

# 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. © 2001 Academic Press

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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.

## WHAT IS A SEXUAL RESPONSE?

Sexual behavior in mammals is a sequence of behavioral responses that includes, but is not limited to, copulation (Ågmo, 1999; Everitt, 1990; Pfaus, 1996, 1999). Animals must respond to a variety of internal and external stimuli that trigger their own sexual desire and signal that of a potential mate. Many of these stimuli are present in the absence of a mate and are important for finding a mate as well as eliciting sexual arousal (defined as increased genital blood flow) and sexual excitement (defined as heightened locomotor activity in anticipation of sexual contact). Other stimuli are derived from a potential mate and may lead to sexual arousal, elicit sexual excitement, or initiate copulatory interactions. An animal's ability to respond appropriately to such stimuli requires not only innate mechanisms, but also a great deal of flexibility in order to learn what stimuli are useful predictors of copulatory success or failure. Although copulation is an unambiguous sexual behavior, it is important to emphasize that it is not the only behavioral sequence that is sexual.

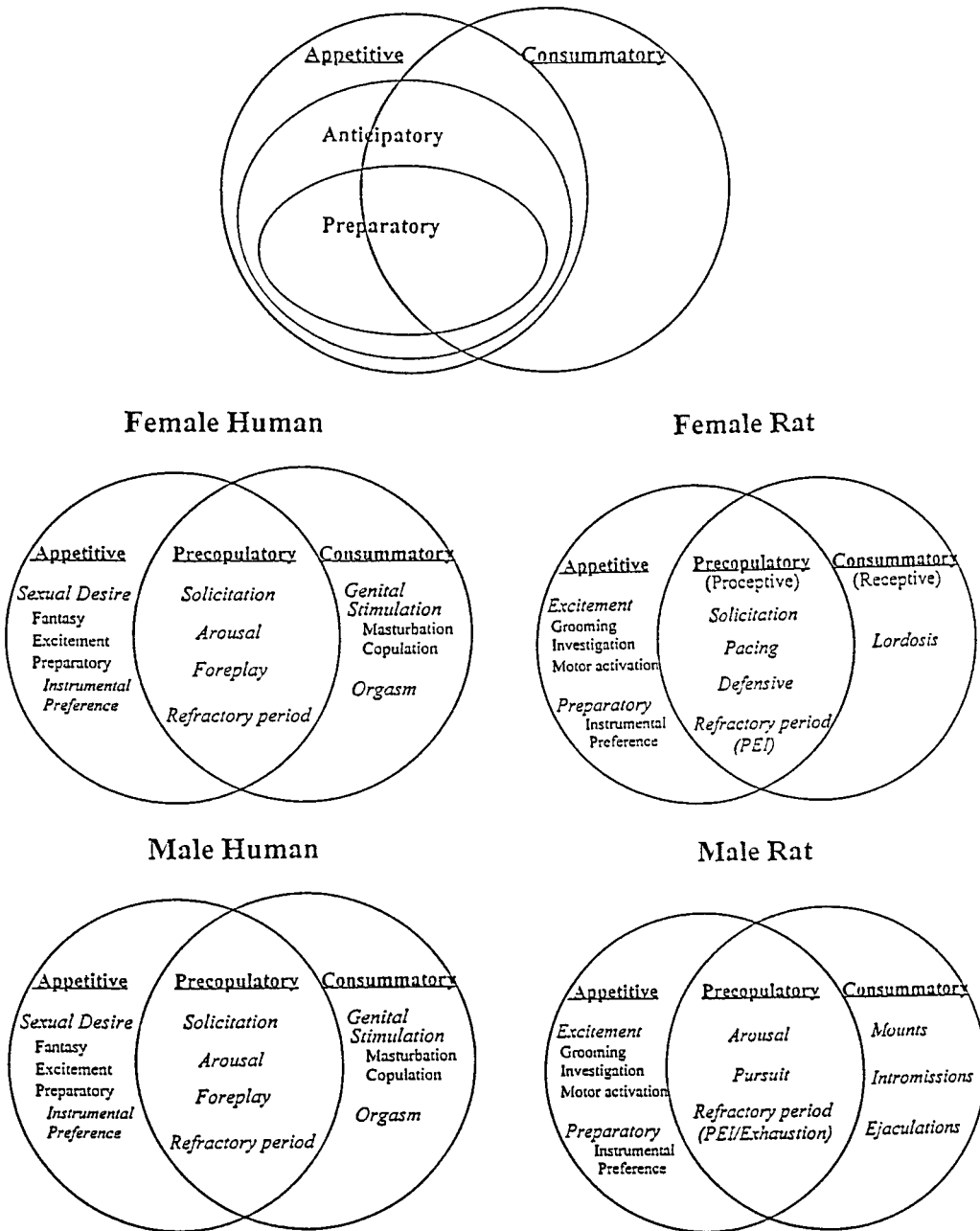
Differentiating sexual behavior from nonsexual behavior can be difficult. The goal here is not to provide a definitive list of behaviors that may be classified as sexual or otherwise, but rather to offer criteria that have an appropriate and meaningful scope. For the purpose of the present article, sexual behaviors are those that are motivated by the desire for, and are reinforced or punished by, copulatory responses. We have found it useful heuristically to conceive of sexual behaviors moving in sequences of responses made to different incentive cues, from distal to proximal to interactive (Pfaus, 1996, 1999). These incentive sequences are viewed as overlapping Venn diagrams (Fig. 1) that comprise the appetitive phase of sexual behavior (behaviors that denote sexual excitement and arousal), the precopulatory phase of behavior (behaviors such as solicitation and courtship), and the consummatory phase of sexual behavior (copulatory responses). Accordingly, we review the empirical evidence regarding the influence of different types of learning on the elicitation of sexual excitement, on behaviors that bring about the opportunity to mate, on courtship and solicitation displays, on sexual arousal and copulatory behaviors, on sexual partner preferences, and the influence of copulatory experience on subsequent sexual and reproductive function.

## INFLUENCE OF LEARNING ON SEXUAL EXCITEMENT

Before an actual sexual encounter, anticipatory responses are often performed with great vigor and excitement in the presence of stimuli that are predictive of such encounters (Pfaus, 1996, 1999). For example, Mendelson and Pfaus (1989) found that male Long-Evans rats will increase the number of level changes made in a bilevel chamber in anticipation of a conspecific if they have previously received access to a sexually receptive female in the bilevel chamber. Males given access to nonreceptive females in bilevel chambers (with intervening access to receptive females in unilevel chambers) failed to develop this behavior. Following the establishment of increased anticipatory level changing in trials with sexually receptive females, this response was extinguished if males received access to no conspecific during the subsequent trials in bilevel chambers, but not if males received access to a nonreceptive female (Mendelson and Pfaus, 1989). The reason for this apparent contradiction in the development and maintenance of conditioned sexual excitement is unclear.

Conversely, Van Furth and Van Ree (1996b) found that male albino Wistar rats exposed to bilevel chambers with either receptive females, nonreceptive females, or no female displayed increased anticipatory level changing. However, in this study, the development of anticipatory level changing was disrupted by anosmia produced by zinc sulfate infusions into the nasal cavity. Based on these results, Van Furth and Van Ree concluded that olfactory stimuli from animals copulating previously in the bilevel chambers are a critical determinant in the development of anticipatory level changing in male Wistar rats. Consistent with this hypothesis is the finding that neurochemical responses to estrous odors in the male rat sensitize with repeated exposure (Mitchell and Gratton, 1991).

The reasons for the discrepancies between these studies is unclear. In both studies, sexually experienced males were examined and the chambers were not cleaned between trials. One possibility is that strain differences contributed to the differences in results. Wistar rats appear to display more robust responses to sex-related odors than do Long-Evans rats (Carr, Loeb, and Dissinger, 1965; Lydell and Doty, 1972; Merkx, 1983; however, see Sachs, 1996, for a failure of estrus odors to induce noncontact penile erections in Wistar albino males relative to pigmented Long-Evans males). However, relative to Long-Evans, Wistar rats have poorer vision and rely more



**FIG. 1.** Incentive sequences for the sexual behavior of humans and rats. In this scheme, the appetitive and consummatory phases of behavior are conceived as two overlapping Venn diagrams in which the overlap defines a class of precopulatory behaviors. The behavioral stream moves from left to right and then back again during consummatory interaction in which behavior occurs in bouts (e.g., copulation in the rat). Three types of appetitive responding reflect relative degrees of learning and necessity. Preparatory behaviors are learned responses that animals *must* make in order to acquire the incentive (e.g., operant behaviors and pursuit); anticipatory behaviors are learned responses that occur in anticipation of the incentive, but are not necessary to obtain it (e.g., conditioned psychomotor stimulation); and unlearned appetitive responses also exist that are instinctual (e.g., unconditioned anogenital investigation). Appetitive responses are generally more flexible than consummatory responses which are more stereotyped, species-specific, and sexually differentiated. Adapted from Pfaus (1999).

heavily on olfactory stimuli (e.g., Boyes and Dyer, 1983; Creel, Dustman, and Beck, 1970; Dyer and Swartzwelder, 1978). Alternatively, in the Mendelson

and Pfaus (1989) experiment, males trained with non-receptive females were allowed to copulate with receptive females between each trial in unilevel cham-

bers; this procedure was not followed in the Van Furth and Van Ree (1996b) study. Thus, males in the Mendelson and Pfaus (1989) study may have been able to discriminate between the value of the two types of chambers for predicting copulation and responded to the odors in the bilevel chambers as predictive of the lack of opportunity to copulate.

Increased locomotor responses to female sex odors can also be observed in chambers bisected by wire-mesh screens. In such studies, males are placed on one side of the screen, and different UCSs or CSs presented on the other side. The presentation of female sex odors in bedding, or glass slides that contain estrous vaginal secretions, elicit large increases in nose-pokes through the wire-mesh screen (Pfaus *et al.*, 1990; Damsma *et al.*, 1992). An analogous finding of increased anticipatory locomotor behavior in the rat has been demonstrated in the Japanese quail. Akins, Domjan, and Gutierrez (1994) found that general activity of the male quail was increased in response to a CS (red light) if the interval between the CS and the UCS (presentation of a receptive female) was 20 min or longer. In contrast, for intervals shorter than 5 min, the male quail approaches and remains near the CS, a behavior similar to that observed with a visible female. These results, along with those of Mendelson and Pfaus (1989), suggest that stimuli present before copulation elicit sexual excitement which is evidenced by increased locomotor activity. One benefit of increased locomotor activity may be to increase the chance of encountering a mate, for example, by stimulating forward-directed locomotion, searches, or navigation of known routes toward places in which potential mates can be found.

The effect of opiates on conditioned sexual excitement has been examined using conditioned level changing in bilevel chambers. Van Furth, Wolterink-Donselaar, and Van Ree (1994) and Van Furth and Van Ree (1996b) found that naloxone (an opiate receptor antagonist) injected systemically prior to each training trial attenuated the development of conditioned level changing. They also found that in males showing high levels of conditioned level changing, naloxone given before each test produced a gradual decrease in conditioned level changing across subsequent trials. However, it was not clear whether the expression of conditioned level changing was blocked or if the behavior was truly extinguished because a final vehicle test was not reported. Van Furth and Van Ree (1996c) also examined the effects of infusions of opioid drugs into the ventral tegmental area (VTA) on the expression of conditioned level changing. Similar to the ef-

fect of systemic administrations, VTA infusions of naloxone given prior to each test session blocked the development of conditioned level changing. In contrast, VTA infusion of  $\beta$ -endorphin given prior to each test session did not block the development of conditioned level changing but instead lowered the frequency of level changes compared to controls. The effects of these manipulations on the expression of previously acquired conditioned level changing were not examined.

The role of dopamine in the expression of conditioned level changing in bilevel chambers was examined by Pfaus and Phillips (1991). Systemic injections of either SCH 23390, a D1 receptor antagonist, or sulpiride, a D2 receptor antagonist, both produced a decrease in the frequency of conditioned level changing in male rats. These effects did not appear to be due to general locomotor impairments as the latencies to level change were not affected. The neuroanatomical basis of the dopaminergic influence on conditioned level changing was also examined following infusions of haloperidol, a nonselective D2/D1 receptor antagonist, into the nucleus accumbens, anteriodorsal striatum, and the medial preoptic area (mPOA). Infusions of haloperidol into the nucleus accumbens or the mPOA, but not into the striatum, decreased conditioned level changing. Interestingly, haloperidol infusions into the mPOA also reduced the amount of pursuit of a receptive female, suggesting that this area is involved in responses to both conditioned and unconditioned sexual stimuli. The effects of manipulations of dopamine systems on the development of conditioned level changing was not examined.

A number of issues remain to be clarified regarding conditioned sexual excitement. First, more attention needs to be paid to the factors that influence the development and/or expression of conditioned sexual excitement. Second, control procedures need to be employed for general performance effects that may be independent of conditioned effects. For instance, decreased level changing may be due to motor effects of a drug independent of stimulus-elicited sexual excitement. Third, although disruptions of conditioned sexual excitement can be interpreted as disruptions of sexual motivation, they could also be produced by disruptions of mnemonic or associative processes independently of purely motivational processes. Rats may fail to make associations or forget the predictive value of stimuli rather than exhibit decreased responsiveness to sexually relevant stimuli. This criticism is relevant to other research attempting to use conditioned behaviors as indices of sexual motivation. One

way to examine memory processes independently from motivational influences is the posttrial manipulation during training method developed by McGaugh and colleagues to examine fear conditioning (for reviews see McGaugh, Cahill, and Rooztdall, 1996; McGaugh, 1989). In this method, subjects are given a conditioning trial or session of trials, receive a manipulation following the training, and then are tested at a later time. For instance, a tone (CS) may be paired with a shock (UCS), followed by drug administration, and tested once the drug is no longer present. In such a case, the drug cannot influence the performance of responses necessary for the development or expression of conditioning, but rather it specifically influences memory retention or consolidation processes. Conversely, manipulations that precede a training or test session may influence motivational, performance, and mnemonic processes.

## INFLUENCE OF LEARNING ON LOCATING A MATE

An initial problem in mating concerns the location of potential mates. Solving this problem might be accomplished simply by relying upon chance encounters; however, unless the individual resides in an area that has a very high density of potential partners, it is unlikely to be a very successful strategy. Accordingly, animals could increase their chances for reproductive success by using past experience in the search for a mate. Studies using both contextual and discrete stimuli demonstrate that animals tend to approach and remain in the vicinity of stimuli that have been paired with copulation.

Animals display a preference to remain in a context that has been paired consistently with access to a mate over a context that has not; this is commonly referred to as a conditioned place preference (CPP). CPP is typically demonstrated using an apparatus with two connected distinctive compartments. First, the compartments are paired differentially with unconditional stimuli (e.g., one side is paired with a sex partner, food, or a rewarding drug and the other side is paired with either nothing or a control manipulation). Then, on a test session, the subject is allowed to move freely between the compartments. CPP is said to have developed when the subject spends more time in the reward-paired compartment than in the other one. UCSs that are capable of supporting CPP are referred to as rewards, as opposed to reinforcers, because the subject

has never been required to move into the paired compartment to experience the UCS. Thus CPP is not reinforced, as it is being displayed spontaneously. In male rats, CPPs have been established with sexual reward using two different conditioning procedures. In one procedure, copulation to ejaculation is allowed to occur within one distinctive environment and this environment is subsequently preferred over the other environment in which copulation was not allowed (e.g., Everitt, 1990); a CPP developed by this procedure is referred to as copulatory CPP. Copulatory CPPs can be maintained by intromissions alone, whereas prevention of intromission disrupts a previously established CPP (Hughes, Everitt, and Herbert, 1990).

In a second procedure, male rats are allowed to copulate to ejaculation in a separate arena and then transferred immediately to one distinctive compartment of the CPP apparatus; following such training this compartment will be preferred over the other compartment (e.g., Ågmo and Berenfeld, 1988); a CPP produced by this procedure is referred to as postejaculatory CPP. Demonstrations of postejaculatory CPP might appear puzzling at first glance because the CS is presented following the UCS or reward (copulation). This appears to involve a "backward" pairing of the stimuli that is not supposed to yield conditional responding to the CS. However, if the neural state induced by ejaculation is considered to be the UCS, then the pairing of CS and UCS is simultaneous and postejaculatory CPP can be accounted for by the rules of Pavlovian conditioning. Although both copulatory and postejaculatory CPP procedures produce effects of similar magnitude, there are differences in the underlying neurobiology as demonstrated by differential effects of drugs (see below).

Conditioned place preferences have also been demonstrated in female rats and hamsters. However, in contrast to the robust preferences seen in males, some reports demonstrate only weak effects in females. Oldenburger *et al.* (1992) found that when copulation occurred within one of the distinctive compartments of a typical CPP apparatus female rats showed only a weak CPP. Conversely, Paredes and Alonso (1997) and Paredes and Vazquez (1999) demonstrated a robust CPP in female rats which depended on whether the females were able to pace the rate of copulation without employing defensive behaviors (referred to as "paced" copulation). Females acquired a strong preference for a context if they were placed into the context immediately following paced copulation. In contrast, no preference was found if the copulation was

unpaced. Thus, for a female rat CPP develops only when she is able to control the temporal aspects of copulation without defensive behavior. Paredes and colleagues have interpreted these results as a post-copulatory reward state in the female rat. Although a sexually vigorous male rat is a clear UCS for approach and solicitation in sexually receptive female rats (Ågmo, 1999), contextual cues associated with pacing elicit a sexual reward state in these females. However, these results may also reflect the presence of aversive properties during unpaced mating conditions given that the female must resort to defensive behavior in an attempt to pace the male's sexual behavior. Examining CPP in female rats produced by paced mating within a distinctive environment would allow researchers to evaluate if paced copulation itself is rewarding.

Copulatory CPPs have also been demonstrated in female hamsters (Meisel and Joppa, 1994). However, females also displayed a CPP for compartments paired with aggressive encounters. Thus, there appears to be a species difference between female hamsters and female rats regarding the rewarding properties of aggressive encounters. In hamsters, aggressive encounters may serve to strengthen a copulatory CPP. Conversely, in rats, aggressive encounters (produced by unpaced mating) may serve to weaken a copulatory CPP. Nevertheless, the body of evidence on sexually rewarded CPP demonstrates that both males and females approach and remain in a context that has previously been paired with sexual stimulation or reward. However, it is not yet clear whether the nature of sexual stimuli capable of supporting CPP are the same or different for males and females.

Discrete stimuli within an environment that are consistently paired with sexual interactions can also elicit conditioned approach behavior. Domjan, Lyons, North, and Bruell (1986) found that when a visual stimulus consistently preceded the arrival of a female, male quail would approach and remain near the stimulus. Similar results have been produced in female quail (Gutierrez and Domjan, 1997). One study in the male gerbil (Villarreal and Domjan, 1998) is of particular interest because it suggests that even when a CS is paired inconsistently with sexual reward it is still able to elicit conditioned approach behavior. In this study, male gerbils were exposed to a neutral odor that was paired with access to their impregnated mates. On some of the training trials, copulation took place, whereas on other trials, no copulation occurred. Despite this, the males displayed conditioned approach behavior to the neutral odor in the absence of their mates.

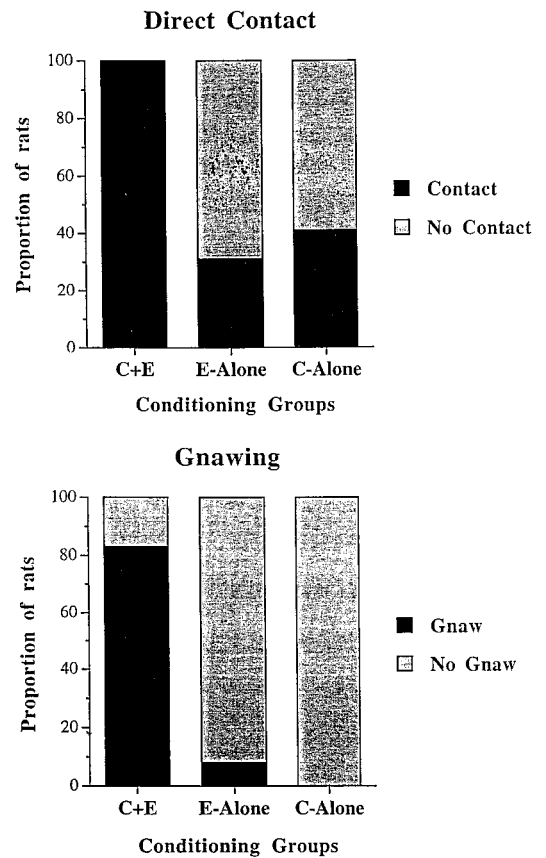


FIG. 2. Proportion of rats that made direct contact with (top) and gnawed on (bottom) a wooden dowel soaked in cadaverine. Males in the C+E group had previously been conditioned to associate cadaverine with the presentation of an estrous female and copulation. Males in the E-alone group received copulation with unscented estrous females and their first exposure to cadaverine during the test. Males in the C-alone group received cadaverine habituation trials prior to the test.

Recently, Pfaus, Theberge, and Kippin (in preparation) found that an initially aversive stimulus paired with copulation can acquire conditional appetitive properties. Cadaverine is an airborne polyamine given off by decaying flesh and is innately aversive to rats (Pinel, Gorzalka, and Ladak, 1981). In this study, groups of male rats were allowed to copulate either with cadaverine-scented females or with unscented females for nine sessions. Following this conditioning procedure, all males were tested in a novel environment into which a wooden dowel wrapped in cotton containing cadaverine was placed. Males that had previously copulated with unscented females avoided the dowel (Fig. 2). Few of these males made contact with it, many tried to escape the test chamber, and all spent more time on the distal side of the chamber. Con-

versely, males that had previously copulated with cadaverine-scented females readily approached and showed appetitive responses toward the scented dowel. All of these males made contact with and remained in close proximity to it, most picked it up, and gnawed on it, and none tried to escape the test chamber. Following subsequent cadaverine habituation sessions, the control group still displayed aversive responses to cadaverine. Thus, pairing the aversive cadaverine odor with copulation not only diminished the aversive properties of the odor but made it conditionally appetitive. This finding may have implications for the formation of sexual paraphilias in humans involving erotic responses to stimulation that may otherwise be perceived as aversive.

Demonstrations of conditioned place preference and conditioned approach behavior are consistent with the much larger literature showing that animals will approach conditioned stimuli that have been paired with rewarding stimuli (for reviews see Nader, Bechara, and van der Kooy, 1997; Tzschentke, 1998; Wise, 1989). Presumably this reflects a cognitive search strategy based on past experience which increases the probability of coming into contact with mates or other rewards. The phenomenon of postejaculatory or drug-induced CPP suggests that it may be the rewarding aspects of mating, but not necessarily the discovery of a mate, that elicit stimulus approach behaviors. However, it is not clear whether copulatory behavior per se is capable of supporting the development of CPP.

The neurochemical substrates of conditioned approach behaviors have been examined primarily using the conditioned place preference model in the male rat. Both copulatory and postejaculatory CPPs have been studied using opioid agents, yielding somewhat inconsistent results. Naloxone appears to disrupt both types of CPP, but in different ways. Ågmo and Berenfield (1988) found that the development of postejaculatory CPP is blocked by naloxone injections prior to each training session. Conversely, the development of copulatory CPP was unaffected by naloxone prior to each training session (Meharra and Baum, 1990). However, once a copulatory CPP had developed, its expression was blocked by an injection of naloxone prior to the test session (Meharra and Baum, 1990; Hughes *et al.*, 1990). There is also evidence that the site of action of naloxone is different for these effects. Ågmo and Gomez (1993) found that naloxone disruption of the development of postejaculatory CPP can be achieved with infusions into the mPOA, whereas naloxone into this brain region prior to a test session did

not disrupt the expression of copulatory CPP (Hughes *et al.*, 1990). Interestingly, lesions of this area caused a time-dependent disruption of a copulatory CPP (Hughes *et al.*, 1990). The differential effects of opioids on the two types CPP suggest that postejaculatory CPP may be less robust than copulatory CPP or that multiple opioid systems are involved in CPPs produced by sexual reward. One way to resolve this issue is to test the influence of a naloxone injection prior to the test on the expression of postejaculatory CPP.

The effect of dopaminergic drugs on conditioned approach behavior has also been examined. Ågmo and Berenfield (1988) found that the development of postejaculatory CPP in male rats was not blocked by injections of pimozide (a D2/D3 receptor antagonist) prior to each training session. Conversely, Meisel, Joppa, and Rowe (1996) found that the development of copulatory CPP in female hamsters was blocked by injections of the D2 receptor antagonists sulpiride or raclopride prior to each training session. No studies have reported on the effects of dopaminergic drugs on the expression of CPP. However, other results suggest involvement of the mesolimbic dopamine systems in responding to conditioned stimuli. For example, West, Clancy, and Michael (1992) examined the responsiveness of the nucleus accumbens in male rats to odors. They found that odors paired previously with a receptive female produced more single-unit activity in medium spiny neurons than odors paired with either a nonreceptive female or with no conspecific. Further, the responsiveness was higher for males that ejaculated during training than in those who did not. Although conditioned approach behaviors would likely have been elicited following this training procedure, no behavioral measures were reported to confirm this and the relation of these conditioned physiological changes to conditioned approach behavior is unclear.

Limited attention has been given to assessing the role of the endocrine system in conditioned approach behavior. Castration disrupts the expression of copulatory CPP on the first postoperative test (Miller and Baum, 1987; Hughes *et al.*, 1990), and acquisition of copulatory CPP was blocked by naloxone in castrated, but not intact, males (Meharra and Baum, 1990). It is interesting to note that endocrine responses have been detected following exposure to either contextual or discrete stimuli paired previously with copulation. Kamel, Mock, Wright, and Frankel (1975) found that testosterone, luteinizing hormone, and prolactin levels were elevated following exposure to an arena in which prior copulation occurred. Similarly, Graham and Desjardin (1980) found that testosterone and luteiniz-



ing hormone were increased following exposure to an odor (methyl salicylate, or wintergreen) paired previously with copulation. However, it is again important to note that no behavioral measures were reported, thus the relation of these conditioned physiological changes to conditioned approach behavior is unclear.

A number of issues remain to be clarified with sexually rewarded CPP. First, the differences between copulatory CPP (which includes ejaculation) and postejaculatory CPP need to be examined further. More work needs to be done to determine whether these types of CPP are mediated by the same or different physiological mechanisms. Also, as with conditioned sexual excitement, more attention needs to be paid to the development and expression of CPP. Similarly, studies need to determine if disruptions of CPP can be attributed to disruptions of sexual motivation or independent disruptions of mnemonic processes.

## INFLUENCE OF LEARNING ON OVERCOMING OBSTACLES TO MATING

In order to gain access to a mate, it may not be sufficient to merely approach a location that has previously been the site of copulation. Sometimes there are obstacles to overcome. Males and females of many species have demonstrated a strong willingness to work for many rewards, including access to a sex partner. The propensity to perform arbitrary behaviors that result in the presentation of a mate has been demonstrated in several species. Anecdotal evidence from human experience tells us that both men and women will perform various operants to attract or gain favor with potential mates; however, empirical data are restricted to studies involving animals.

Numerous studies have demonstrated that male rats can learn to bar press to receive access to a receptive female (Beck, 1971, 1978; Beck and Chmielewska, 1976; Jowaises, Taylor, Dewsbury, and Malagodi, 1971; Larsson, 1956; Schwartz, 1956). Other studies have demonstrated that female rats learn to bar press for a sexually active male (Beck, 1971, 1974, 1978; Bermant, 1961; Bermant and Westbrook, 1966; French, Fitzpatrick, and Law, 1972). Typically, these studies involve the subject learning to bar press in a modified Skinner box in order to cause a mate to be delivered into the box allowing copulation to commence. Bar pressing for mates has also been demonstrated in both male (Micheal and Keverne, 1968) and female (Keverne, 1972) rhesus monkeys. Similar studies dem-

onstrate that male pigeons will key peck (Gilbertson, 1975) and male stickleback fish will swim through a ring (Sevenster, 1973) in order to gain access to a receptive female. Correct performance of a T-maze in order to locate a mate is also performed by male rats (Drewett, 1973; Hetta and Meyerson, 1978; Kagan, 1955; Whalen, 1961) and female rats (Drewett, 1973; Meyerson and Lindstrom, 1973; Eliasson and Meyerson, 1975). Other studies found that male rats (Beach and Jordan, 1956a; Ware, 1968) and guinea pigs (Seward and Seward, 1940) will run an alley, and male rats will climb over a hurdle (Sheffield, Wulff, and Backer, 1951), dig through sand (Anderson, 1938), cross shock grids or perform other aversive tasks (Anderson, 1938; Meyerson and Lindstrom, 1973; Warner, 1927), turn a wheel (Denniston, 1954), and master obstruction boxes (Moss, 1924; Warner, 1927; Jenkins, 1928; Stone, Barker, and Tomlin, 1935) to gain access to a receptive female. These results demonstrate that males and females of many species have the ability to learn to overcome many obstacles, as well as to endure painful stimulation, in order to gain access to a mate.

The effect of allowing only incomplete copulation (i.e., intromission without ejaculation) on several operants has been examined. In contrast to males allowed to mount and intromit only, males allowed to copulate to ejaculation made more consistent choices (Kagan, 1955) and developed faster running speeds (Whalen, 1961) in T-mazes and hurdle climbing (Sheffield *et al.*, 1951). Bermant and Westbrook (1966) examined lever press latencies following intromission alone or with ejaculation in male and female rats. They found that for both sexes the longer response latencies were obtained with the completion of the entire sequence of sexual behavior. This suggested that a transient sexual satiety is produced by ejaculation. These results support the notion that copulation and ejaculation have differential effects on behavior; however, they do not indicate whether such differences are quantitative or qualitative in nature.

Everitt and colleagues have used a modified version of lever pressing for a receptive female to examine the neurobiology of sexually reinforced operant behavior in male rats. Everitt, Fray, Kostarcyzk, Taylor, and Stacey (1987) demonstrated that rats trained to bar press for a receptive female can subsequently be trained to bar press for a light or tone that is paired with copulation on a second-order (FI: FR10) schedule of reinforcement. Using this procedure, they were able to obtain high and consistent rates of lever pressing, allowing an examination of the neurochemical basis of

the expression of this conditioned responding. Dopamine antagonism by intraperitoneal injection of  $\alpha$ -flupentixol dose dependently decreased, whereas infusion of amphetamine into the nucleus accumbens increased, instrumental responding under this second-order reinforcement schedule (Everitt, 1990). Lesions of the basolateral amygdala selectively disrupted conditioned lever pressing for a secondary reinforcer, and this effect was reversed by infusion of amphetamine into the nucleus accumbens. Such lesions did not affect copulation (Everitt, Cador, and Robbins, 1989). These results implicate a projection from basolateral amygdala to nucleus accumbens in the control of operant responding for sexual incentives. However, it appears that this circuit is not specialized for sexual incentives, as similar disruptions are seen in responding for ingestive incentives (Everitt, 1990). In contrast, lesions of the mPOA disrupted copulation, but had a small, indirect influence on conditioned lever pressing; in initial postlesion tests, responding was high and decreased with subsequent testing. This suggests that lever pressing was extinguished due to an inability to obtain reinforcement through copulation (Everitt and Stacey, 1987). The effects of castration on lever pressing were similar to those of mPOA lesions: initially normal rates followed by extinction. Additionally, systemic injections, but not intra-mPOA infusions, of naloxone reduced conditioned responding for second-order reinforcement (Hughes *et al.*, 1990).

## INFLUENCE OF LEARNING ON COURTSHIP BEHAVIOR

Once animals come into contact with a conspecific that is sexually receptive, copulation is typically preceded by one or both potential partners engaging in behaviors which entice the other partner to mate. A number of studies have reported that certain components of courtship or behavior in males can be elicited by stimuli associated with a mate. Studies in rodents have found that learning plays an important role in the production of vocalizations associated with copulation. For example, ultrasonic vocalizations in response to sex-related olfactory stimuli in male mice were dependent on prior sexual experience for their expression (Maggio, Maggio, and Whitney, 1983; Dizinno, Whitney, and Nyby, 1978).

Classical conditioning has been implicated in the elicitation of courtship behaviors in several studies. Nyby and his colleagues (Nyby, Bigelow, Kerchner,

and Barbehenn, 1983; Nyby, Whitney, Schmitz, and Dizinno, 1978) have demonstrated that artificial odors paired with access to receptive female mice become capable of eliciting ultrasonic vocalizations from male mice. Hollis and colleagues (Hollis, Cadieux, and Colbert, 1989; Hollis, Pharr, Dumas, Britton, and Field, 1997) demonstrated that repeatedly pairing a light with noncontact exposure to a receptive female resulted in conditioning of the sexual behavior in male gouramies. Following training, males responded to the light alone with fin displays that are normally associated only with courtship. Sevenster (1973) reported that male stickleback fish made courtship displays toward a floating ring that they had been trained to swim through in order to gain access to a female. Similar results have been obtained in avian species. Gilbertson (1975) reported that courtship displays were elicited in male pigeons during operant key pecking for a female, and Farris (1967) found that male Japanese quail made courtship displays following a tone that had reliably predicted presentation of a female. Interestingly, in several studies using a visual CS, Domjan and colleagues (for a review see Crawford, Holloway, and Domjan, 1993) have failed to replicate the conditioned courtship displays reported by Farris. This inconsistency may indicate the differential effects of conditioning produced by stimuli that affect different sensory modalities and may thus reflect constraints on learning regarding the conditioned elicitation of courtship behaviors.

Conditioning can also attenuate preparatory and courting behaviors. Peters, Koch, Blythe, and Sufka (1988) found that ultrasonic vocalizations preceding copulation were inhibited in male rats that had previously received illness-inducing injections of lithium chloride (LiCl) paired with access to a receptive female. Like male rats, male hamsters not only learn to prefer the odors of estrous females but they also readily lick and consume vaginal secretions when presented on a slide (Johnston, 1972, 1974). Johnston and colleagues have produced a conditioned taste aversion to this normally attractive stimulus through a punishment procedure that pairs vaginal secretions with an injection of LiCl. Male hamsters treated in such a manner took longer to initiate licking, spent less time licking, consumed less vaginal secretions presented on a slide than did control animals (Johnston and Zahorik, 1975; Zahorik and Johnston, 1976; Johnston, Zahorik, Immler, and Zakon, 1978), and consumed less of a dilute solution of vaginal secretions than control males (Zahorik and Johnston, 1976). Moreover, when given the opportunity to interact with an estrous

female, conditioned males had increased latencies for orogenital contact with a receptive female (Johnston *et al.*, 1978).

## INFLUENCE OF LEARNING ON SEXUAL AROUSAL AND COPULATORY BEHAVIORS

Once two or more potential mates have come in contact with each other and engaged in courtship behavior and are mutually receptive, copulation may begin. For all mammals, copulation involves the insertion of the male's penis into the female's vagina to allow sperm delivery to produce fertilization and for vaginocervical stimulation to facilitate pregnancy. For males of most mammalian species, this involves obtaining an erection, mounting a receptive female, and pelvic thrusting with the subsequent achievement of penile intromission that eventually culminates in ejaculation and the postejaculatory refractory period. For females of most species, copulation involves the act of assuming appropriate positioning to facilitate intromission by the male, solicitation and pacing the male's copulatory behavior, and a period of quiescence following ejaculation. Although the behavioral cascade of copulatory behavior necessitates a high level of similarity between species, there is substantial diversity in copulatory patterns. For instance, in a comparative analysis, Dewsbury (1972, 1973, 1975) found that the copulatory behavior of male rodents differs qualitatively from other species based on the presence of a copulatory lock, thrusting, multiple intromission, or multiple ejaculations.

### *Sexual Arousal*

Perhaps the most widely studied dependent measure of conditioning of sexual behavior has been the study of sexual arousal. Sexual arousal is one of the few components of sexual behavior to which there are both substantial human and animal literatures. Assessment of sexual arousal in human studies is strictly defined as the measurement of blood flow to the genitalia—penile erection in men and vaginal pulse in women. Penile erections elicited by nonaccessible females are also measured in primates (e.g., Nadler and Bartlett, 1997; Pomerantz, 1990) and rats (Sachs, Akasofu, Citron, Daniels, and Natoli, 1994; Sachs, 1995a). Additionally, penile erection produced by manual stimulation by the experimenter is also widely studied

in rodents (see Meisel and Sachs, 1994). The more common approach in animal models has been to use the latencies to intromit and ejaculate as indices of sexual arousal. Thus, the measures of sexual arousal used in humans and animals studies have often not been the same. This is especially true for the case of studies of conditioned sexual arousal.

Studies using human subjects have demonstrated that sexual arousal can be altered through the use of a number of manipulations, including habituation, classical conditioning, and instrumental learning. Habituation of erectile responses in men has been demonstrated with repeated exposure to the same erotic slides (O'Donohue and Geer, 1985) or audiotapes (O'Donohue and Plaud, 1991). Using women subjects, Meuwissen and Over (1990) found that vaginal pulse habituated with repeated presentations of the same erotic film segment and then dishabituated with novel film segments.

A number of studies have demonstrated that classical conditioning can produce sexual arousal. Sachs and Garinello (1978) reported that placing male rats into a chamber in which copulation had previously occurred dramatically reduced the latency for males to display penile erections. Rachman (1966) and Rachman and Hodgson (1968) found that following pairing with erotic slides, a pair of women's boots was able to elicit erections in men. Similarly, McConaghy (1970, 1974) demonstrated conditioned erection in heterosexual and homosexual men elicited by colored circles or squares paired previously with erotic videotapes or still pictures. A particularly informative study by Kantorowitz (1978) further examined the nature of association between the UCS and conditioned arousal induced by still pictures. For each subject, three different slides were paired with the plateau, refractory, and resolution stages of masturbation. During subsequent testing, stimuli paired with the plateau phase produced an increase in penile erection, stimuli paired with the refractory phase produced a decrease in erection, and stimuli paired with the resolution phase had no effect. Remarkably these responses were still present after 3 months. Only one study has examined the classical conditioning of sexual arousal in women. Letourneau and O'Donohue (1997) failed to find significant effects of conditioning on sexual arousal in women. However, the authors note that the UCSs (erotic films) produced only moderate levels of arousal, whereas in studies with male subjects such stimuli produced high levels of arousal. Thus, this failure to demonstrate conditioned arousal in women may have been due to an ineffective UCS.

Several studies have attempted to demonstrate instrumental control of sexual arousal in men and women. Rosen, Shapiro, and Schwartz (1975) found that, given feedback and contingent monetary reinforcement, men learned to become sexually aroused in the absence of erotic stimuli. Other studies have found that men, as instructed, can suppress (Rosen and Koppel, 1977; Rosen, 1973) or increase (Reynolds, 1980) penile erection with feedback; however, these studies failed to demonstrate learning effects across trials. Given similar instructions, women can increase their vaginal pulse in the absence of erotic stimulation (Zingheim and Sandman, 1978) or decrease vaginal pulse in the presence of erotic stimulation (Cerny, 1978), but again, no learning effects occurred. In summary, the evidence regarding instrumental control of sexual arousal is limited to the one report in which monetary reinforcement and feedback were provided.

### *Copulation*

Evidence from animal studies has demonstrated a clear influence of previous sexual experience in the speed of copulation. Larsson (1956), and subsequently Dewsbury (1969), reported the effect of sexual experience on the development of sexual behavior. They both found that ejaculation latency was reduced as a function of prior copulation and Dewsbury found that mount and intromission latencies were also reduced. Similar results have been obtained with mice (McGill, 1962b), cats (Michael, 1961), and guinea pigs (Valenstein and Goy, 1957). Additionally, McGill (1962a) reported that, in mice, the number of mounts inappropriately directed toward the female's head decreased with sexual experience. These effects of experience on sexual behavior are likely due to instrumental learning and appear to bring male copulatory responses to a homogenous form. However, no studies have reported the effect of sexual experience on the sexual efficiency of female animals or humans of either gender.

A necessary UCS for the development of sexual behavior in male rodents is the penile stimulation received during intromission. Whalen (1961) examined the influence of penile stimulation without ejaculation on the development of sexual behavior. Male rats were allowed to mount four times each day, with or without intromission, for a total of 33 days. At the end of this training period, males that mounted with intromission displayed relatively short latencies to copulate and brief intermount intervals compared to males that mounted without intromission, many of

which had ceased to copulate altogether. In a similar study, Kippin, Talianakis, and Pfaus (1997) examined the influence of ejaculation on the development of sexual behavior. Male rats were allowed to display intromissions but without ejaculation, intromit to one ejaculation, or two ejaculations on each of nine training sessions, then all males were allowed to copulate for a 30-min test. There were no differences between groups on a range of copulatory parameters, including intromission latency, ejaculation latency, intromission frequency, interintromission interval, and postejaculatory interval. Thus, similar to the development of sexually reinforced maze learning (Sheffield, Wulff, and Backer, 1951; Whalen, 1961), the penile stimulation received from intromission alone appears to be sufficient for the development of copulatory efficiency. Other sensory stimulation may be important as a UCS. Hayashi and Kimura (1976) found that the latency to initiate copulation and to ejaculate was greatly reduced in sexually naive male mice if they were allowed to observe a male and a female conspecific engaging in sexual behavior. It is not clear whether the sexually naive males could also sense odors from the copulating pair.

Other learning effects on copulatory behaviors have also been reported. Silberberg and Adler (1974) reported that rats can learn to control their intromission frequency under a negative punishment schedule of responding. They found that rats decreased the number of intromissions required to ejaculate if they were limited to seven per copulation session, whereas control rats showed no alteration in intromission frequency. Jowaisas, Taylor, Dewsbury, and Malagodi (1971) found that rats allowed to copulate under an imposed operant requirement produced altered intromission patterns similar to that produced by an "enforced interval effect" (see Larsson, 1956) in which males ejaculated with fewer intromissions. Female quail display increased squatting (a measure of sexual receptivity) frequency and duration if the appearance of a male quail is signalled visually (Gutierrez and Domjan, 1998).

Classically conditioned stimuli are also capable of increasing sexual arousal as reflected by copulatory rate measures. Zamble and his colleagues (Zamble, Hadad, Mitchell, and Cutmore, 1985; Zamble, Mitchell, and Findlay, 1986) used placement of male rats in a holding cage as a conditioned stimulus to signal noncopulatory exposure to a receptive female on several training trials. On test trials, they found that placing the males into the holding cage prior to copulation resulted in significantly shorter latencies to intromit

and ejaculate than if the conditioned stimulus was omitted. Subsequent studies found that second-order conditioned stimuli were effective at eliciting arousal (Zamble *et al.*, 1985). Hollis, Cadieux, and Colbert (1989) demonstrated that repeatedly pairing a light with noncontact exposure to a receptive female resulted in conditioning of sexual behavior in male gouramies. They found that males receiving the conditioning treatment displayed significantly lower latencies to initiate copulation and lower levels of aggression toward females when the conditioned stimulus was presented before access to a female. Similar results have been demonstrated in Japanese quail. Males that had previously received repeated exposure to females following the presentation of a conditioned stimulus displayed significantly shorter latencies to initiate copulation when the stimulus was present compared to when it was absent (Domjan, O'Vary, and Greene, 1988). Pfaus, Talianakis, and Kipin (in preparation) have recently found evidence that somatosensory stimuli can be used to condition sexual arousal. Male rats that had received prior sexual experience with receptive females while wearing an unattached harness jacket displayed faster intromission and ejaculation latencies if tested with the jacket than without it.

Aversive conditioning can also influence copulatory latencies. Male hamsters and rats injected with LiCl following copulation subsequently displayed significantly longer intromission latencies than controls (hamsters: Johnston *et al.*, 1978; rats: Peters, 1983). However, Emmerick and Snowdon (1976) failed to find inhibition following a similar treatment. In rats, the addition of a neutral stimulus (almond odor: Lawrence and Kiefer, 1987) or a component of scent marking (phenylacetic acid: Emmerick and Snowdon, 1976) facilitated the conditioned aversion to females. Similarly, juvenile rats injected with LiCl following exposure to estrous females displayed longer latencies to intromit during copulation in adulthood (Koch and Peters, 1987). Finally, Sachs (1995b) reported that in male rats erections elicited by noncontact exposure to a female were attenuated by prior pairings of such exposure with injections of LiCl.

Copulatory behaviors can be affected by CSs that have been paired with either arousing or rewarding stimuli of a nonsexual nature. Fillion and Blass (1986) found that adult male rats displayed shorter ejaculation latencies with receptive female rats bearing an odor paired with nursing during infancy compared with receptive females not bearing the odor (see also Marr and Gardner, 1965). It has been demonstrated

that moderately painful stimuli have a facilitatory effect on copulation in male rats. For example, administration of painful skin shock decreased intromission latency and postejaculatory refractory period (Barfield and Sachs, 1968) and administration of painful tailshock can induce sexually sluggish rats to copulate (Caggiula and Elbergen, 1969). Moreover, the presentation of a CS previously paired with shock can induce noncopulating male rats to copulate (Crowley, Popolow, and Ward, 1973). Contextual stimuli paired with drug administration also have effects on copulation. Mitchell and Stewart (1990) found that a context previously paired with morphine increased the amount of female-directed behaviors in intact male rats and decreased the intromission latencies in castrated male rats. The influence on sexual behavior of stimuli paired with other drugs or aversive stimuli in males or any drugs or aversive stimuli in females have not been reported; such studies would be of great importance to understanding how sexual arousal and motivation interacts with motivational and arousal mechanisms for nonsexual incentives.

## INFLUENCE OF LEARNING ON SEXUAL PARTNER PREFERENCES

Individuals exhibit preferences not only for sexually receptive versus nonreceptive conspecifics, but also among potential sexually receptive mates in which the features of one are preferred over another. There has been much theoretical speculation and some empirical evidence that learning plays a role in the development of these preferences, and mate preferences appear to be influenced by experiences both early in life and in adulthood.

Preferences for specific mates is determined, at least in part, by sexual imprinting. Several studies have demonstrated that adult males preferentially mate with females that have attributes similar to those of the female that nursed them early in life. Yamazaki *et al.* (1988) found that male mice nursed by foster mothers choose to mate with females that resembled their foster mother rather than their biological mother. Similarly, Cooke and colleagues have determined that the coloration of the nursing lesser snow goose is preferred by adult ganders both in laboratory experiments (Cooke and McNally, 1975) and field studies (Cooke, Finney, and Rockwell, 1976; Cooke, Mirsky, and Seiger, 1972). Bateson (1978a) argued that sexual imprinting allows adult males to mate using an opti-

mal outbreeding strategy in order to avoid inbreeding. He provided evidence for this hypothesis from a study in Japanese quail using three distinctively colored strains. In a series of mate-choice tests, males showed the highest preference to approach and to copulate with females whose color differed slightly from that of their foster mothers compared to females with the exact same color or completely different color. Perhaps the most provocative report of sexual imprinting is that of Kendrick, Hinton, and Atkins (1998), who demonstrated that sexual partner preferences can be achieved between goats and sheep using cross-fostering to manipulate the imprinting process. In males and females of both species, sexual partner preferences were toward members of the opposite sex of the species of the foster, rather than biological, mother.

Another approach to studying sexual imprinting has been to examine the influence of artificial stimuli attached to nursing mothers. Two such studies have examined the influence of pairing novel odors with nursing dams on subsequent conspecific preferences in male rats. Marr and Gardener (1965) found that subjects that had a novel odor paired with nursing until weaning displayed an approach preference for conspecifics bearing that odor. Similarly, subjects with normal scented dams showed a preference for unscented females. Recently, Moore, Jordan, and Wong (1996) failed to replicate these findings. However, during preference tests in the latter study, the subjects were allowed to contact conspecifics, whereas in the former study no contact could occur. As well, different odors were used. Why these methodological differences would produce different results is unclear and this contradiction needs to be clarified. Moore *et al.* (1996) also found no differences during contact with anaesthetized conspecifics or during a simultaneous sexual test with a scented and unscented female. These studies have been performed only in rats using odors as stimuli; it would be interesting to examine whether these findings can generalize to other sensory modalities and to other species.

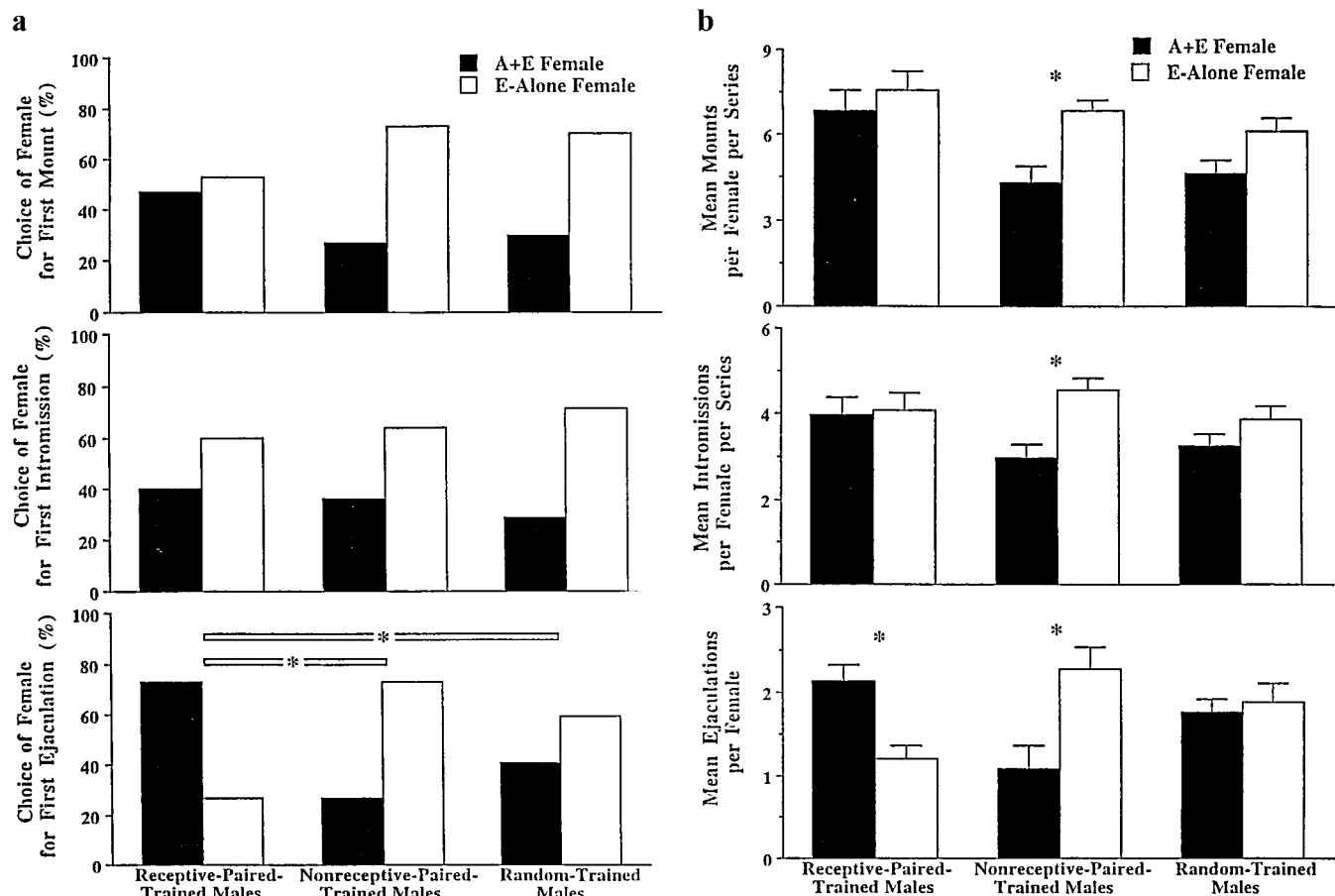
The importance of adult sexual experience on partner preferences has been clearly demonstrated in three lines of research. First, studies of social interaction in pair-bonded prairie voles, a socially monogamous species, show preferential responding to partners that are sexually familiar over partners that are novel. Second, studies of social interaction in animals that are seasonally socially monogamous, such as Japanese quail, have shown that pairing neutral stimuli with copulation produces subsequent preferential responding toward individuals bearing the familiar stimuli.

And recently, we have shown that the polygamous male rat displays a preference to ejaculate with a female bearing an odor previously paired with copulation.

The behavioral consequences of past sexual interactions on sexual preferences have been studied extensively in voles. Such studies employ a comparative framework in which socially monogamous prairie voles (*Microtus orchrogaster*) are compared to polygamous montane voles (*Microtus montanus*). The results of research from several laboratories demonstrates that prairie voles, but not montane voles, prefer an opposite-sex conspecific with whom they have previously copulated and/or cohabited over an opposite-sex conspecific that is unfamiliar. Although well-established breeding pairs show sexual preferences for each other (Getz, Carter, and Gavish, 1981), sexual preferences are rarely studied in this model (Carter, DeVries, and Getz, 1995). Typically, noncopulatory social interactions are studied because they are displayed by newly formed pairs. The primary measure used in these studies has been the amount of side-to-side contact exhibited by female prairie voles during the opportunity to interact with one familiar and one unfamiliar male. In such tests, females will mate indiscriminately with both males, but will show more contact with the familiar male (Williams, Catania, and Carter, 1992). This preference is independent of behavioral responses of the males as females still display preferences when the males are anesthetized.

Classical conditioning of stimuli associated with sexual behavior plays a role in the development of mate-choice preferences in the seasonally monogamous Japanese quail. Studies by Domjan and colleagues show that male Japanese quail respond differentially to females based on the presence of stimuli paired previously with copulation. Nash and Domjan (1991) allowed male quail to copulate with females of two strains of quail that have different plumage color (brown versus blond). Subsequently, males choose to spend more time in the proximity of females whose color was the same as that of females with whom they had copulated previously (Nash and Domjan, 1991). Similarly, males allowed to copulate with females that were adorned with bright orange feathers subsequently spent more time near, and engaged in more sexual activity with, females similarly adorned than unadorned females. Moreover, males trained with adorned females engaged in mating behavior with a taxidermic model of a female quail only if it was adorned with the feathers (Domjan, O'Vary, and Greene, 1988).

Recently, we have developed a model to examine



**FIG. 3.** (a) Proportional distribution by female type of first mount (top), first intromission (middle), and first ejaculation (bottom) during the copulatory preference test with two estrous females, one bearing the almond scent and one unscented. \*  $P < 0.05$  for between-groups comparison. (b) Distribution of mean (+SEM) mounts per female per ejaculatory series (top), mean (+SEM) intromissions per female per ejaculatory series (middle), and mean (+SEM) ejaculations per female (bottom) during the copulatory preference test. \*  $P < 0.05$  for between female types comparison. Adapted from Kippin *et al.* (1998).

the role of associative learning in sexual partner preferences in the male rat. In our model of conditioned sexual partner preferences an initially neutral odor (e.g., almond or lemon) is used as a CS and is physically attached to a potential sexual partner. During training, male rats have access to females bearing the CS odor. Then, during a test session, the male has access to two females, one bearing the CS and one not. Under these conditions males trained with scented females (Paired-Trained) tend to ejaculate first and more frequently with a scented female than an unscented female. Conversely, these males do not tend to mount or intromit first or more often with either female (Fig. 3). Under the same testing conditions, males with equivalent sexual experience and odor exposure but in an unpaired or random paired fashion do not exhibit a preference for the scented female (see Kippin

*et al.*, 1998 for more details). We have termed this phenomenon conditioned ejaculatory preference (CEP) because it is specific to ejaculation and develops according to the rules of associative learning. These findings are particularly remarkable because they demonstrate that in a polygamous species mate selection is influenced by previous sexual experience, as it is in monogamous species. Moreover, mate preferences in polygamous males can be toward sexual partners which resemble previous ones rather than toward novel ones, as would have been predicted by the Coolidge effect (see Dewsbury, 1981).

We have also found that the UCS necessary to support the development of CEP is an event triggered by ejaculation, but not ejaculation per se. When males are allowed to copulate to ejaculation with a scented female and the female is removed immediately follow-

ing ejaculation, males fail to display CEP. Conversely, when a scented female is present following ejaculation produced by copulation with either a scented or an unscented female, males display CEP for the scented female (Kippin and Pfaus, 2001b). Thus, males need not actually to copulate with the female, but merely have to be exposed to a scented female during the postejaculatory refractory period for CEP to develop. These findings demonstrate that postejaculatory events are capable of supporting conditioning of sexual partner preferences and are similar to those found in place conditioning with sexual reward (see Ågmo and Berenfeld, 1990; Paredes and Alonso, 1997).

We have also studied the CR that underlies CEP (Kippin and Pfaus, 2001a). Given equal distribution of mounts and intromissions and the unequal distribution of ejaculations, there are at least two ways in which CEP could be mediated. First, males trained with scented females may have a lower threshold to ejaculate with a scented female than an unscented one. Alternatively, the male may select one female preferentially over the other for ejaculation but not for mounts or intromissions. During a copulatory preference test with one scented and one unscented female, Paired-Trained males do not demonstrate any evidence of facilitated ejaculation with the scented female; ejaculation latency, mount frequency, intromission frequency, or interintromission interval did not differ as a function of ejaculating with the scented or unscented female. Similarly, when males were trained with scented females then given an opportunity to copulate with an unscented female during a dyad test, no difference were found for ejaculation latency, mount frequency, intromission frequency, interintromission interval, postejaculatory interval, or number of ejaculation in a 30-min test. Conversely, when males trained with scented females were given the opportunity to interact with scented, sexually nonreceptive females, they displayed more mounts and mount attempts than did controls indicating that the CS alone is capable of eliciting sexual responses. Additionally, when the distribution of mounts during the copulatory preference test was analyzed at different points of an ejaculatory series, males displaying CEP mounted the scented female more often than the unscented one immediately prior to ejaculation, but not at other times (Kippin and Pfaus, 2001a). These results demonstrate that CEP is mediated by a preference to mount the scented female at or near the point of ejaculation. Accordingly, we hypothesize that the ability of the CS to direct copulatory behavior is modulated by physiological changes produced by copula-

tion such that the CS is a relatively more attractive stimulus when the male is about to ejaculate.

The neurobiology of sexual partner preference has been examined using the comparative approach in voles and in our CEP model. Extensive research has determined that pituitary hormones control social proximity preferences in both male and female prairie voles; however, the hormones responsible appear to be different in males and females. In female prairie voles, partner preferences are controlled by oxytocin, whereas in males, partner preferences are controlled by vasopressin (for reviews, see Carter, DeVries, and Getz, 1995; Insel, Winslow, Wang, and Young, 1998; Young, Wang, and Insel, 1998). Further, the adrenal hormone, corticosterone, inhibits social proximity preference in females, but facilitates it in males (Carter *et al.*, 1995; DeVries *et al.*, 1995; DeVries, Taymans, and Carter, 1997). Additional comparative investigations of the oxytocin and vasopressin systems have revealed differences in brain organization that may underlie species differences in partner preferences. The distribution of oxytocin and vasopressin cells appears to be similar between socially monogamous and nonmonogamous species (Wang, Zhou, Hulihan, and Insel, 1996). Conversely, receptor autoradiography has revealed differences in receptor densities between monogamous and nonmonogamous voles for vasopressin in the thalamus and septal nuclei (Insel, Wang, and Ferris, 1994) and for oxytocin in prelimbic cortex, nucleus accumbens, amygdalar nuclei, septum, thalamus, and hypothalamus (Insel and Shapiro, 1992). Together these findings suggest that differences in cellular responses to, rather than release of, oxytocin and vasopressin mediate species differences in partner preferences.

We have begun to investigate the neural substrates underlying the learning in sexual partner preferences using our CEP model. Fos immunoreactivity was used to assess activation of neural pathways by an odor paired with copulation in order to identify putative substrates of CEP (Kippin and Pfaus, in preparation). In this study, CS-induced increases in Fos expression were found in the piriform cortex, nucleus accumbens, basolateral amygdala, and lateral hypothalamus. By comparison, estrous odors have been shown to increase Fos expression in the accessory olfactory bulb, medial preoptic area, medial amygdala, nucleus accumbens, bed nucleus of the stria terminalis, and ventromedial hypothalamus (Bakker, Baum, and Slob, 1996; Bressler and Baum, 1996; Kippin and Pfaus, in preparation). Thus, it appears that conditioned and pheromonal sexual odors activate similar and inde-



pendent pathways in the limbic system and hypothalamus.

A number of issues regarding the role of learning in sexual partner preferences still remain to be addressed. Specifically, do monogamy and polygamy represent completely distinct mating strategies or do they share some elements in common? Given our demonstration that the polygamous male rat displays CEP and the resemblance of CEP to monogamous sexual partner preference, the relation between mating strategies used by monogamous and polygamous or other nonmonogamous species should be readdressed. This needs to be done on a behavioral level, for instance, using a comparative approach to examine how monogamous and polygamous species respond to conditioned sexual incentives. As well, comparisons of the neurobiology underlying partner preferences in prairie voles and CEP in rats may reveal physiological similarities and differences between species with divergent mating strategies.

Finally, in the course of our initial studies on CEP (Kippin *et al.*, 1998), we employed an explicitly unpaired control procedure (see Rescorla, 1967) in which males learned to differentiate between unscented, sexually receptive females and scented, sexually nonreceptive females (i.e., the odor predicted sexual nonreceptivity), using the same sequential training paradigm as Pfaus and Pinel (1989) to condition males not to copulate with nonreceptive females. All males attempted to copulate with the nonreceptive females during the first trial, but the proportion that attempted copulation declined precipitously to zero in the next few trials. In the final mate choice test with two receptive females, one scented and one unscented, these males displayed the opposite preference to that shown by paired-trained males: strong preferences to ejaculate with the unscented female over the scented female (Fig. 3). In fact, several males that had shown robust and stable copulatory behavior with unscented females during training, and that had learned to suppress their copulatory responses with the scented, nonreceptive females, did not attempt copulation during the final test, despite the obvious proceptive behavior of the females and intense anogenital investigation of both females by the males. Although this paradigm fit the definition of an explicitly unpaired control, it was in fact another kind of training: conditioned inhibition. Instead of being a true CS<sup>-</sup> (a stimulus that predicts no contingency, in this case, no relation to sexual behavior), the odor had become a CS<sup>+</sup> for sexual nonreceptivity. We are currently using this conditioning procedure to examine the disinhibi-

tory effects of several drugs of abuse, notably alcohol and cocaine.

## EFFECTS OF COPULATORY EXPERIENCE ON SEXUAL AND PARENTAL BEHAVIOR

Copulatory experience has pronounced effects on sexual and reproductive processes in male rats. Compared to sexually inexperienced males, sexually experienced males have larger testes (Drori and Folman, 1964), heavier penises (Herz, Folman, and Drori, 1969), lighter body weights (Siegel, Nunez, and Wade, 1981), and increased secretions from accessory sex glands (Drori and Folman, 1964). Sexual experience has also been shown to block the disruptive effects of anosmia (Thor and Flannelly 1977), castration (Centeno, Coopersmith, and Pfaus, 2000; Lisk and Heiman, 1980), penile deafferentation (Lodder, 1975), and age (Gray, Smith, Dorsa, and Davidson, 1981). Intact, sexually experienced males prefer the odors of sexually receptive females over those of sexually nonreceptive females, whereas sexually inexperienced males do not show a significant preference (Carr, Loeb, and Dissinger, 1965; Carr, Loeb, and Wylie, 1966).

We have shown previously that sexually naive males are susceptible to the disruptive effects of novelty stress on copulation, whereas sexually experienced males are not (Pfaus and Wilkins, 1995). Although both sexually naive and experienced males that were placed into a novel testing apparatus displayed behaviors consistent with a fear state (e.g., freezing followed by careful exploration near the walls of the chamber), the sexually experienced males responded immediately to the presentation of a sexually receptive female with the initiation of copulation, whereas most of the sexually naive males ignored the female for a long period of time. Systemic administration of the opioid receptor antagonist naloxone, or preexposure of the naive males to the testing chamber, were equally effective in increasing the proportion of males that eventually copulated to ejaculation during their first sexual encounter. These findings suggest that novelty-induced opioid release in certain brain regions may lead to an endogenous state in which copulatory behavior is suppressed. However, the induction of this state in males with sexual experience was not sufficient to suppress copulation once the female was placed into the chamber, suggesting that the female had acquired conditioned incentive properties that actively inhibited the state.

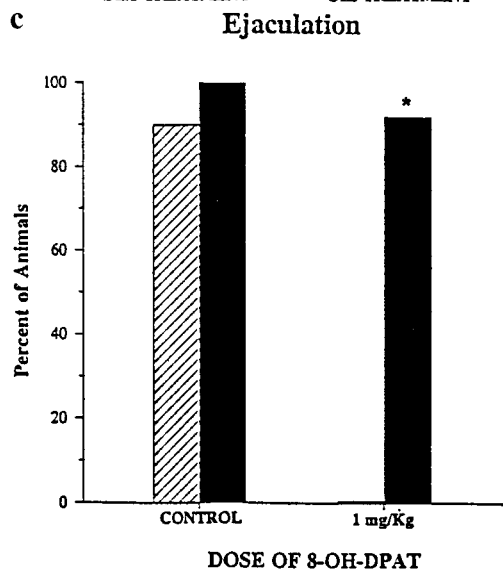
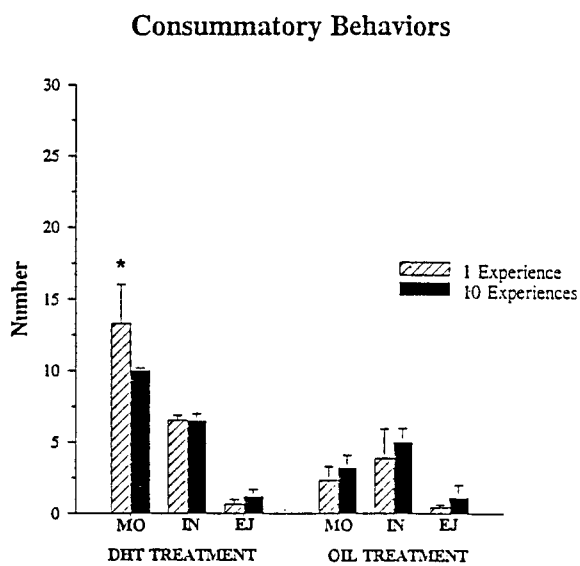
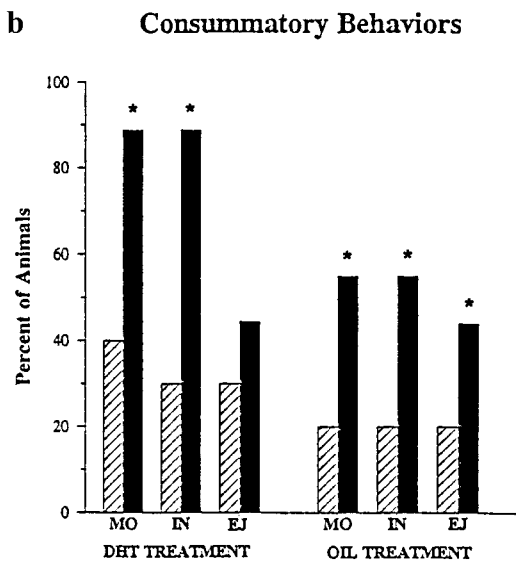
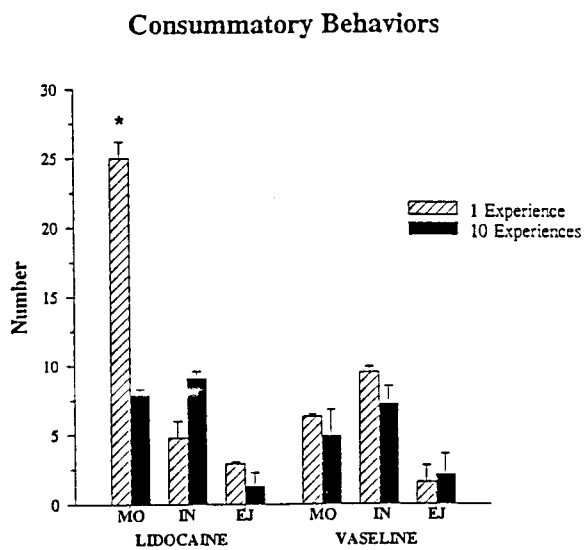
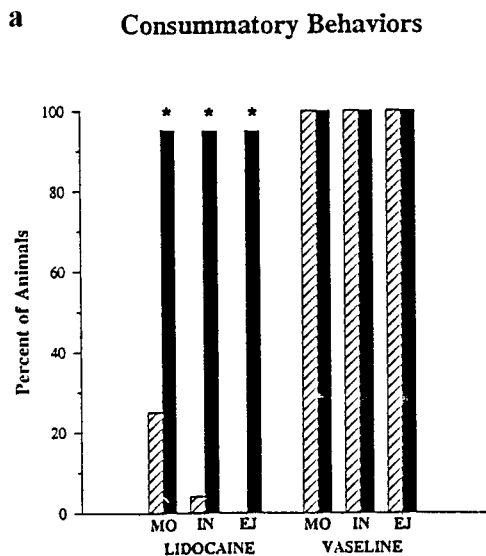
A similar “buffering” effect was recently observed for other inhibitory influences on sexual behavior, most notably castration, penile anesthesia, and the effect of the 5-HT<sub>1a</sub> receptor agonist 8-OH-DPAT (Centeno, Coopersmith, and Pfaus, 2001). In this study, male rats received either 1 (inexperienced) or 10 (experienced) copulatory experiences to at least one ejaculation each with sexually receptive females at 4-day intervals. These males were given a final copulatory test following either penile anesthesia (5% lidocaine versus vaseline rubbed on the penis), castration with an intervening month, or treatment with 1 mg/kg of 8-OH-DPAT, a drug that dramatically facilitates ejaculation, often on the first intromission, once copulation is initiated. All sexually experienced males showed normal patterns of mounts, intromissions, and ejaculations following penile anesthesia, whereas significantly fewer sexually inexperienced males mounted repeatedly but did not intromit or ejaculate (Fig. 4a). Significantly more sexually experienced males maintained their ability to mount, intromit, and ejaculate 1 month after castration compared to sexually inexperienced males (Fig. 4b). Finally, sexually experienced males treated with 8-OH-DPAT were able to ejaculate, whereas none of the sexually inexperienced males attempted to copulate following this treatment, although nearly all of the sexually inexperienced males copulated to ejaculation following control treatment with saline (Fig. 4c). Copulatory experience thus provides a powerful disinhibitory influence on sexual behavior.

Copulatory experience can alter other reproductive behaviors in rodents, especially the propensity for males to display infanticide or parental behavior. In many rodent species, adult virgin males tend to kill conspecific young that they encounter. Such infanticide is thought to serve as a male reproductive strategy because infanticidal males may then mate with the lactation-interrupted females whose pups were killed. In contrast to virgin males, males that have sired a litter only rarely kill young and are thus “protected” from harming their own progeny. There is now general agreement that the transition from the infanticidal

behavior seen in virgin males to the noninfanticidal behavior characteristic of reproductively active males is dependent on both copulation and postcopulatory cohabitation with the pregnant female. However, the relative importance of these two variables is also dependent on the species or strain under examination. In some rodents, copulation alone is sufficient to inhibit infanticide in virtually all males by the time their own progeny are born 3 weeks later (Elwood and Kennedy, 1991). In CF-1 mice, this copulation-induced inhibition of infanticide is dependent on ejaculation having occurred (vom Saal, 1985), and a similar observation has been made for males of the Wistar albino strain (Mennella and Moltz, 1988). In contrast, although sexual experience (trials with multiple ejaculations) or cohabitation with a pregnant female for 14 days were both effective in reducing rates of infanticide in laboratory-reared Long-Evans males, both experiences together were necessary to reduce infanticide in Long-Evans males purchased from a commercial breeder (Brown, 1988). However, copulation followed by cohabitation with a nonpregnant female was not sufficient to reduce infanticide in males from a commercial breeder, indicating that close proximity to, or experience with, pregnant females was critical.

Coopersmith and Pfaus (1997) examined the type of sexual experience necessary to disrupt infanticide in Wistar males and whether pelvic nerve transection would eliminate the effect of sexual experience. Adult virgin Wistar males were given an initial 30-min infanticide test to determine their baseline responsiveness toward a 1-day-old rat pup, after which they were categorized as either infanticidal (90%) or noninfanticidal (10%). A week later, males received different types of sexual experience with a receptive female for 20 min in a semicircular arena. Control males were placed into an empty arena for 20 min. All males received a second infanticide test 3 weeks later. Previously infanticidal males allowed to copulate to one ejaculation were significantly less likely to display infanticidal behaviors during the second test compared to males that were allowed only to intromit or males that were exposed to the empty mating arena

**FIG. 4.** (a, left) Proportion of rats with 1 or 10 prior sexual experiences to ejaculation that displayed mounts (MO), intromissions (IN), and ejaculations (EJ) as a function of penile anesthesia following lidocaine treatment or sham treatment with vaseline. (Right) Mean number (+SEM) of mounts, intromissions, and ejaculations in the same group of rats. (b, left) Proportion of rats with 1 or 10 prior sexual experiences to ejaculation that displayed mounts, intromissions, and ejaculations following castration and subsequent daily treatment with either dihydrotestosterone (DHT) or the oil vehicle. (Right) Mean number (+SEM) of mounts, intromissions, and ejaculations in the same group of rats. (c) Proportion of rats with 1 or 10 prior sexual experiences to ejaculation that achieved ejaculation following treatment with 8-OH-DPAT or saline.



DOSE OF 8-OH-DPAT

(Fig. 5a). However, none of the males that achieved more than nine intromissions before their first ejaculation displayed infanticidal behaviors, whereas males with fewer than nine intromissions before ejaculation were just as likely to display infanticide as those males that received nine or more intromissions only or were exposed to the empty mating arena (Fig. 5b). Likewise, rates of infanticide were high in males that were treated with the 5-HT<sub>1a</sub> agonist 8-OH DPAT, which causes males to ejaculate with few, if any, prior intromissions, whereas pelvic nerve transections abolished the inhibitory effect of intromissions and ejaculation (Figs. 5c and 5d). Taken together, our results indicated that a sufficient amount of genital stimulation prior to and including ejaculation is necessary to inhibit the tendency of Wistar males to display infanticidal behaviors 3 weeks later and that stimulation of the pelvic nerve is critical for this inhibition.

## SYNTHESIS AND GENERAL DISCUSSION

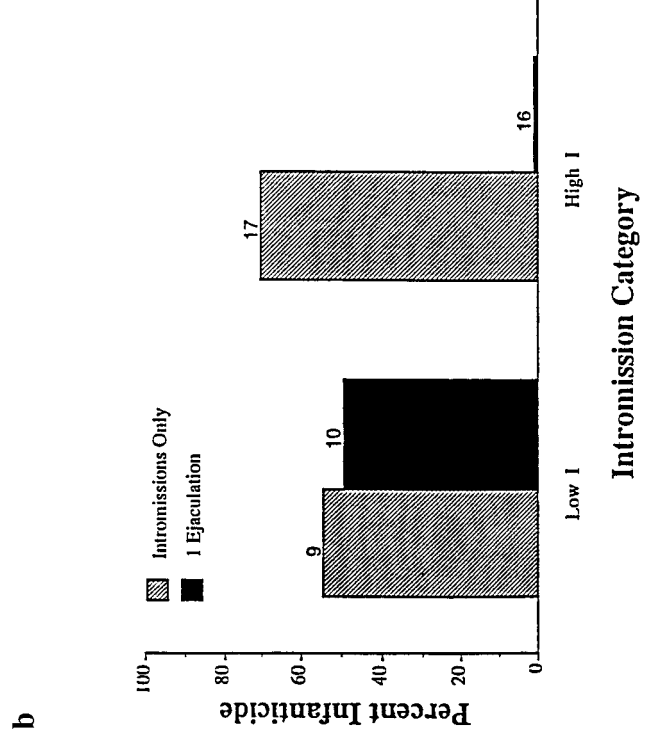
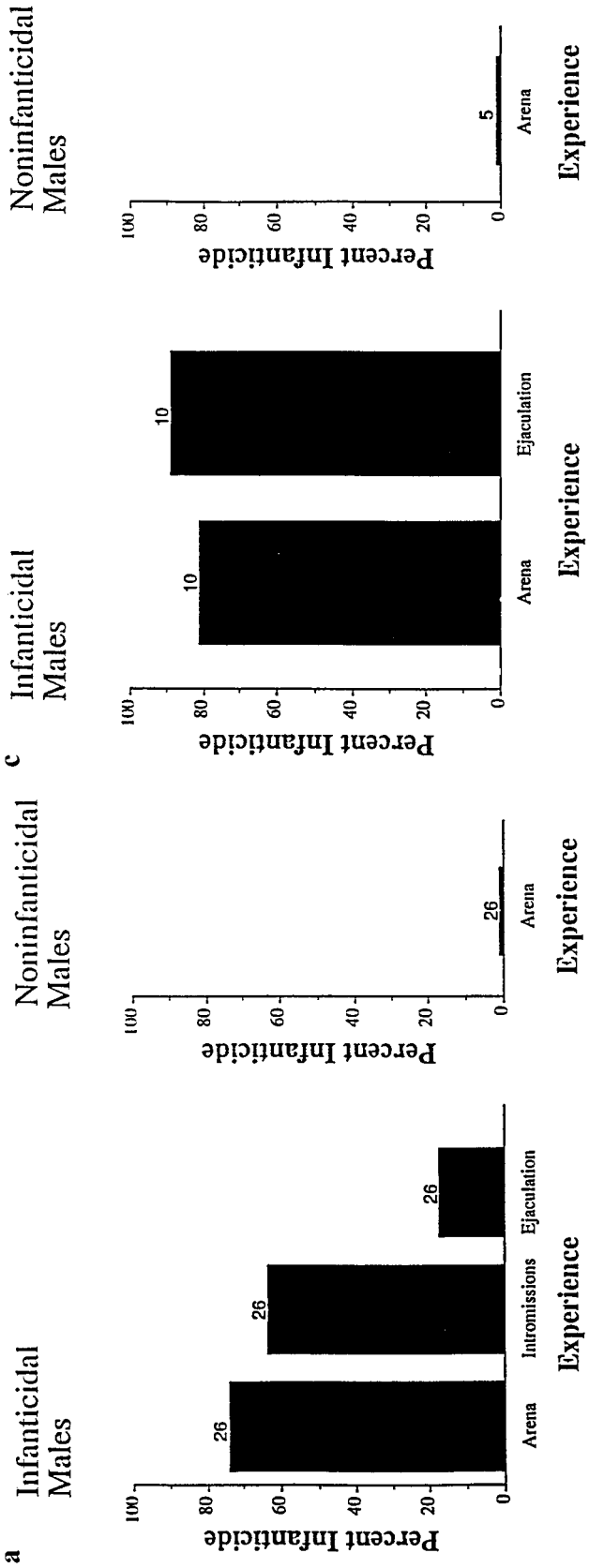
In this article, we have provided evidence that learning produces both short- and long-term changes in appetitive, precopulatory, and consummatory aspects of sexual behavior. In some cases, learning can alter behaviors that are typically considered instinctual or “hardwired” such as certain mating strategies, in addition to those that are generated by hormone actions in the brain, such as copulatory responses. By analogy, instinct and hormones appear to “set the stage” for sexual responding, whereas learning appears to “write the play,” to determine the kinds of stimuli that animals will respond to and how vigorously such responses will be made. This interplay is exemplified in conditioned sexual partner preference: although ejaculation is clearly determined by hormone actions in the brain and periphery, the direction of the ejaculation, i.e., the female that receives it in a group-mating situation, is determined by previous sexual experience. This conditioned ejaculatory pref-

erence also reveals a division between copulation and mating, in which the expression of mounts and intromissions appears to be indiscriminant during the early consummatory period, but become more discriminating as the male nears ejaculation. This results in the male directing his ejaculations toward females bearing cues that were paired previously with sexual reward. Likewise, a high degree of sexual experience can “buffer” males partially or completely from the disruptive effects of certain physiological treatments, such as castration, penile desensitization, or deafferentation; psychological treatments such as novelty stress; or the effects of certain drugs.

### Neural Correlates

A number of studies have examined the neuroanatomical correlates of copulatory stimulation in male and female rats using the stimulation of immediate-early genes as markers of neuronal “activation” (Baum and Everitt, 1992; Coolen, Peters, and Veening, 1996; Dudley, Rajendren, and Moss, 1992; Greco, Edwards, Michael, and Clancy, 1998; Heeb and Yahr, 1996; Kollack and Newman, 1992; Meddle *et al.*, 1997; Polston and Erskine, 1995; Pfaus *et al.*, 1993, 1996; Tetel, Getzinger, and Blaustein, 1993; Wersinger, Baum, and Erskine, 1993; Wood and Newman, 1993). Distinct patterns of activation have been found in hypothalamic and limbic structures, including hormone-concentrating regions of the medial preoptic area, bed nucleus of the stria terminalis, lateral hypothalamus, paraventricular hypothalamus, ventromedial hypothalamus, medial amygdala, lateral septum, hippocampus, ventral premammillary nucleus, subparafascicular thalamus, ventral tegmentum, central grey, along with other limbic and motor structures, such as the accessory olfactory bulbs, nucleus accumbens, caudate-putamen, cingulate and piriform cortex (reviewed in Pfaus and Heeb, 1997). Taken together with electrophysiological and lesion data, some of these structures appear vitally important for the generation of sexual arousal and copulatory responses (e.g., medial preop-

**FIG. 5.** (a) Proportion of rats that displayed infanticidal behavior following copulation to ejaculation, copulation with intromissions but no ejaculation, or exposure to the mating arena without copulation. The propensity of noninfanticidal males not to display infanticide was not altered by exposure to the mating arena. (b) Proportion of rats that displayed infanticidal behavior following intromissions alone or ejaculation with either a low (i.e., >9) or a high (<9) number of preceding intromissions. (c) Proportion of rats that displayed infanticidal behavior following exposure to the test arena or copulation to ejaculation after treatment with 8-OH-DPAT. (d) Proportion of rats that displayed infanticidal behavior following exposure to the test arena or copulation to ejaculation after pelvic nerve transection.



**Experience**

**Experience**

**Intrusion Category**

tic area, ventromedial hypothalamus, and ventral tegmentum), whereas others are important for the generation of sexual excitement and instrumental responses for secondary sexual reinforcers (e.g., accessory olfactory bulb, basolateral and medial amygdala, nucleus accumbens). Still others may be important for sexual inhibition, especially the refractory period following ejaculation or a large number of vaginocervical stimulations (e.g., medial preoptic area, lateral septum, lateral hypothalamus, ventromedial hypothalamus, and medial amygdala).

We have found increases in Fos expression in piriform cortex, nucleus accumbens, basolateral amygdala, and lateral hypothalamus in the brains of male rats following the presentation of an odor that had been paired previously with sexually receptive females. Likewise, engaging in a learned social proximity response induces Fos in regions of the male Japanese quail brain, including the ventral hyperstriatum (a homolog of the mammalian nucleus accumbens), medial archistriatum, and nuclei of the stria terminalis (Tlemcani *et al.*, 2000). Although our understanding of the neuroanatomy of conditioned sexual responding is still rudimentary, these findings suggest that conditioned cues can tap into existing copulatory pathways. The conditional activation of these pathways by distal or proximal CSs may be sufficient to drive sexual excitement and arousal in experienced animals, thus focusing their attention toward sexual incentives and appetitive sexual behaviors and away from competing incentives or behaviors.

### ***What Is the "Purpose" of Learning in Sexual Behavior?***

Why do animals need to learn about sex? Would it not be simpler for sexual response systems to be fixed and hardwired? Hardwired systems lack flexibility, and a lack of flexibility in sexual responding would result in mating systems that could only exist under certain optimal internal and/or external conditions and in which only a limited kind of sexual selection could take place. Flexibility in responding gives different species an enormous amount of chance to recombine in different ways, yielding a higher degree of diversity. But therein lies a paradox: Although experience and learning provide the basis for this flexibility within and across species, these processes constrain the individual's attention to sets of stimuli and patterns of behavior that are known to "work," i.e., that result in the proximal goal of sexual reward. Such stimuli and behavior are likely to differ from animal to

animal based on each animal's sexual experience. How excited an animal gets in anticipation of sex; how willing an animal is to work for sexual reinforcement; where an animal goes to find a mate; how vigorous the courtship, solicitation, and copulation; and which potential mate an animal chooses to copulate or ejaculate with are all determined by the counterbalancing of experience and conditioning on one hand and instinctual responses to unconditionally arousing stimuli (both internal secretions and external cues) on the other. The integration of these two influences may occur in the theoretical construct of "sexual arousability" as defined by Whalen (1966). Whalen argued that steroid hormones induce sexual motivation essentially by inducing the ability to be aroused by sexual incentives in the environment (e.g., Alexander and Sherwin, 1991). However, the ability to be aroused or excited by sexual incentives also requires previous experience with the incentive, and such experience in highly trained individuals can lead to expectations of normal performance that can sometimes supplement or even substitute for decreased hormone actions.

### ***What Do Females Learn?***

Currently, we know much more about the role of learning in the sexual behavior of males. This is especially true in rats and is due, in part, to a greater number of appetitive responses that have been identified and studied in males. It is also due to a concentration on sexual receptivity (i.e., the lordosis reflex) as the defining measure of female sexual behavior. And yet, females display complex patterns of behavior that allow them to control virtually all aspects of sexual interaction with males. Females attract and solicit males (Beach, 1976; Erskine, 1989; McClintock, 1984; Wallen, 1995); pace the rate of sexual interaction (Erskine, 1989; Pfaus *et al.*, 1999); and show a variety of appetitive behaviors, including wheel running (Richter, 1927), maze learning (Drewett, 1973; Meyerson and Lindstrom, 1973; Eliasson and Meyerson, 1975), operant bar pressing (Beck, 1971, 1974, 1978; Bermant, 1961; Bermant and Westbrook, 1966; French, Fitzpatrick, and Law, 1972; Keverne, 1972), conditioned place preference (Oldenburger, 1992; Paredes and Alonso, 1997; Paredes and Vazquez, 1999), and level changing in bilevel chambers (Pfaus *et al.*, 1999). These occur either in anticipation of sex, as a function of steroid hormone action, or as an interaction of the two. In rats, the patterns of solicitation and copulation differ in group mating situations between dominant and subordinate females and also between wild and do-

mesticated females (McClintock, 1984; McClintock, Anisko, and Adler, 1982). It is not clear to what extent hormone-driven behaviors, such as solicitation, pacing, or even the display of lordosis, can come under operant control or be augmented by classically conditioned stimuli. Indeed, a sexually active male may be an unconditioned incentive to a sexually receptive female (e.g., Ågmo, 1999). It is clear, however, that sexually receptive females learn to use the environment to maximize their ability to pace copulatory contact with males (Pfaus *et al.*, 1999) and that they can alter their appetitive and precopulatory behaviors accordingly in different environments.

### Human Considerations

A role for learning in the sexual behavior of animals also has profound implications for our understanding of human sexual arousal and sexual preferences, especially as they concern the development of extreme forms of sexual behavior, including paraphilias or deviant sexual preferences. Deviant sexual preferences and behaviors are thought to develop through conditioning processes (e.g., Abel and Blanchard, 1974; Laws and Marshall, 1990; McGuire, Carlisle, and Young, 1965), and conditioning techniques are often employed in an attempt to reduce or eliminate these preferences. Common techniques include directed masturbation (in which subjects masturbate to nondeviant themes), satiation (in which subjects masturbate well past the first orgasm to deviant themes), and masturbatory reconditioning (in which subjects masturbate to nondeviant themes followed by fantasizing to deviant themes) (Brownell, Hayes, and Barlow, 1977; Marquis, 1970; Marshall, 1979). These techniques are often employed despite limited evidence of their effectiveness (Laws and Marshall, 1991; Johnston, Hudson, and Marshall, 1992). The finding that pairing a stimulus with sexual reward (i.e., during the postejaculatory period) increases the incentive value of sex partners bearing that stimulus suggest that directed masturbation should be followed by exposure (either real or fantasized) to nondeviant stimuli and may explain the weak effects of satiation and masturbatory reconditioning. Additionally, the findings that a stimulus paired with sexual frustration (i.e., sexual stimulation that does not accompany sexual reward) or with lack of sexual stimulation in a sexual context (i.e., with a sexually nonreceptive partner, as in the CEP for an unscented female if the conditioned odor is paired with a nonreceptive female) decreases the incentive value of sex partners bearing that stimulus

suggest new venues for conditioning of sexual preferences in clinical treatment. Pairing deviant stimuli with sexual frustration or with diminished sexual stimulation or gratification may enhance the therapeutic effectiveness of directed masturbation to alter sexual preferences.

It is not known to what extent the attraction to more "normal" physical attributes (e.g., a certain body type, shape of face, and eye and hair color) are also produced by conditioning, especially during an individual's early sexual experience. Many factors appear to be related to the attractiveness of a mate in humans, including physical, personality, and social features (see Buss and Schimdt, 1993; Townsend and Law, 1990). Humans also form pairbonds of variable length. Buss and colleagues have described long- and short-term mating strategies with their primary focus and evidence stemming from studies of sex differences. From their studies, it is clear that different features are preferred and different criteria are used for different types of relationships. Like the prairie vole, people tend to enter into relationships that are of a long-term nature in which selective aggression, biparental care, cohabitation, and perhaps social preferences are displayed (Kenrick *et al.*, 1990). Moreover, despite implicit expectations of sexual exclusivity, pair-bonded humans also engage in extrapair copulation. Accordingly, it appears that human mating patterns have much in common with mating patterns observed in other species. Preferences are not global, but are composed of several competing factors. People exhibit preferences for copulatory partners. Buss and colleagues have used the phrase "short-term mating" to describe transient relationships that are unrelated to child rearing and characterized by partner preferences that rely most heavily on physical characteristics for both men and women. These are essentially copulatory preferences. Although Buss and colleagues posit that evolved psychological mechanisms underlie these preferences, they offer no proximal mechanism for the establishment of these preferences. Evidence of learned sexual preferences may fill this void.

CEP may occur during actual copulation or during masturbation, with the features of real or fantasized partners becoming preferred. The development of preferences during actual copulation would explain the anecdotal evidence that individuals often pursue new partners with some features similar to previous partners (e.g., Stendahl, 1821/1959). Even following past abuse, partners with similar features are often sought despite the negative consequences. Preferences developed during masturbation may also contribute

to the adherence to cultural values. The features of fantasized partners could be composed of culturally valued characteristics such that when these are paired with sexual reward, preferences would be established or strengthened. Thus, cultural values may also determine what features will be preferred in a mate. This can explain not only the status quo of physical preferences within a culture, but also how those cultural preferences can change from era to era.

Accordingly, the “evolved psychological mechanism” that guides copulatory preferences according to Buss may in fact be learning. Learning provides an efficient mechanism to guide behavior toward the stimuli that are predictive of fertility and reproductive success. Sexually imprinted maternal stimuli may be excellent predictors of fertility. Classically conditioned stimuli paired with sexual reward are likely to be excellent predictors of receptivity. Moreover, the relative impact of imprinted and conditioned stimuli in sexual preferences in humans may be magnified in comparison to the rat because sexual status (i.e., menstrual cycle) is masked in women (Alexander and Noonan, 1979). In an incentive motivation analysis, sexually imprinted and conditioned stimuli would be expected to have more powerful influences in the absence of direct sexual UCSs. This would indeed be the case in men for whom the reproductive status of women cannot be determined directly. Accordingly, copulatory attempts may be appropriately or inappropriately directed toward or away from women based largely on learned stimuli rather than actual reproductive status.

Finally, the finding that the male’s first ejaculation and postejaculatory interval were sufficient for the induction of CEP in our studies would seem to suggest that a “critical period” for the development of conditioned sexual responses might exist in other mammalian species. Secondary stimuli associated with the initial experience of sexual arousal and/or gratification may become conditioned such that they are designated subsequently as attractive and preferred. Even if some stimuli are innately preferred, others could be added by experience which would maintain a degree of diversity in features that are considered attractive within a single human social system or culture. By not having to vie for a few partners that possess a narrow range of desired features, human sexual behavior is free to vary, with humans free to discover their own optimal modes of sexual attraction and expression.

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