacal contact responses more than conditioned approach to the CS (Experiment 3). These results demonstrate a functional dissociation between conditioned appetitive and consummatory responses and imply that the motivational and/or associative mechanisms underlying the two types of behavior are distinct.

Ethologists have long viewed behavior in terms of sequences of motor patterns that progress toward the attainment of a biologically important goal (Craig, 1918; Hinde, 1953; Lorenz, 1981; Tinbergen, 1951). Early components of behavioral sequences were referred to as "appetitive" and were assumed to mobilize the animal and bring it into contact with species-typical sign stimuli. Later components were labeled "consummatory" and were thought to enable the animal to interact in a conclusive and adaptive fashion with those sign stimuli. Progress from appetitive to consummatory stages was presumed to be regulated by interaction with specific stimuli that gated the transitions from one stage to the next (Baerends, 1988; Hinde & Stevenson, 1969).

Investigators of animal behavior in laboratory paradigms have also distinguished between "early" and "late" response components in considerations of complex behavior. For instance, Konorski (1967) viewed feeding behavior in terms of preparatory and consummatory responses. Preparatory responses involved the elicitation of hunger and searching behavior, whereas consummatory responses involved reflexes beginning with the arrival of food in the mouth. According to Konorski's model, when a cue was paired with the opportunity to eat, the re-

sultant conditioned response (CR) involved parallel conditioning of preparatory and consummatory responses relevant to feeding—a "hunger CR" to the cues of the experimental context and a "food CR" to the conditioned stimulus (CS). As conditioning became better established, food CRs tended to supplant hunger CRs.

Konorski's (1967) theorizing was an early "functional" or "biological" account in which the topography of the CR was viewed as the result of superimposing contingent relations between stimuli on a naturally organized response system. This idea has been elaborated more recently by Timberlake and his associates in behavior systems theory (Timberlake, 1994; Timberlake & Lucas, 1989). Behavior systems theory invokes a hierarchy of control mechanisms consisting of *system* (e.g., feeding), *subsystem* (e.g., predating), *mode* (e.g., general search), *module* (e.g., chase), and specific *action pattern* (e.g., pounce).

Behavior systems are far more complex than the binary distinction between appetitive and consummatory responses (Timberlake & Silva, 1995). Nonetheless, all behavior system models incorporate the appetitive–consummatory concept in some way. They feature a continuum, running from behaviors that are variously characterized as general, diffuse, or flexible, to responses that are viewed as conclusive, more stereotyped, and more specifically related to a biologically important stimulus such as a sexually receptive conspecific (Domjan, 1994), an encounter with a predator (Fanselow & Lester, 1988), or food (Timberlake, 1990).

Traditional ethological theory held that each of the responses in a complex chain leading to biological consummation was supplied with a separate motivation or

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“action-specific” energy that impelled that response (Lorenz, 1981). In a similar vein, the behavior system account claims that multiple “motivational substates” intervene between the highest level of a system and the events at the level of action patterns (Timberlake & Silva, 1995). Therefore, an important question is whether the constructs said to underlie an appetitive-to-consummatory response chain are motivationally independent. This question can be addressed by identifying the individual elements in a behavioral chain or sequence and then using various techniques to investigate the relationships between these elements.

For instance, following Beach (1956), contemporary investigators have applied the appetitive-consummatory distinction to sexual behavior (e.g., Pfau, 1996). Action patterns “anticipatory” to copulation, such as activity changes or approach to a potential sexual partner, are deemed to be appetitive, whereas copulation itself is said to be consummatory (Balthazart & Ball, 1992; Domjan, 1994; Pfau, Mendelson, & Phillips, 1990). Numerous studies with rats have supported the idea that appetitive and consummatory sexual behavior are mediated by separate mechanisms (Blackburn, Pfau, & Phillips, 1992; Everitt, 1990). For instance, Pfau and Phillips (1991) found that high doses of the dopamine antagonist clozapine abolished copulatory behavior, but not sexually conditioned increases in locomotor activity. In contrast, bilateral infusions of the dopamine antagonist haloperidol into the nucleus accumbens attenuated conditioned increases in locomotor activity but did not suppress copulation.

Appetitive and consummatory components have also been identified in the sexual behavior of male Japanese quail (*Coturnix japonica*) and have been incorporated into a behavior system model of sexual conditioning (Domjan, 1994). According to this model, sexual behavior starts with general search behavior elicited by endogenous factors and nonspecific environmental cues, proceeds to focal search once localized cues predictive of a female bird are perceived, and concludes with copulation once contact with the female has been established. Focal search in male Japanese quail is viewed as appetitive behavior (Balthazart, Reid, Absil, Foidart, & Ball, 1995; Domjan, 1994) and is operationalized as approaching and remaining near either species-specific female cues (Domjan & Hall, 1986) or conditioned stimuli predicting the impending presentation of a female (Domjan, Lyons, North, & Bruell, 1986). Consummatory responding consists of a highly stereotyped sequence of behaviors in which the male first grabs the back of the female’s head or neck, steps onto her back, and then exhibits cloacal contact movements (Wilson & Bermant, 1972).

Domjan’s model borrows from Timberlake’s scheme of progressively narrowing search modes (general search, focal search, and consummatory responding) leading to biological consummation, but the underlying structure of the modes, and their degree of independence, have not been empirically investigated. In fact, thus far the commonalities between appetitive and consummatory ele-

ments in the response chain have been more remarkable than the differences. For instance, appetitive sexual behavior in male Japanese quail appears to be activated in adulthood by the aromatization of testosterone into estrogen (Balthazart et al., 1995) in the same way that consummatory behaviors are (Balthazart & Foidart, 1993). In addition, both appetitive and consummatory responses are modifiable by Pavlovian conditioning procedures (Domjan, Huber-McDonald, & Holloway, 1992; Domjan et al., 1986; Domjan, O’Vary, & Greene, 1988).

Timberlake has recommended the integration of behavior systems and traditional associative accounts of learning by using the rich arsenal of laboratory learning paradigms to explore the structure of behavior systems (Timberlake & Silva, 1995; see also Williams, 1981). We further suggest that because behavior systems theory has little to say about the contents of learning, analysis of the associations exhibited at various stages in the appetitive-to-consummatory continuum may contribute significantly to the characterization of the system.

A well-established method for analyzing the contents of an association involves changing the value of the unconditioned stimulus (US) after acquisition. For instance, by using various methods to reduce the affective value of a food US after conditioning (such as pairing the food with LiCl- or rotation-induced illness), it has been established that whereas first-order Pavlovian conditioning is mediated by stimulus-stimulus associations, second-order conditioning is mediated by stimulus-response linkages (Holland & Rescorla, 1975; Holland & Straub, 1979). The critical evidence in these experiments is a dissociation: US devaluation suppresses conditioned responding to a first-order CS but spares responding to a second-order CS (Stanhope, 1992).

Another way to devalue an appetitive US is through satiation. Satiation has proven to be a particularly effective way to reveal functional dissociations between appetitive and consummatory components of feeding behavior (Morgan, 1974). Appetitive aspects of feeding, such as orientation to signals for food (Cleland & Davey, 1982), leverpressing (Balleine, 1992; Davidson, 1971), or predatory attack of mice by cats (Leyhausen, 1975) may all persist after satiation has abolished eating.

Satiation has also been used to investigate the contents of sexual conditioning. Hilliard and Domjan (1995) found that sexual satiation reduced the tendency of male quail to approach a CS that signaled access to a sexually receptive female. However, even when the male subjects were satiated to the point that they no longer copulated with females, they continued to approach the CS to an appreciable extent. This suggests that appetitive and consummatory aspects of male sexual responding in Japanese quail may be mediated by distinct mechanisms.

Although a large number of investigators have reported evidence for functional dissociations between appetitive and consummatory behaviors, in much of this research the appetitive response examined was a conditioned behavior, whereas the consummatory response was an un-

conditioned behavior (Hilliard & Domjan, 1995; Holland & Straub, 1979; Pfaus & Phillips, 1991). For instance, Everitt and Stacey (1987) observed that male rats with lesions of the preoptic area of the hypothalamus continued to barpress to gain access to a sexually receptive female rat, even though they no longer copulated with that female. It could be argued that the dissociations observed in these studies were related to the difference between conditioned and unconditioned behavior rather than to the distinction between appetitive and consummatory responses.

In the present study, we employed a standard associative learning paradigm to explore the modes or "motivational substates" (Timberlake & Silva, 1995) underlying appetitive and consummatory sexual responding in male Japanese quail. Specifically, we tested the functional independence of the focal search and copulation modes proposed to underlie sexual responding in male Japanese quail (Domjan, 1994). In addition, we sought to exploit the well-established US revaluation strategy (see, e.g., Holland & Rescorla, 1975; Holland & Straub, 1979; Rescorla, 1973; Stanhope, 1992) to assess the contributions of stimulus-stimulus and stimulus-response mechanisms to appetitive versus consummatory conditioned sexual responses.

The experiments avoided confounding the appetitive-consummatory distinction with conditioned versus unconditioned behavior (and enabled analysis of the contents of learning of conditioned appetitive versus conditioned consummatory responses) by using as the CS a 3-D object that supported conditioned copulation as well as conditioned approach behavior. Male subjects were conditioned to approach and copulate with the CS object by having it paired with access to a sexually receptive female. In Experiment 1, different CS-US intervals were employed to verify the associative basis of this conditioned responding. In Experiments 2 and 3, appetitive and consummatory conditioned sexual responses were compared following sexual satiation and extinction manipulations.

EXPERIMENT 1

Male Japanese quail quickly learn to approach and remain near a CS that predicts access to a sexually receptive female (Domjan et al., 1986). This conditioned sexual approach behavior appears to be a function of Pavlovian sign tracking rather than instrumental goal tracking. Crawford and Domjan (1993) demonstrated that the conditioned approach response is acquired even with an omission control procedure, and Burns and Domjan (1996) found that quail continue to approach a CS paired with sexual reinforcement even when the site of presentation of the CS is moved 91 cm away from the site where the US is delivered.

Under certain circumstances, male quail will also display consummatory sexual responses directed toward a CS. In particular, this occurs if the CS is a 3-D object that incorporates the head and some of the plumage of a female quail (Domjan et al., 1992). Although such an object contains some species-specific stimuli, male quail show

only modest levels of approach and copulation behavior toward the object in the absence of some type of sexual conditioning (Köksal, Domjan, & Weisman, 1994).

If approach and copulation with a CS object depends on an association between the CS and sexual reinforcement, then procedures designed to weaken the association should disrupt acquisition of the approach and copulatory responses. One such procedure involves introducing a trace interval between the CS and the US. Trace conditioning is generally less effective than delay conditioning, especially at longer trace intervals (Mackintosh, 1974). Experiment 1 was conducted to evaluate the associative basis of sexually conditioned approach and copulatory behavior using a trace conditioning manipulation. Independent groups of male Japanese quail received sexual conditioning with trace intervals of 0 sec, 10 min, and 20 min.

Method

Subjects. Twelve naive male Japanese quail (3 months old) were obtained from a randomly bred colony maintained at the University of Texas at Austin. At 30 days of age, the birds were moved from mixed-sex groups to individual wire mesh cages (GQF Manufacturing Co., Savannah, GA), where they remained until the experiment began. Six adult female Japanese quail served as copulation partners to provide sexual reinforcement (the US) during the acquisition trials. Overhead lights in the laboratory were on from 6:00 a.m. to 10:00 p.m. daily, which provided sufficient photostimulation to maintain the birds in reproductive readiness. Food and water were available at all times.

The male subjects were selected for participation in the experiment on the basis of a pretest for sexual competence. A female was placed in their home cages for 5 min to determine whether they would display the full copulatory sequence of neck grab, mount, and cloacal contact movement (Schein, Diamond, & Carter, 1972).

Apparatus. Experimental procedures were conducted in six identical chambers (67.3 cm high $\times$ 121.9 cm wide $\times$ 121.9 cm deep) walled with plywood on the ceiling, sides, and back; floored with wire mesh; and closed at the front by a hinged wire mesh door. A smaller side cage (35.8 cm high $\times$ 61.5 cm wide $\times$ 29.8 cm deep) was attached to the middle of the left or right side wall of each experimental chamber. A female quail was housed in each side cage. A 20.5-cm² vertically sliding door (the US door) separated the experimental chamber from the female side cage.

A CS object (Figure 1) was made for each experimental chamber by removing the head and approximately 2.5 cm of the neck of a female Japanese quail, cleaning out soft tissue and brain, stuffing the head and neck with Poly-fil (Fairfield Processing Corp.), and mounting them on top of an artificial "body." The body was composed of two ovoids of dark blue terry cloth stuffed with Poly-fil: one approximately 8 cm long and 13 cm in circumference, and the other approximately 10 cm long and 20 cm in circumference. The larger ovoid was glued to a plywood platform (approximately 12 $\times$ 9 cm), while the smaller one was mounted vertically directly in front of it and was crowned with the taxidermically prepared female head.

The platform holding the CS object was suspended from the ceiling of the experimental chamber. A hood mounted on the ceiling served to conceal the CS from the male birds when it was in the raised position. When lowered to the floor, the CS object rested approximately 16 cm from the US door, with the head facing the door.

Procedure The subjects were conditioned and tested in two squads of 6 birds each. Each squad was housed in the experimental chambers during alternate 24-h periods. While the males of one squad stayed in the experimental chambers, the subjects in the other

Figure 1. The conditioned stimulus object consisted of a taxidermically prepared female quail head and neck on top of two fiber-filled terry-cloth ovoids. Following conditioning, a male quail will exhibit copulatory responding to such an object that is similar to his behavior with a female quail. From "One-Trial Appetitive Conditioning in the Sexual Behavior System," by S. Hilliard, M. Nguyen, and M. Domjan, 1997, *Psychonomic Bulletin & Review*, 4, p. 238. Copyright 1997 by the Psychonomic Society, Inc.

squad were housed in their colony cages. The birds were exchanged each day 15 min after the first squad's trials were completed. The second squad of the day was given 45 min to acclimate to the experimental chambers before its trials began. The alternate housing procedure commenced 10 days before any experimental treatments in order to habituate the subjects to the experimental chambers and to the handling involved. During the last 5 days of the habituation procedure, all males received three mock trials daily. Mock trials consisted of 2-min presentations of the CS platform (without the CS object), separated from each other by 10–15 min. This was done to habituate the subjects to the noise and movement of the CS platform.

Female quail were placed in the side cages 10 days prior to the experiment and remained there throughout the study. Because they were present at all times rather than just during conditioning trials, the presence of females in the side cages was not a cue for impending copulatory opportunity. The assignment of females to males was rotated across trials so that a given male did not encounter the same female on successive days.

Immediately following the habituation phase, seven conditioning trials were provided, one per day. During each trial, the CS object was lowered to the floor for 2 min. The CS was then raised, and the US door was opened either immediately (for Group Paired, $n = 4$) or 10 or 20 min later (for Groups 10-Trace and 20-Trace, $ns = 4$). The US female remained in the male's chamber for 5 min, during which copulation invariably took place.

Response measures. A video camera recorded the 2 min during which the subjects had access to the CS object. The videotape was scored for three response measures. Approach was measured in terms of seconds spent in the CS zone, a rectangular area (46×42 cm) around the CS delineated by a bright-colored string fixed to the floor. A subject was considered to be "in" the CS zone if at least one foot was seen to cross the string.

The frequencies of mounts and cloacal contact movements directed at the CS object were also counted. While copulating with a female quail, a male bird first seizes the feathers of her neck in his

beak, steps onto her back, and then engages in a complex but highly stereotyped action pattern: He opens his wings, often using them to balance by propping his primary flight feathers against the ground, rocks backwards in a movement that lowers his cloaca and brings it into apposition with the female's, and then displays a rapid "shivering" movement that concludes in a few moments of immobility, still in the wingspread, arched position of copulation. A mount was scored when the subject placed one or both feet on the CS object. If, while standing on the CS object, the subject placed one foot on the floor of the cage or on the plywood base of the object and then replaced it on the object again, this was scored as another mount. A cloacal contact movement was scored when the three copulatory elements (wingspread, back arch, and "shiver") occurred together, regardless of how briefly they were displayed.

One experimenter scored all of the trials, and his data were used for the statistical analyses. A second observer scored every other trial throughout the course of the experiment to obtain estimates of interobserver reliability. Pearson product-moment correlations between the scores of the two independent observers for time in the CS zone, mount, and cloacal contact movement measures were .94, .95, and .97, respectively.

Results

The results of Experiment 1 are summarized in Figure 2. Subjects in Group Paired displayed a rapid increase in their approach to the CS object, reaching an asymptote of approximately 80 sec by the fourth trial. In contrast, Groups 10-Trace and 20-Trace did not display an orderly increase in their approach to the CS object. In fact, after a burst of activity on Trial 2 suggestive of sensitization, mean times near the CS systematically declined across trials in Group 20-Trace.

The data were first evaluated with a 3 (groups) $\times$ 7 (trials) analysis of variance (ANOVA), which showed a significant interaction between groups and trials [$F(12,54) = 2.91, p < .01$]. Subsequent analysis of responding on Trial 7 demonstrated that Groups Paired, 10-Trace, and 20-Trace reached different response levels [$F(2,9) = 8.87, p < .05$]. Post hoc Newman–Keuls comparisons ($p < .05$) showed that whereas the approach scores for Groups 10-Trace and 20-Trace did not differ from each other ($Ms = 9.75$ and 4.75 sec, respectively), each of these groups approached the CS object significantly less frequently than did Group Paired ($M = 78.50$ sec).

Subjects in Group Paired also displayed more mounts of the CS object ($M = 5.43$) than did birds in Groups 10-Trace or 20-Trace ($Ms = 0.07$ and 0.25 , respectively). A group $\times$ trials ANOVA demonstrated that the main effect of group was significant [$F(2,9) = 7.27, p < .05$]. Newman–Keuls post hoc paired comparisons ($p < .05$) showed that subjects in Group Paired mounted the CS object significantly more frequently than those in Groups 10-Trace and 20-Trace, which did not differ significantly from one another.

Only the subjects in Group Paired showed cloacal contact responses toward the CS object. In addition, they also displayed an increase in cloacal contact movements across trials. Analysis of the data showed a significant main effect of trials [$F(6,54) = 2.37, p < .05$], as well as a significant group $\times$ trials interaction [$F(12,54) = 2.37, p < .05$].

Figure 2. Sexual responding to the conditioned stimulus (CS) object by subjects in Experiment 1 that experienced closely contiguous pairing of CS and copulatory access to a female (Group Paired) and subjects that experienced delays of 10 and 20 min between CS and copulatory access (Groups 10-Trace and 20-Trace): (a) mean ($\pm$ SE) seconds spent near the CS object during the CS period; (b) mean ($\pm$ SE) number of mounts of the CS object; and (c) mean ($\pm$ SE) number of cloacal contact movements (CCMs) directed at the CS object.

Discussion

The subjects in Group Paired displayed significant increases in approach and copulatory behavior directed at the CS object. In contrast, systematic increases in approach behavior were not evident in Groups 10-Trace and 20-Trace. The trace groups showed minimal mounting behavior and no cloacal contact responses. These results indicate that the conditioned approach and copulatory responses exhibited by Group Paired reflected primarily associative processes.

Akins, Domjan, and Gutiérrez (1994, Experiment 2) previously reported evidence of learning with a 20-min delay between onset of the CS and presentation of the US female. This learning was manifest in conditioned changes in locomotor activity—crossings between the two halves of an experimental chamber considerably larger than those used in the present experiment. There were many procedural differences between the Akins et al. study and the present experiment. Most importantly, Akins et al. employed a 20-min delayed conditioning procedure, whereas subjects in Group 20-Trace in Experiment 1 encountered a female bird after a 20-min trace interval. Because trace conditioning is notably less effective than delay conditioning, especially at longer trace intervals (Mackintosh, 1974), it is not likely that conditioned locomotor behavior would have been evident in Group 20-Trace even if the chambers employed had been large enough to support such behavior. Whether or not other response measures might have revealed some associative learning with the 10- and 20-min trace intervals, the results of Experiment 1 demonstrate that increases in the behaviors under consideration (approach to the CS object and copulation with it) were a function of associations formed between the CS object and sexual opportunity.

EXPERIMENT 2

If male quail are given access to females, they will copulate repeatedly. The greatest number and rate of copulations appear to be produced by successive presentation of several females one at a time, rather than in a group (Hilliard & Domjan, 1995). Given enough serially presented female quail (8 females presented at 5-min intervals), males will cease copulating altogether, even if a new female is presented following a sexually conditioned CS. We refer to this effect as “sexual satiation.”

In Experiment 2, we tested the effects of sexual satiation on conditioned appetitive and consummatory sexual behavior by allowing the subjects to copulate with 0, 1, 4, or 8 females presented serially prior to a test using the same 3-D CS object employed in Experiment 1.

Method

Subjects. Twelve male Japanese quail, 3.5–9 months old and hatched in the colony at the University of Texas, served as subjects. The birds were pretested for sexual competence in the same way as the birds in Experiment 1. Six of the subjects had no other prior experimental experience; the other 6 had served as noncopulating controls in a prior instrumental conditioning experiment. Thirty-six female quail, at least 3.5 months of age, served as copulation partners.

Apparatus. The subjects were trained and tested in 12 experimental chambers similar to those used in Experiment 1. In the middle of one side wall of each chamber there was a vertically sliding door (the US door) that controlled access to a small chamber in which a female bird (the US) could be placed. The same type of CS object was used as in Experiment 1. During both acquisition and test trials, the CS object was located on the floor approximately 4.5 cm in front of the US door, with the head facing the door, as in Experiment 1. Between trials, a 19-cm² opaque plywood box (the CS box) was lowered over the CS object to hide it from the subject.

Procedure. Throughout the experiment, the subjects were continually housed in the experimental chambers. The experiment began with 8 days of habituation to the chambers. During the last 4 days, eight mock trials (two per day) were conducted, during which the CS box was raised to the ceiling of the chamber. Two minutes later the US door was raised for a moment, and then the US door and the CS box were lowered. During the mock trials, the CS object was not present and a female was not released from the US door. On the last 4 days of the habituation period, the subjects were also handled for 30 sec each day.

Following the habituation phase, the subjects experienced seven acquisition trials, during which the CS object was paired with access to a female quail. An acquisition trial began with the raising of the CS box to allow the subject to see the CS object. After 2 min of exposure to the CS, the US door was raised, releasing a female quail into the chamber for 5 min. Nine of the 12 male subjects invariably copulated with the female.

The day after the seventh acquisition trial, a series of three blocks of satiation test trials were started. Before each satiation test, the subject was confined under a small box. The CS object was then removed from the chamber, both CS box and US door were raised, and the aperture behind the US door was blocked with a clear Plexiglas partition that could be removed to introduce female birds into the chamber. Each subject experienced one of four satiation conditions during the next 40 min. In the 0-female condition (0-fem), the subject remained alone in the test chamber without female quail. In the 1-female condition (1-fem), 1 female was placed in the chamber during the last 5 min of the satiation period. In the 4-female condition (4-fem), 4 females were introduced sequentially into the cage at 5-min intervals during the last 20 min of the satiation period. Previous females were not removed as new ones were introduced. The 8-female condition (8-fem) involved an identical procedure except that twice as many females were introduced sequentially at 5-min intervals throughout the 40 min of satiation. After the satiation period, all the subjects were again confined under a small wooden box, the females were removed, the CS object was returned, the US door was closed, and the CS box was lowered to cover the CS object.

A test trial was then conducted during which each subject's CS box was raised, allowing the male to interact freely with the CS object for 2 min. The delay between the end of the 40-min satiation period and the beginning of the test ranged between 5 and 15 min and did not vary systematically across the different satiation conditions.

Three test blocks were conducted over 12 days, with each subject being tested once a day. During each test block, every subject experienced each of the four satiation conditions (0-fem, 1-fem, 4-fem, or 8-fem) once. In addition, each satiation condition appeared in each ordinal position (1st, 2nd, 3rd, or 4th day) an equal number of times across the 12 subjects.

Between the first test block and the second, two additional conditioning trials were conducted. Between the second and the third test blocks, the subjects experienced three more conditioning trials.

Response measures. Responses were scored from videotaped records of the conditioning and test trials using the same procedures as in Experiment 1. Pearson product-moment interobserver reliability correlations were .99, .97, and .93, respectively, for measures

of time in the CS zone and frequency of mount and cloacal contact responses.

Three of the subjects failed to reliably display mounting and cloacal contact movements during the course of acquisition. Because it is impossible to examine the effect of satiation on a behavior that does not occur, the data from these subjects were omitted from the analyses.

Results

Acquisition. The subjects rapidly learned to approach and remain near the CS object. A one-factor repeated measures ANOVA revealed a significant increase in time spent near the CS across trials [$F(6,48) = 18.74, p < .01$]. Separate ANOVAs revealed that the subjects also rapidly learned to mount the CS object [$F(6,48) = 16.69, p < .01$] and display cloacal contact movements [$F(6,48) = 8.38, p < .01$]. The mean ($\pm SE$) seconds spent in the CS zone, number of mounts, and number of cloacal contact movements at the end of acquisition (Trial 7) were 116.04 (± 2.20), 11.56 (± 1.92), and 3.44 (± 0.93), respectively.

Satiation testing: Multivariate analyses. Responding during the satiation tests was analyzed using a multivariate repeated measures analysis of variance (MANOVA). Due to the small sample size ($n = 9$), we focused on the averaged MANOVA output from SPSS MANOVA (Norris, 1994). The design featured test blocks and satiation conditions as repeated measures and incorporated approach (time in the CS zone), mounts, and cloacal contact movements as the multiple dependent measures.

The MANOVA revealed that there was no significant effect of test block on sexual responding [Pillai's trace = 0.63, $F(6,30) = 2.29, p > .05$]. Nor was there a significant block $\times$ condition effect [Pillai's trace = 0.47, $F(18,144) = 1.47, p > .05$]. However, satiation condition significantly affected responding to the CS object. Across the 0-, 1-, 4-, and 8-fem conditions, there was a significant decrement in overall conditioned responding [Pillai's trace = 0.93, $F(9,72) = 3.57, p < .01$]. These results are summarized in Figure 3.

The averaged F -statistic provided by the MANOVA is advantageous under small sample conditions where power is at a premium. However, the averaged F depends upon meeting the assumption of sphericity that is integral to all repeated measures designs involving three or more levels of an independent variable. Unfortunately, there is no readily available test for sphericity in a repeated measures design featuring multiple dependent measures at each measurement occasion. Accordingly, the approach, mount, and cloacal contact movement scores from the test phase were also examined separately, employing supplemental univariate repeated measures ANOVAs. Univariate repeated measures ANOVAs can easily be corrected for violations of the assumption of sphericity. Using the most rigorous correction available, the Greenhouse-Geisser epsilon (Stevens, 1996), ANOVA revealed no significant effect of test blocks on time spent in the CS zone [$F(1.59,16) = 3.34, p > .05$], nor was there a sig-

Figure 3. Mean seconds spent near the conditioned stimulus (CS) object (a), number of mounts (b), and number of cloacal contact movements (CCMs; c) during successive test blocks as a function of the number of females (0, 1, 4, or 8) introduced before each test in Experiment 2.

nificant blocks $\times$ conditions interaction [$F(3.07, 48) = 2.58, p > .05$]. However, satiation suppressed approach to the CS object, as revealed by an effect of condition [$F(1.72, 24) = 27.33, p < .01$]. The supplemental univariate ANOVAs conducted on mounting and cloacal contact movements showed similar results, in each case revealing a main effect of condition [$F(1.46, 24) = 41.43, p < .01$, and $F(1.09, 24) = 7.12, p < .05$, respectively] and no inter-

action of block with condition. The fact that the supplemental univariate ANOVAs all resulted in significant Greenhouse–Geisser corrected F s for condition suggests that the main effect of satiation condition seen in the MANOVA was not a sphericity-based artifact.

In order to assess the magnitudes of the successive, stepwise decreases in sexual responding (Figure 3) from one satiation condition to the next, post hoc comparisons were carried out with three separate MANOVAs (0 fem vs. 1 fem, 1 fem vs. 4 fem, and 4 fem vs. 8 fem). Overall sexual responding was significantly less frequent in the 1-fem condition than in the 0-fem condition [Pillai's trace = 0.88, $F(3, 6) = 14.05, p < .01$]. However, the decreases in responding from 1-fem to 4-fem and from 4-fem to 8-fem conditions were not statistically significant [Pillai's trace = 0.36, $F(3, 6) = 1.11$, and Pillai's trace = 0.56, $F(3, 6) = 2.56$, respectively, p s $> .05$].

Satiation testing: Conditional probability analyses. Because MANOVA treats the various response measures as an optimally weighted linear composite, it yields only one test statistic for the pooled dependent measures (for a general discussion of multivariate models, see Stevens, 1996). Therefore, MANOVA cannot tell us whether sexual satiation suppressed conditioned copulatory responses more than conditioned approach behavior.

The univariate analyses reported above indicated that both appetitive and consummatory responses were disrupted by sexual satiation. Given that sexual satiation disrupted CS approach, some suppression of mount and copulatory behavior was bound to occur because subjects cannot copulate with an object that they do not approach. A comparison of the effects of sexual satiation on appetitive versus consummatory behavior must take into account reductions in the opportunity to perform the consummatory responses caused by disruptions of approach to the CS.

To adjust the data for this "indirect" effect of satiation through reduced opportunities to make contact with the CS object in the 1-, 4-, and 8-fem conditions, we first calculated the baseline conditional probability of mount responses (and of cloacal contact responses) per second of approach in the 0-fem condition. Because the MANOVA revealed no main effect of test block or interaction between test block and satiation condition, the means for the three test blocks were used in these calculations. The average observed number of mounts (and cloacal contacts) in the 0-fem condition for each subject was divided by the average observed number of seconds spent near the CS by that subject in the 0-fem condition to yield that bird's baseline probability of mounts (and cloacal contacts) per second of approach to the CS. These values were then multiplied by the seconds the subjects spent near the CS in the 1-, 4-, and 8-fem conditions.

The response frequencies obtained by the above calculations represent how many mount and cloacal contact responses were expected to occur in the 1-, 4-, and 8-fem conditions simply as a consequence of reductions in opportunity to contact the CS object—the "indirect" effect

of satiation on mounting (and cloacal contact) behavior. If mount (and cloacal contact) responses were suppressed beyond what we would expect as a result of this "indirect" effect, then we may assume that there is also some "direct" effect of satiation on copulatory responding. Our primary concern was whether this "direct" effect of satiation on mount (and cloacal contact) responses was greater than the effect of satiation on approach to the CS.

To address this concern, the response frequencies adjusted for reduced opportunity for sexual contact were further adjusted to reflect the size of the suppression effect of satiation on approach behavior. To estimate how much CS approach was disrupted in the 1-, 4-, and 8-fem conditions in comparison with the control 0-fem condition, time spent in the 1-, 4-, and 8-fem conditions was divided by time spent near the CS in the 0-fem condition. The frequencies of mounts and cloacal contacts adjusted for response opportunity were then multiplied by these proportions to yield expected frequencies of mounts and cloacal contact responses. These expected frequencies provide conservative estimates of the number of mounts and cloacal contacts that should have occurred if satiation suppresses these responses about as much as it suppresses approach to the CS. (The estimates are conservative because they independently take into account both the "indirect" effect of reduction in physical opportunity to copulate and the magnitude of the effect of satiation on CS approach.)

Figure 4 shows the mean ($\pm SE$) of the observed numbers of mounts and cloacal contact movements that occurred at each level of satiation in comparison with the expected values that were obtained by the above calculations. In each case, the mean obtained values were lower than the mean expected values. To determine whether these differences were statistically significant, the data for each response measure were entered into a 2×3 ANOVA in which data source (predicted vs. obtained) and satiation condition (1, 4, or 8 fem) served as factors. These analyses showed a significant effect of data source for cloacal contacts [$F(1,8) = 5.45, p < .05$]. However, the effect of data source for mounts did not attain conventional levels of significance [$F(1,8) = 3.59, p < .10$]. The source $\times$ condition interaction and the main effect of satiation condition were not significant for either response. These results indicate that conditioned cloacal contact behavior was suppressed by satiation more than conditioned approach to the CS. However, conditioned mounting was not suppressed significantly more than conditioned approach.

Discussion

Exposure to 1, 4, or 8 female quail prior to testing significantly suppressed conditioned sexual responding to the CS object, presumably as a result of a decrease in sexual motivation. This suppression reached nearly its full extent after exposure to only 1 female quail for a period of 5 min; exposure to 4 or 8 female quail did not result in significantly greater suppression of conditioned sexual

Figure 4. Mean ($\pm SE$) expected and obtained number of mount responses (a) and number of cloacal contact movements (CCMs; b) after exposure to 1, 4, or 8 females in Experiment 2. The expected values were frequencies of mount and cloacal contact responses that should have occurred after exposure to 1, 4, or 8 females if sexual satiation directly depressed these responses as much as it depressed approach to the conditioned stimulus (CS). The expected values were corrected for reduced opportunities to contact the CS object caused by reductions in conditioned approach behavior (see text for details).

responding. More importantly, the results of Experiment 2 show that exposure to females suppressed conditioned copulatory behavior (cloacal contact responses) more than conditioned appetitive behavior (approach and proximity to the CS object). Conditioned mount responses were also suppressed by sexual satiation, but in this case the degree of response suppression was not significantly greater than the extent to which satiation suppressed conditioned approach behavior. These results suggest that the last component of the sexual behavior sequence is more easily disrupted by satiation than earlier components.

The present findings are the first demonstration of suppression of *conditioned* sexual consummatory behavior by satiation. Satiation, as well as other US devaluation procedures, is commonly used to determine whether Pavlovian conditioned responses are mediated by a direct association between the CS and the conditioned response (stimulus–response, or S–R, learning) or by an association of the CS with a memorial representation of the US (stimulus–stimulus, or S–S, learning). If devaluation of the US causes suppression of the CR in the absence of further training or extinction of the CS, it is assumed that devaluation must have served to decrease the strength or motivational significance of a memorial US representation, which then supports less conditioned responding (see, e.g., Holland & Rescorla, 1975; Holland & Straub, 1979; Rescorla, 1973; Stanhope, 1992). Earlier reports of the suppression of conditioned appetitive sexual responses by US devaluation suggested that responding by male Japanese quail to a sexually conditioned CS is mediated at least in part by S–S learning (Hilliard & Domjan, 1995; Holloway & Domjan, 1993). The present findings show for the first time that US devaluation, and presumably a change in the memorial representation of the US, also suppresses conditioned consummatory sexual responding. Furthermore, conditioned consummatory behavior is suppressed by US devaluation more than conditioned appetitive behavior.

EXPERIMENT 3

Experiment 3 was conducted to evaluate the generality of the findings of Experiment 2 by using another procedure to attenuate conditioned behavior—extinction. Previous studies (e.g., Domjan et al., 1986) demonstrated that conditioned sexual approach in Japanese quail declines with repeated presentations of the CS alone, in a manner consistent with other Pavlovian conditioned responses. However, the effects of extinction on conditioned copulatory behavior have not been explored, and we do not know whether consummatory aspects of conditioned sexual behavior become extinguished at the same rate as appetitive aspects. In Experiment 3, we employed a procedure that involved both short- and long-term extinction to compare the rates of extinction of conditioned approach and copulatory behavior.

Method

Subjects and Apparatus. The subjects were 12 male Japanese quail, 5–11.5 months of age. Other than a pretest for sexual competence (5 min in the home cage with a female), the birds had no sexual experience prior to the experiment. They were housed, conditioned, and tested in the same experimental chambers that were used in Experiment 2, and the same group of 36 female quail served as sexual partners.

Procedure. The procedures were the same as those of Experiment 2 in all unspecified respects. The subjects were given six acquisition trials (one per day) involving a 2-min presentation of the CS object followed by access to a female quail for 5 min. At the conclusion of the acquisition phase, the subjects received 4 extinction trials on each of the next 8 days, for a total of 32 extinction tri-

als. Each extinction trial involved a 2-min unreinforced presentation of the CS object. The intertrial interval during the daily sessions was about 35 min.

Throughout acquisition and testing, the trials were videotaped and scored for approach (time in CS zone), mounting, and cloacal contact responses by two independent observers, as in Experiments 1 and 2. Interobserver reliability correlations were .98, .97, and .98, respectively.

Results

Acquisition. Acquisition proceeded as in the previous experiments. The subjects quickly learned to display both appetitive and consummatory responses to the CS object. One-factor, within-subjects ANOVAs revealed significant increases in time spent near the CS [$F(5,55) = 25.47, p < .01$], mounting [$F(5,55) = 13.56, p < .01$], and cloacal contact movements [$F(5,55) = 3.48, p < .01$]. The mean ($\pm SE$) seconds spent in the CS zone, number of mounts, and number of cloacal contact movements on Trial 6 were 110.57 (± 5.14), 15.08 (± 2.05), and 4.67 (± 1.40), respectively.

Extinction: Multivariate analyses. To assess the effect of extinction on conditioned sexual responding, the data were analyzed using an averaged MANOVA (as in Experiment 2) incorporating sessions and trials (within sessions) as repeated measures in an 8 (sessions) $\times$ 4 (trials) design. The effect of extinction sessions was not statistically significant [Pillai's trace = 0.39, $F(21,210) = 1.50, p > .05$]. However, conditioned sexual responding decreased significantly across the four trials given each day, as shown by a significant main effect of trials [Pillai's trace = 0.62, $F(9,90) = 2.61, p < .025$]. Sessions did not interact significantly with trials [Pillai's trace = 0.34, $F(63,630) = 1.27, p > .05$]. The effects of the extinction trials are summarized in Figure 5.

As in Experiment 2, supplemental univariate ANOVAs using the Greenhouse–Geisser correction were applied to the approach, mounting, and cloacal contact data. These ANOVAs in each case yielded significant effects of trials [$F(1.91,30) = 5.31, p < .05$, $F(1.66,30) = 14.35, p < .01$, and $F(1.36,30) = 8.22, p < .01$, respectively]. These results suggest that the main effect of trials in the MANOVA was not the result of an artificially inflated F .

To assess the magnitudes of the decreases in sexual responding (Figure 5) from one trial to the next, post hoc comparisons were carried out with three separate MANOVAs. Overall sexual responding was significantly less frequent on Trial 2 than on Trial 1, as demonstrated by a main effect of trial in the first post hoc MANOVA [Pillai's trace = .717, $F(3,8) = 6.75, p < .01$]. However, the decrease in responding from Trial 2 to Trial 3 was not statistically significant [Pillai's trace = .112, $F(3,9) = .378, p > .05$], nor was the decrease from Trial 3 to Trial 4 [Pillai's trace = .425, $F(3,9) = 2.215, p > .05$].

Extinction: Conditional probability analyses. To determine if within-session extinction trials suppressed conditioned consummatory behavior more than conditioned approach to the CS, conditional probability analyses were conducted as in Experiment 2. First, the baseline

Figure 5. Mean seconds spent near the conditioned stimulus (CS) object (a), number of mounts (b), and number of cloacal contact responses (CCMs; c) as a function of trials (1–4) across the eight extinction sessions of Experiment 3.

conditional probability of making a mount or cloacal contact response per seconds of approach to the CS was calculated for each subject using data for extinction Trial 1, averaged across the eight extinction sessions. The conditional probabilities were then used to calculate how many mount and cloacal contact responses should have occurred on extinction Trials 2, 3, and 4 given the reductions in time spent near the CS that occurred on those trials. Finally, these scores were multiplied by estimates of the

size of the extinction effect on conditioned approach behavior, as in Experiment 2. The size of the extinction effect was estimated by dividing time spent near the CS during extinction Trials 2, 3, and 4 by time spent near the CS during Trial 1. The final results of these calculations were the frequencies of mount and cloacal contact movements that should have occurred on Trials 2, 3, and 4 if extinction suppressed these responses no more than it suppressed approach to the CS.

Figure 6 shows the mean ($\pm SE$) of the observed numbers of mounts and cloacal contact movements that occurred on extinction Trials 2, 3, and 4 (averaged across extinction sessions) in comparison with the expected values

Figure 6. Mean ($\pm SE$) expected and obtained number of mount responses (a) and number of cloacal contact movements or CCMs (b) during within-session extinction Trials 2, 3, and 4 in Experiment 3. The expected values were frequencies of mount and cloacal contact responses that should have occurred on Trials 2, 3, and 4 if extinction directly depressed these responses as much as it depressed approach to the conditioned stimulus (CS). The expected values were corrected for reduced opportunities to contact the CS object caused by reductions in conditioned approach behavior (see text for details). Note that the scale of the ordinate in Figure 6b is different from that of Figure 4b.

that were obtained by the above calculations. Each of the obtained values was lower than the expected values. To determine whether these differences were statistically significant, the data for each response measure were entered into a 2×3 ANOVA in which data source (predicted vs. obtained) and extinction trial (2, 3, and 4) served as variables. These analyses showed a significant effect of data source for both mounts and cloacal contacts [$F_s(1,11) = 12.33$ and 11.56 , respectively, $ps < .01$]. The main effect of trials and the source $\times$ trials interactions were not significant. These results indicate that within-session extinction suppressed conditioned mount and cloacal contact responses significantly more than conditioned approach to the CS.

Discussion

Konorski (1967; see also Mackintosh, 1974) distinguished between "acute" extinction procedures, in which an unreinforced CS is presented in massed trials, and "chronic" extinction procedures, in which an unreinforced CS is presented only once a day. The procedure employed in Experiment 2 was designed to reveal the effects of both acute and chronic extinction processes. However, as illustrated by the absence of a main effect of sessions and no interaction of sessions and trials (within sessions) in the MANOVA, 32 unreinforced trials resulted in very little chronic extinction. For instance, on Trial 1 of Day 8 (which was the 29th extinction trial), time spent near the CS, mounting, and cloacal contact movements were preserved at 91%, 74%, and 95%, respectively, of the scores obtained on the last trial of acquisition.

There are few reports of the extinction of conditioned sexual responses with which to compare the present results. Zamble, Mitchell, and Findlay (1986) found that conditioned sexual arousal in rats is significantly decreased by 20 extinction trials administered one per day. Male Japanese quail, trained to approach a red light CS by pairing it with access to a female bird, significantly decrease their responding to the light after 40 daily extinction trials (Domjan et al., 1986). A chronic extinction effect might also have occurred in the present experiment if additional extinction sessions had been conducted.

In contrast to the absence of chronic extinction, acute extinction was clearly evident across the four extinction trials conducted each day. This suppression of responding was primarily the result of Trial 1; further decreases in responding as a result of Trials 2 and 3 were not statistically significant. Konorski attributed the response decrements generated by "acute" extinction to a decrease in motivation or expectancy (Konorski, 1967; see also Zielinski, 1979). Consistent with Konorski's motivational interpretation, responding spontaneously recovered on Trial 1 of each day to a level similar to that observed on the first trial of the preceding day. If we view the acute extinction effects as nonassociative in nature, and if we assume that copulations with the CS object

during extinction produce sexual satiation (copulation with the CS object conforms to a topography that is indistinguishable from copulation with a female quail), then the results of Experiments 2 and 3 may be regarded as two examples of much the same thing—suppression of appetitive and consummatory aspects of conditioned sexual behavior by a decrease in motivation.

The major result of Experiment 3 was that massed, unreinforced exposures to the CS object suppressed conditioned consummatory sexual behavior more than conditioned appetitive behavior. Across Trials 2–4 each day, mounting and cloacal contact movements were suppressed more than approach, even after reductions in the opportunity to contact the CS were taken into account. The obtained frequencies of mounts and cloacal contacts for Trials 2, 3, and 4 were significantly less than what was predicted if massed extinction had suppressed mount and cloacal contact responses to the same extent that it suppressed CS approach.

GENERAL DISCUSSION

A wide range of behavioral, pharmacological, and neurosurgical interventions have been shown to influence appetitive and consummatory behavior differentially. However, in many of these studies, learning was confounded with the appetitive–consummatory distinction because the investigators compared conditioned appetitive behavior with unconditioned consummatory behavior (e.g., Everitt & Stacey, 1987; Hilliard & Domjan, 1995; Holland & Straub, 1979; Pfaus & Phillips, 1991). This confound was avoided in the present experiments by conditioning both appetitive and consummatory sexual responses to a 3-D CS object that elicited minimal responding unconditionally.

In Experiment 1, male Japanese quail that received copulatory opportunity immediately after exposure to the CS object displayed systematic and significant increases in sexual behavior directed toward the CS. In contrast, control subjects that received the US 10 or 20 min after CS onset made virtually no mount and copulatory responses. Although Groups 10-Trace and 20-Trace showed some approach to the CS, their approach behavior had largely dissipated by the end of the experiment. These results indicate that sexual behavior directed toward the CS object was mediated by association of the CS with the US, rather than by context–US associations or sensitization effects (see also Cusato & Domjan, in press).

In Experiment 2, sexual satiation suppressed consummatory sexual behavior (cloacal contact responses) more than appetitive sexual behavior (approach and proximity to the CS object). In Experiment 3, massed unreinforced presentations of the CS object ("acute extinction") decreased both mounting and cloacal contact responses more than approach and proximity behavior. If we agree with Konorski (1967) that acute extinction procedures

exert their effects primarily by motivational mechanisms, both Experiments 2 and 3 are instances in which conditioned appetitive sexual behavior was less sensitive to decreases in sexual motivation than conditioned consummatory sexual behaviors.

Taken together, the results of Experiments 2 and 3 support the traditional distinction between appetitive and consummatory aspects of sexual behavior and allow us to formulate some preliminary conclusions about the structure of the sexual behavior system in quail. Inspired by Timberlake's (e.g., 1990) behavior system perspective, Domjan (1994) proposed that distinct response modes govern general search, focal search, and copulatory behavior in the male Japanese quail. As in Timberlake (1994), these modes were proposed as a way to understand why different temporal arrangements of CS and US may produce very different conditioned response topographies (Akens et al., 1994). The results of Experiments 2 and 3 provide evidence for separate motivational subsystems or "modes" that mediate focal search and copulatory behavior.

Although behavior systems accounts stop short of claiming that modes involve independent motivational mechanisms, some ethological theories have stipulated that different stages in the appetitive-to-consummatory continuum are mediated by distinct endogenous motivations. Classical ethologists emphasized that adaptation may place different demands on initial versus concluding elements of complex chains of behavior. Thus, in reference to Leyhausen's (1975) result, in which cats given the opportunity to kill and eat an unlimited number of mice stopped eating before they stopped killing, and stopped killing before they stopped predatory orientation and approach, Lorenz (1981) proposed that appetitive and consummatory aspects of predatory behavior were motivationally autonomous. He reasoned that because in a natural setting a cat will be forced to stalk more mice than it can actually catch, and perhaps catch more than it manages to kill, appetitive elements of behavior are more abundantly supplied with motivation ("drive") than consummatory elements.

Although Lorenz's (1981) proposal is couched in dated terminology, it captures an important feature of the appetitive-consummatory distinction. The fact that appetitive behaviors are more resistant to satiation than consummatory behaviors is consistent with the idea that the motivational substrates of these two aspects of conditioned sexual behavior are to some extent independent.

The present results are also relevant to the suggestion that consummatory behaviors are more "rigid" and "inflexible" than appetitive responses (Tinbergen, 1951). In Japanese quail, appetitive sexual responses are indeed more easily conditioned than consummatory responses. Male birds quickly learn to approach a wide range of arbitrary localized stimuli if these cues are reliably paired with sexual reinforcement (Domjan et al., 1988; Köksal et al., 1994). Although consummatory sexual behavior can also be conditioned, such learning is limited to CS

objects that have some of the features of a female bird (Cusato & Domjan, in press; Domjan et al., 1992; Domjan et al., 1988). The results of Experiments 2 and 3 show that consummatory sexual responding is also limited to a narrower range of motivational states than appetitive sexual responding.

The present experiments also speak to the nature of Pavlovian conditioned behavior. Pavlovian conditioning was originally conceptualized as the attachment to the CS of a reflex previously elicited only by the US (Jenkins & Moore, 1973; Moore, 1973; Pavlov, 1927). The failure of this view to account for the various CRs that can develop has resulted in more elaborate theories (e.g., Williams, 1981). For instance, Konorski (1967) conceptualized the CR in terms of a dynamic integration of two independently acquired responses ("food" and "hunger" CRs) determined by the preorganized behavior system of the animal. Konorski's view of the CR as the amalgam of multiple conditioning components remains influential, stimulating empirical testing and contemporary theorizing that unite traditional associative accounts of the topography of the CR with behavior systems views (Clelland & Davey, 1982; Davey, Clelland, & Oakley, 1982).

The present findings are also consistent with the view that Pavlovian conditioned behavior consists of the convergent action of multiple, independently formed associations (Holland, 1977, 1979, 1980). To borrow a phrase from Holland and Straub's (1979) work on food conditioning, the results of Experiments 2 and 3 indicate that conditioned appetitive and consummatory sexual behaviors "are to some extent independent and cannot be viewed as forming a unitary conditioned response" to sexually conditioned stimuli (p. 78).

Prior copulation with a female and acute extinction may disrupt consummatory behavior more easily than appetitive behavior through a number of different mechanisms. One possibility is that conditioned approach and copulatory responses to the CS reflect associations with different components of the sexual US, and those US components are differentially devalued by sexual satiation. (For a similar argument concerning food conditioning, see Holland and Straub, 1979.) The female bird used in the present experiments as the US provides both visual and tactile stimuli. Approach behavior in males is stimulated by the visual aspects of the female (Domjan & Hall, 1986). In contrast, copulation is probably a response to tactile stimulation arising from contact with the female, since mounting is invariably preceded by a neck grab. Sexual satiation might devalue the tactile component of the US more than its visual features, or it may devalue a specific aspect of those visual features that is not involved in approach. The visual cues provided by a female quail at a distance (upon first encounter) are not the same as the visual cues she affords to a male quail that is in very close contact with her (during copulation). Thus, the visual stimulus that elicits approach may be substantially different than the visual stimulus that is devalued

by persistent copulation, and the hedonic value of the former may be relatively unaffected by devaluation of the latter. In addition, during the close, physical interaction that characterizes copulation, tactile cues may take precedence and be more salient, and thus more subject to devaluation, than visual cues. This may be why sexual satiation disrupts conditioned copulatory behavior more than conditioned approach behavior.

Another possibility is that conditioned approach and conditioned copulation are mediated to different degrees by S–R and S–S associations. Holland (1977, 1979, 1980) suggested that CS–US relations result in “two quite independent types of conditioned behavior to the CS—a response appropriate to the US, perhaps as a consequence of a stimulus substitution process (e.g., Mackintosh, 1974), and enhancement of the orienting response originally elicited by the CS” (1979, p. 431). Holland based this proposal in part on the observation that certain “early” components of the CR antecedent to food delivery were less influenced by the nature (food vs. sucrose) and the magnitude of the US than “later” components. It is possible that, in the sexual behavior system of Japanese quail, conditioned appetitive behavior arises in part from enhancement of the original orienting response to the CS through an S–R mechanism that is relatively unaffected by US devaluation. In contrast, conditioned consummatory behavior may reflect US-relevant responses largely through S–S associations.

A third possibility worth considering is that appetitive behavior was less disrupted than consummatory behavior because the subjects approached the CS to some degree as an unconditioned or sensitized response. The extent to which the CS elicited approach nonassociatively may be estimated from the behavior of Groups 10-Trace and 20-Trace in Experiment 1. At the end of Experiment 1 (which is comparable to when the test sessions were conducted in Experiments 2 and 3), Groups 10-Trace and 20-Trace exhibited no mount or cloacal contact responses, but they spent a mean ($\pm SE$) of 7.25 sec (± 3.41) near the CS object during a 2-min period. However, this was much less than the CS approach behavior of the subjects in Experiment 2 after copulating with 1 or more females (overall mean = 46.40 sec, ± 5.22) or the approach behavior of the subjects in Experiment 3 after one or more acute extinction trials (overall mean = 92.51 sec, ± 2.12). These data suggest that the residual CS approach responding that occurred in Experiment 2 after female exposure and in Experiment 3 after acute extinction was associatively mediated.

We have examined the present results from two different perspectives: as the result of functional independence of the mechanisms that supply motivation for appetitive and consummatory responding, and as the consequence of multiple associations determining complex CR topography. These two perspectives are not mutually exclusive. That is, approach and proximity behaviors and copulation may be mediated by relatively independent motivations, as suggested by behavior systems accounts (Tim-

berlake & Silva, 1995), and they may also be conditioned by the US through distinct mechanisms, as proposed by some associationist theories (Holland, 1977, 1979, 1980).

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