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The Cognitive Animal

Empirical and Theoretical Perspectives on Animal Cognition

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12 Cognitive Modulation of Sexual Behavior

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Were it not for sexual behavior, you and I would not be here, nor would many animal species. Given its critical role, it is not surprising that sexual behavior is multiply determined. Hormonal and neuroendocrine processes mediate sexual motivation or readiness to respond to environmental sexual stimuli. These responses are in turn mediated by both preprogrammed instinctive mechanisms as well as learning and memory.

The role of learning and memory in the control of sexual behavior has been recognized for a long time. For example, Craig (1918, p. 100) noted that “the sexual tendency is . . . directed, *with much guidance by experience*, toward securing the stimulation required for discharging the sexual reflex” (emphasis added). However, only recently have the precise learning mechanisms involved in sexual behavior been empirically documented. These more analytic empirical studies have also helped to identify a number of cognitive factors involved in sexual conditioning. The evidence suggests that sexual behavior is delicately tuned by learning and memory mechanisms that shape both the stimulus control and the effectiveness of sexual responses.

Conditioning of Sexual Anticipatory Behavior

In many situations, learning is manifest in the development of anticipatory behavior. The proverbial Pavlovian dog salivates in anticipation of the presentation of food. Rats freeze in anticipation of painful stimulation, and pigeons peck a lighted key that signals brief access to grain. Conditioned anticipatory behavior is also readily evident in sexual situations.

Conditioned anticipatory behavior has been examined most extensively in male domesticated quail (*Coturnix japonica*). Male quail learn to approach a localized stimulus (a light, for example) that is presented shortly before each time

they receive access to a sexually receptive female. In such situations, the light is referred to as the conditioned stimulus or CS, and access to the female serves as the unconditioned stimulus or US. The development of sexually conditioned approach behavior requires the pairing of the conditioned stimulus with copulatory opportunity (Domjan et al. 1986). Beyond that requirement, however, the learning occurs under a remarkably wide range of circumstances. Conditioned approach behavior develops, for example, even if the conditioned stimulus is presented more than 2 m away from the location of a female that provides copulatory opportunity (Burns and Domjan 2000) and even if contingencies are introduced so that the CS is followed by the US only on those trials when the subject fails to make the conditioned response (Crawford and Domjan 1993).

Under special circumstances, sexual conditioning can also result in conditioned copulatory responses directed toward the conditioned stimulus. Copulation in quail consists of the male grabbing the back of the female’s head and/or neck feathers (the grab response), mounting the female’s back with both feet (the mount response), and making cloacal thrusts that bring the male’s cloaca in contact with the female’s (cloacal contact responses). Conditioned grab, mount, and cloacal contact responses occur if the CS is a three-dimensional object that can support copulatory behavior. Figure 12.1 shows an example of such behavior. The conditioned stimulus in this study was a terrycloth object that included a taxidermically prepared head and some neck feathers of a female quail. The pairing of such a CS object with copulatory opportunity results in conditioned grab, mount, and cloacal contact responses if the conditioning trials involve a relatively short interval between the CS and the US (e.g., Akins 2000; Cusato and Domjan 1998).



Figure 12.1

Male quail performing a conditioned grab, mount, and cloacal contact response on a conditioned stimulus object that includes a taxidermically prepared head and partial neck feathers of a female quail.

Sexually conditioned behavior shows many features common to a conditioned responses, including acquisition, extinction, retention, blocking, stimulus discrimination, trace conditioning, second-order conditioning, and conditioned inhibition (Akins and Domjan 1996; Crawford and Domjan 1995, 1996; Domjan et al. 1986; Köksal et al. 1994). To the extent that these features of Pavlovian conditioning reflect cognitive mechanisms, one may assume that cognitive mechanisms also occur in the sexual behavior system.

Stimulus-Response vs. Stimulus-Stimulus Learning

The development of an anticipatory conditioned response suggests that cognitive processes are involved in sexual behavior. However, the complexity of the underlying cognitive mechanisms is not revealed by a simple demonstration of sexual conditioning. In particular, the fact that a male quail responds to a signal for a female does not mean that it is doing so because the signal activates a representation of the female. It may be that the signal or CS automatically activates the conditioned response without activating a representation of the female that serves as the US.

In the Pavlovian conditioning literature, whether a CS activates a conditioned response directly or by first activating a representation of the US is addressed in terms of the distinction between stimulus-response (S-R) and stimulus-stimulus (S-S) learning. An S-R association is one in which the CS automatically elicits the conditioned response, without activating a representation of the US. Thus, an S-R association involves minimal cognitive processing. In contrast, an S-S association is one in which the CS first activates a representation of the US and the conditioned response is a manifestation of this activated representation. Only if sexual conditioning reflected S-S learning could one conclude that the sexual conditioned response reflects cognitive anticipation of the forthcoming sexual encounter.

S-R learning can be distinguished empirically from S-S learning on the basis of manipulations intended to alter the value or attractiveness of the anticipated event or US after conditioning has taken place (e.g., Holland and Rescorla 1975). If the US is food, for example, the attractiveness of the US may be reduced by conditioning an aversion to the food or by making the subjects not hungry. If the conditioned re-

sponse reflects the cognitive anticipation of food, then procedures that reduce the value or attractiveness of food should reduce the vigor of the conditioned response. In contrast, if the vigor of the conditioned response is not changed by reducing the value or attractiveness of food, then one may conclude that the conditioned response is generated by an S-R mechanism and does not reflect anticipatory cognitions about food.

The available evidence indicates that conditioned sexual behavior is mediated by S-S rather than S-R mechanisms. Thus, conditioned sexual behavior appears to involve the activation of a cognitive representation of the female that is signaled by the CS. In one experiment, for example, Holloway and Domjan (1993) first established a sexually conditioned approach response by pairing a CS with access to a female with whom the males could copulate. The value or attractiveness of the female was then reduced by reducing the sexual motivation of the subjects. This was accomplished by restricting their exposure to light from 16 hours a day to 6 hours a day. Testosterone production (and concomitant sexual motivation) was disrupted by this restricted exposure to light. The reduced sexual motivation (and interest in females) produced a corresponding reduction in the sexually conditioned approach behavior. Conditioned responding was restored when the photoperiod was returned to 16 hours a day.

Subsequent experiments confirmed these findings with direct manipulations of serum testosterone levels and showed that reduced sexual motivation affects sexually conditioned behavior, but does not affect responding conditioned with a food US (Holloway and Domjan 1993). These results indicate that sexually conditioned behavior is mediated by cognitive anticipation of the female that was previously paired with the CS. Alterations in the attractiveness of the female produce corresponding changes in sexually conditioned behavior.

Further evidence of the role of S-S mechanisms in sexual conditioning has been obtained by Hilliard and Domjan (1995), who showed

that sexual satiation also reduces sexual conditioned approach behavior. In a subsequent study, Hilliard et al. (1998) tested the effects of sexual satiation on conditioned responses to a three-dimensional CS object that supported both conditioned approach and conditioned copulatory responses. Sexual satiation reduced both types of conditioned responses, but not to the same extent. Conditioned copulatory responses (mounts and cloacal contacts) were suppressed more by sexual satiation than was conditioned approach behavior.

One interpretation of these results is that S-S mechanisms (or activated representations of a female) have a greater role in conditioned copulatory responses than they do in conditioned approach behavior. Thus, Hilliard et al.'s (1998) findings suggest that cognitive mechanisms may be more important in the control of copulatory or sexual consummatory behavior than they are in the control of approach or appetitive responses that are a precursor to copulation.

Temporal Encoding in the Control of Sexual Anticipatory Behavior

Perception of time is a traditional area of animal cognition (Gibbon and Allan 1984). Most studies of animal timing or temporal coding have been conducted with food and aversive USs. Recent evidence indicates that temporal factors are also important in the control of sexual anticipatory behavior. Furthermore, some of the temporal relations that have been obtained in sexual conditioning are similar to those that have been documented in more conventional learning situations.

Important evidence of the temporal control of sexual anticipatory behavior was first obtained by Akins et al. (1994) in a study of the CS-US interval in sexual conditioning. Male quail received a training procedure in which a CS was presented for either 1 or 20 minutes immediately before access to a sexually receptive female. One conditioning trial was conducted each day, for a

total of 15 trials. Control groups received the CS and US in an unpaired fashion. The CS (a foam block) was presented at one end of an experimental chamber that was unusually large (1.2×1.8 m). With such a large chamber, approach to the CS could be easily distinguished from nonlocalized locomotor behavior or pacing. Approaching the location of the CS may be considered to be a form of focal search for a potential sexual partner. In contrast, pacing from one side of the experimental chamber to the other may be considered to be akin to a non-localized general search response. The short and long CS-US intervals selectively activated these two types of behaviors. Subjects that received the 1-minute CS-US interval came to approach the CS as learning progressed. In contrast, subjects that received the 20-minute CS-US interval developed pacing behavior as the conditioned response. These results were confirmed in a subsequent study by Akins (2000).

These findings are unusual because they contradict the common assumption that learning is disrupted by increasing the CS-US interval. Rather, they indicate that different conditioned responses are activated by short in contrast to long CS-US intervals. Based on extensive analyses of the temporal organization of the behaviors involved in foraging for and eating food, Timberlake (2001) suggested that short and long CS-US intervals activate different response modes. Signals that occur just before an animal encounters food are presumed to activate focal search and food-handling response modes. In contrast, signals that are more remotely related to food are presumed to activate a general search mode. Whether the CS approach and pacing responses identified by Akins et al. in sexual conditioning reflect focal search rather than general search modes is speculative. Nevertheless, the development of different conditioned responses indicates that the subjects encoded the temporal differences between the short and long CS-US intervals.

Further evidence for the importance of temporal factors in sexual anticipatory behavior was

recently reported by Burns and Domjan (2001). Unlike Akins et al. (1994), who focused on effects of the CS duration, Burns and Domjan examined how conditioned sexual behavior is influenced by the temporal context in which a given CS duration is presented. In particular, they focused on the ratio of the duration of exposure to the experimental context (C) compared with the duration of the conditioning trial (T) or conditioned stimulus. Studies with both food and aversive USs had shown that conditioned responding is an increasing function of the C/T ratio (see Gallistel and Gibbon 2000 for a review). Burns and Domjan found that sexually conditioned CS approach behavior is also directly related to the C/T ratio. Subjects that are conditioned with a high C/T ratio spend more time near the CS.

In addition to measuring CS-directed conditioned behavior, Burns and Domjan (2001) also measured conditioned behavior directed toward the location of the US (goal tracking). Unlike CS-directed behavior, US-directed conditioned behavior was inversely related to the C/T ratio. The contrasting effects of the C/T ratio on CS-directed and US-directed conditioned behavior are unprecedented in the literature. Furthermore, both findings provide evidence that conditioned behavior reflects encoding of not just the duration of the conditioned stimulus but also the relation between the CS duration and the duration of exposure to the contextual cues in which the CS is embedded.

Modulation of Responding to Sexual Sign Stimuli

As we have seen, depending on temporal factors, sexual anticipation established through Pavlovian conditioning can be manifest in different types of responses elicited by the conditioned stimulus. Another consequence of sexual anticipation is that it enhances responding to the sexual sign stimuli that are provided by a copu-

lation partner. In fact, this modulation of responding to sexual sign stimuli may be of greater functional significance than CS-directed conditioned behavior.

Early evidence that sexual anticipation can enhance responding to sexual sign stimuli was obtained by Zamble et al. (1985) in male rats. In one experiment, for example, the CS was provided by placing the subjects in a plastic tub before exposing them to a receptive female. Sexual conditioning of the CS did not elicit readily identifiable conditioned responses. However, males exposed to the CS just before being allowed to copulate with a female achieved ejaculation significantly faster. Thus, exposure to the CS enhanced the effectiveness of the sexual sign stimuli that were provided by the female copulation partner. Similar facilitation of copulatory behavior in response to a sexual partner has been obtained in studies with male Japanese quail (Domjan et al. 1986).

The increased effectiveness of sign stimuli for sexual behavior engendered by sexual anticipation is clearly illustrated by studies in which only partial sexual sign stimuli are presented. Experiments of this sort have been conducted with male Japanese quail. The sexual behavior of male quail can be triggered by the visual cues of a receptive female, even if those visual cues are provided by a taxidermic model of a female. Partial sign stimuli can be constructed by providing exposure to just the head and neck of a female. Ordinarily, such head and neck cues are not sufficient to elicit sexual behavior on the part of most male quail. However, the limited cues of a female's head can elicit substantial approach and copulatory responses if those sign stimuli are presented in the presence of contextual cues that were previously associated with copulation with a live female.

In the first study of this effect (Domjan et al. 1989), males were alternatively housed in an experimental chamber and in their home cages. One group was allowed to copulate with a female on 15 occasions in the experimental cham-

ber; the other subjects received these copulatory opportunities in their home cage. All of the subjects were then tested with a head and neck model of a female in the experimental chambers. Significantly more grab, mount, and cloacal contact responses were elicited by the female head and neck cues in subjects for whom the experimental chamber had been paired with sexual reinforcement. A subsequent study demonstrated that such enhanced responding to sexual sign stimuli can develop with just one context conditioning trial (Hilliard et al. 1997).

Enhanced responding to the sign stimuli provided by a sexual partner has been also demonstrated in a fish species, the blue gourami (Hollis et al. 1997). A light served as the CS, and conditioning consisted of presenting the light for 10 seconds paired with visual access to a sexual partner. (The CS and US were presented unpaired for a control group.) After 18 daily conditioning trials, the barrier separating the male and female was removed after the CS presentation to enable the fish to engage in their full range of reproductive behavior responses.

The most significant data in the experiment were not provided by what occurred during the CS, but by what occurred when the male and female were allowed to interact after the CS. The results indicated that prior exposure to the CS facilitated the reproductive interactions of the male and female (by decreasing aggressive responses and increasing nesting and copulatory responses) and resulted in significantly more offspring being produced. Related studies with quail have shown that exposure to a sexually conditioned stimulus increases sperm output (Domjan et al. 1998) and results in greater numbers of fertilized eggs (Domjan 2000).

Observational Conditioning of Sexual Behavior

Additional evidence of cognitive modulation of sexual behavior is provided by studies demonstrating observational conditioning of sexual

behavior (Köksal and Domjan 1998). In these experiments, a terrycloth object was presented as the CS and paired with the release of a sexually receptive female from a side cage. Male quail in an experimental group were permitted to observe this sequence of events from the other side of a wire mesh barrier on 12 occasions. Conditioning trials were then continued, but now with the observers allowed to interact with the CS object and copulate with the female that was released after the CS presentation. The acquisition of approach to the CS object was measured during this second phase. Males that previously received observational conditioning acquired the conditioned approach response faster than subjects in a control group that observed the CS and US in an unpaired fashion. These results suggest that the observation of a CS paired with the sight of a receptive female is sufficient to establish an association between these events.

Further evidence of observational learning in sexual situations has been obtained by Galef and White (1998), who showed that female quail increase their preference for a male as a result of seeing that male copulate with another female. In contrast, males that observe a female mating with another male show reduced preference for that female (White and Galef 1999a; see also White and Galef 1999b, 2000).

Conclusion

The results of sexual conditioning experiments provide substantial evidence of cognitive mediation of sexual behavior. Sexual anticipatory behavior becomes readily established in male quail and other species through Pavlovian pairings of a signal with sexual reinforcement. Evidence indicates that the conditioned sexual behavior is mediated by activation of a representation of the potential sexual partner. The sexual anticipatory behavior also reflects temporal coding of the duration of the conditioned sexual signal and the relation between the signal's duration and the duration of exposure to the context in which

the CS is presented. Sexually conditioned stimuli modulate the effectiveness of the species' typical sign stimuli that are provided by a sexual partner. Further evidence of cognitive mediation is provided by demonstrations of the conditioning of sexual behavior by observation.

Taken together, these findings suggest that sexual behavior is not an automatic outcome of exposure to sexual sign stimuli provided by a potential sexual partner. Rather, the effectiveness of these stimuli is fine tuned by contextual cues, temporal factors, and learning and memory of previous sexual experiences. As Craig (1918) surmised nearly a century ago, sexual behavior is "directed, with much guidance by experience."

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