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Conditioning and Sexual Behavior: A Review

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Sexual behavior is directed by a sophisticated interplay between steroid hormone actions in the brain that give rise to sexual arousability and experience with sexual reward that gives rise to expectations of competent sexual activity, sexual desire, arousal, and performance. Sexual experience allows animals to form instrumental associations between internal or external stimuli and behaviors that lead to different sexual rewards. Furthermore, Pavlovian associations between internal and external stimuli allow animals to predict sexual outcomes. These two types of learning build upon instinctual mechanisms to create distinctive, and seemingly "automated," patterns of sexual response. This article reviews the literature on conditioning and sexual behavior with a particular emphasis on incentive sequences of sexual behavior that move animals from distal to proximal with regard to sexual stimuli during appetitive phases of behavior and ultimately result in copulatory interaction and mating during consummatory phases of behavior. Accordingly, the role of learning in sexual excitement, in behaviors that bring about the opportunity to mate, in courtship and solicitation displays, in sexual arousal and copulatory behaviors, in sexual partner preferences, and the short- and long-term influence of copulatory experience on sexual and reproductive function is examined. Although hormone actions set the stage for sexual activity by generating the ability of animals to become sexually excited and aroused, it is each animal's unique experience with sexual behavior and sexual reward that molds the strength of responses made toward sexual incentives.

Key Words: **learning; motivation; Pavlovian; Operant; sexual desire; sexual arousal; copulation.**

For successful copulation to occur, animals must be able to respond to hormonal and neurochemical changes that signal their own sexual desire and arousal, to identify external stimuli that predict where potential sex partners can be found, to actively seek out or work to obtain sex partners, to distinguish external chemosensory cues or behavioral patterns of potential sex partners from those that are not sexually receptive, and to pursue desired sex partners once sexual contact has been solicited. At each step, animals depend not only on the perception of their own internal state, but on an accurate prediction of external events. Such predictions are based on experience, both with the relation between external and internal stimuli and the relation of these stimuli to their sexual consequences. Such experience makes sexual behavior appear competent and "automated." Thus, the development of successful sexual behavior involves not only important neuroendocrine changes that begin at puberty, but also psychological and social influences that occur both before and after puberty.

Although the contribution of experience and learning to the expression of sexual activity has long been recognized (Ågmo, 1999; Freud, 1905; O'Donohue and Plaud, 1994; Pavlov, 1927; Stendahl, 1821/1959; Watson, 1925), it has not been well understood. Larsson (1956) was one of the first to describe the role of copulatory experience in sexual behavior, although others (e.g., Stone, 1922; Beach, 1942) had made significant observations about the role of different kinds of sensory experience in rat sexual behavior. In humans, Krafft-Ebing's *Psychopathia Sexualis* (1929) was explicit in delineating how paraphilias were almost always reinforced by sexual arousal or genital gratification. These observations beg several questions: How much of what is considered "normal" about human sexual behavior is likewise reinforced by genital gratification? What do humans or other animals really learn about sexual arousal, copulation, and gratification? Are certain kinds of external stimuli more easily associated with sexual arousal than others? Can conditioning compensate for disruptions of neuroendo-

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crine or sensory functioning? Are there long-term changes that occur as a function of sexual stimulation? This article addresses these questions by examining how both classical (Pavlovian) and operant (instrumental) conditioning conspire to direct particular sexual and copulatory responses of males toward primary and conditioned sexual incentives. We include work from our own laboratory on the role of sexual experience in the formation of different sexual behaviors and copulatory partner preferences and in the ability of males to retain normal sexual functioning following surgical, hormonal, and drug treatments that disrupt sexual behavior. This article also ties sexual learning into a more general framework of incentive motivational theory (Bindra, 1974, 1978; Toates, 1986, 1998).

FORMS OF LEARNING

Learning processes are relatively permanent changes in behavior or the potential for behavior which occur as a result of experience (Flaherty, 1987; Kimble, 1961; Pearce, 1997). Although it is not our central goal to distinguish between different types of learning processes, it is necessary to briefly describe the forms of learning that have been implicated in sexual behavior.

Experience early in life that has a latent effect on subsequent sexual behavior has been termed sexual imprinting (Bateson, 1978a,b). As with other forms of imprinting (see Lorenz, 1970), the exact nature of associations and reinforcement contingencies involved in this type of learning are not well understood. However, it has been argued that imprinting follows contingency rules similar to those important for classical conditioning (Hollis, ten Cate, and Bateson, 1991).

When an association is formed between two stimuli, the type of learning is termed classical or Pavlovian conditioning. As described originally by Pavlov (1927), and later by Kimble (1961), Macintosh (1974), and Rescorla (1980, 1988), when an initially neutral stimulus (one that does not elicit the specific behavioral response) is paired with a second unconditioned stimulus (UCS) that unconditionally elicits the specific behavioral response, the neutral stimulus will gain the ability to elicit a conditioned response (CR) by itself, with the previously neutral stimulus now becoming a conditioned stimulus (CS). The CR does not necessarily have to be exactly the same as the UCR, but can serve to prepare the organism for the performance of the UCR (see, e.g., Hollis, 1984). Thus, a mate can be conceived as an array of stimuli, some of which will unconditionally elicit sexually relevant responses and others of which will not. With sexual experience, initially ineffective stimuli become associated with behaviorally significant ones and thereby come to elicit sexually relevant responses. Second, initially neutral stimuli that are arbitrary and separated physically from the UCS can, through contiguous pairings, come to elicit sexually relevant responses.

Instrumental learning is said to occur when there is a change in the frequency or effectiveness of a behavioral response as a result of contingent reinforcement or punishment (Ferster and Skinner, 1957; Kimble, 1961; Macintosh, 1974; Skinner, 1938). Response-contingent reinforcement (either "positive" in which an animal moves toward a reward or "negative" in which an animal moves away from an aversive event) increases the frequency of behavioral responses. Response-contingent punishment decreases the frequency of behavioral responses. Traditionally, it has been assumed that operant learning is the result of an association between a behavioral response and its consequences, i.e., response–outcome associations are formed (Thorndike, 1911). Several variants of instrumental conditioning are of interest to the study of sexual behavior. For example, successful mounting and intromitting appear to be reinforced by sensory feedback; performance of arbitrary responses can be positively reinforced by mate presentation; and behavioral responses may be diminished by the removal of sexual partners or sexual reward, such as intromission or ejaculation.

We adopt a neural perspective in this article. In such a perspective, it is the *neural representations* of stimuli and events that are paired (e.g., Pavlov, 1927) rather than the events themselves. Consider a male rat exposed to a sexually receptive female bearing a neutral odor (e.g., almond). The representation of the CS is relatively easy to define as the neural activity generated by the odor. The representation of the UCS is the pattern of neural stimulation generated by salient features of the female as well as those generated by feedback from copulatory stimulation. In a simple conditioning trial in which the male is allowed to copulate with the female, there are multiple UCSs that evoke separate aspects of behavior and that are paired with the CS. Further, the context in which the encounter occurs may also gain control over behavior if its neural representation is paired with that of the sexual UCSs. Thus, a high degree of plasticity exists in the generation of sexually relevant conditioned stimuli.