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The Role of Pavlovian Conditioning in Sexual Behavior: A Comparative Analysis of Human and Nonhuman Animals

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The literature on human sexual deviations is replete with case studies and behavior therapies that demonstrate successful treatment of maladaptive sexual behavior acquired through Pavlovian conditioning. Ironically, the empirical research with humans in this area is limited and plagued by methodological confounds. Nonhuman animal studies have provided some information about the mechanisms of the role of Pavlovian conditioning in sexual arousal/behavior but have not been well coordinated with clinical research. The present paper serves to highlight the major empirical findings and theories of these two disparate bodies of literature, briefly discuss how they have emerged over time, and finally discuss their overlap and make connections between animal and human research on sexual arousal.

It has been widely accepted that learning factors contribute to the etiology of human sexual deviations. For the purposes of this paper, "sexual deviations" are defined as aberrant, maladaptive, and compulsive behaviors such as paraphilias, fetishes, and sexual offenses. Research on the role of Pavlovian conditioning in human sexual arousal has been focused heavily on the acquisition, development, and treatment of sexual deviations. The literature on humans includes a mixture of empirical research, theories of sexual deviations and an abundance of literature on treatment and case studies demonstrating the effectiveness of behavioral therapy. The role of learning in the sexual behavior of animals may have important implications for our understanding of human sexual arousal and sexual deviations, in particular with regard to the development of certain forms of sexual behavior such as paraphilias or sexual fetishes. However, the potentially relevant research on nonhuman animals has not been well-integrated with the clinical literature.

Although a thorough review of the human and animal literature on sexual arousal is beyond the scope of this paper, the paper will attempt to briefly review these two bodies of literature, discuss how these areas have changed over time, and draw parallels and overlap between them. The organization of this paper is first to review theories, behavior therapies for sexual deviations, and empirical studies conducted with humans. Second, a description of the research that has been conducted with animals within the framework of several theories will be presented. Third, the paper will describe parallels and make connections between clinical and animal research.

Research with Humans

Theories of Deviant Sexual Behavior as Mediated by Pavlovian conditioning

Although there are a wide variety of theories of abnormal sexual behavior (e.g., Geer & O'Donohue, 1987), common to most of these theories is the

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involvement of conditioning processes. Behavioral theories have most strongly emphasized the role of Pavlovian conditioning in the development of sexual deviations. Krafft-Ebing (1886) implicated conditioning in describing a case of masochism that was suggested to have developed as a result of the child feeling friction on the penis while being held across a parent's lap when being spanked. Alfred Binet, the French psychologist best known for developing intelligence tests for school children, proposed that sexual deviations were often the result of accidental experiences with a deviant act that was presumably rewarding (Binet, 1888). Later, Jaspers (1963) and Rachman (1961) independently proposed that sexual deviations were the result of an accidental pairing of an abnormal stimulus with sexual arousal or ejaculation. Laws and Marshall (1991a) proposed a similar model to those of Jaspers (1963) and Rachman (1961) except that, in addition, they included the involvement of second order conditioning such that once a stimulus was conditioned, it came to serve the same role as the unconditioned stimulus (sexual arousal) and became paired with another conditioned stimulus that would come to acquire sexual properties. Laws and Marshall (1991a) also emphasized the importance of operant conditioning and social learning in developing and conserving deviant interests.

McGuire, Carlisle, and Young's (1965) hypothesis is similar as those discussed above except that "fantasy" is suggested to play a pivotal part of the process. They proposed that accidental early sexual experiences later resulted in the pairing of masturbatory activity with fantasy. They suggested that through this process of higher order conditioning, deviant preferences became predominant and nondeviant preferences either dramatically dropped in value or simply faded away. More recently, Marshall and Eccles (1993) proposed a similar theory by suggesting that Pavlovian conditioning processes could be initiated by pairing a conditioned stimulus (CS) with tactile-induced sexual arousal (e.g., a first order elicitor, such as genital contact) or with a nontactile stimulus that elicited sexual arousal. In the latter case, the nontactile stimulus served as a second-order elicitor of sexual arousal after it has been paired with the first order elicitor.

Clinical theories of sexual deviations have been focused on sex offenders. According to the deviant arousal theory (Abel & Blanchard, 1974), sex offenders are more sexually aroused by stimuli associated with the sexual offense (e.g., thoughts of rape or sex with a child) than by stimuli that are relevant to the crime but occur between mutually consenting individuals. This has been addressed mainly in laboratory studies using plethysmograph measures of genital arousal (changes in penile circumference). Participants in these studies are typically told to imagine the sexual activity described while listening to audiotapes or viewing slides. The results of these studies have provided only mixed support with the strongest support found in nonfamilial child molesters. In the most convincing research conducted with this population (Barbaree & Marshall, 1989; Marshall, Barbaree, & Christophe, 1986), 35% to 40% of convicted male child molesters exhibited greater sexual arousal to children than to adults; an additional 15% showed equally high arousal to both young children and adults; and none of the non-deviant control group adults showed greater arousal to children than adults. In contrast, most evidence from plethysmograph studies fail to demonstrate that rapists might be more sexually aroused by fantasizing about rape imagery rather than mutually consenting sexual imagery (for review, see Barbaree, 1990). Thus, there has been little support for the deviant sexual arousal theory.

A recent and multifactorial theory of sexual offending has been proposed by Marshall and colleagues (Marshall, 1989; Marshall, Hudson, & Hodgkinson, 1993). They suggest that a lack of intimacy in adulthood and the resulting experience of loneliness predispose some individuals to be sexually aggressive. This deficiency in adult intimacy may interact with sociocultural influences, conditioning events, and biological factors in the development and maintenance of deviant sexuality (Marshall & Eccles, 1993). According to the model, the developmental history of sex offenders renders them vulnerable to various influences and events (Smallbone & Dadds, 1998; Weeks & Widom, 1998). Presumably, the vulnerability may arise from failure during childhood of the parents to form a secure attachment bond between themselves and the child. At puberty, the vulnerable male may begin to develop sexual urges yet feel socially inept, especially with female peers. Finally, the individual develops nonthreatening sexual thoughts that may include child molestation, voyeurism, and fetishism (Marshall & Eccles, 1993). These nonthreatening and distorted thoughts may become incorporated into masturbatory practices and serve to initiate Pavlovian conditioning (McGuire et al., 1965). In addition, the individual may become attracted to cultural messages that perpetuate gender role stereotypes, such as the view that males are naturally aggressive and women are inherently passive. Therefore, this multifactorial theory and others like it (e.g., Finkelhor, 1984; Marshall, 1989, Marshall & Barbaree, 1990) combine various nonconditioning factors such as vulnerability with Pavlovian conditioning to account for the acquisition and maintenance sexual deviations.

Behavior-Therapy Techniques

To date, there are various types of therapies and techniques (e.g., cognitive, social, surgical castration, and psychopharmacology including antiandrogens, self-regulation and self control, and combinations of these) used to treat deviant sexual behavior. However, behavior therapy techniques have been developed to specifically target conditioning in its role in the acquisition and maintenance of deviant sexual behavior. These techniques have been focused on both reducing deviant sexual arousal and behavior to deviant stimuli, and increasing sexual arousal and behavior to nondeviant stimuli. Two major behavior-therapy techniques that have typically been used are masturbatory reconditioning and aversive conditioning.

Masturbatory reconditioning involves several different procedures for the clinical modification of sexual arousal (Laws & Marshall, 1991b). Orgasmic reconditioning, first described in detail by Marquis (1970), is a form of masturbatory reconditioning in which the client masturbates while fantasizing normative sexual behavior with adult partners. If fantasizing is involved, it may require the client to switch from a deviant fantasy to a conventional one at the point of orgasm. The rationale is that repeated pairings of appropriate images with masturbatory-induced arousal or orgasm would gradually come to replace deviant images as the preferred fantasies via Pavlovian conditioning.

Another masturbatory reconditioning technique is based on a suggestion by Guthrie (1935) that by repeatedly presenting a stimulus and evoking the undesirable response, exhaustion of the undesirable response would occur and an alternative response would come to be associated with the stimulus. Marshall (1979) and Marshall and Lippens (1977) later developed a variation of this

procedure that they called “satiation.” The procedure involves having men masturbate to images related to their deviant behavior immediately after they have ejaculated and when they usually cannot be aroused again. Some researchers (e.g., Davison, 1968; Jackson, 1969) have reported success in having clients masturbate up to the point of orgasm to appropriate fantasies followed by satiation as a means to replace deviant interests with more acceptable sexual desires. However, evidence in support of these variants on masturbatory reconditioning is weak (Laws & Marshall, 1991b).

Aversive conditioning is another major approach to altering undesirable sexual behavior (Quinsey & Earls, 1990; Quinsey & Marshall, 1983; Rachman & Teasdale, 1969). This approach involves pairing an aversive stimulus, such as an odor, with deviant behavior, slides of deviant behavior, or fantasies of deviant behavior. Chemical treatments that induced nausea, such as apomorphine were first used as aversive stimuli (e.g., Raymond, 1956; Freund, 1960; Blackmore et al., 1963) but they were quickly replaced with mild electric shock delivered to the forearm or leg (e.g., Marks & Gelder, 1967; McGuire & Vallence, 1964; Earls & Castonguay, 1989; Marshall, 1971; 1973). Due to changes in procedural standards in human experimentation and ethical concerns (American Psychological Association, 1973), researchers sought out alternatives to using electric shock in aversive conditioning. Noxious odors were one alternative (e.g., Laws, Meyer, & Holmen, 1978). Bancroft (1974) summarized the results of studies that used electric shock as the aversive stimulus, including controlled comparative studies, and concluded that shock was effective in reducing deviant sexual responses. However, there was limited evidence on the long-term effects of this technique. It is also not clear whether electric shock is a more effective treatment than olfactory aversion. Some researchers question whether aversion therapy in any form has ever convincingly demonstrated permanent changes in sexual behavior (Quinsey & Earls, 1990; Quinsey & Marshall, 1983). Nevertheless, electric shock is rarely used today.

Another form of aversive conditioning is referred to as “covert sensitization.” In this procedure, a person imagines himself or herself engaging in the deviant behavior and when he/she has achieved a vivid image, they are asked to imagine a highly unpleasant scene such as nausea, being caught, or embarrassment (Cautela, 1967; 1971). The procedure is called “covert” because the individual has to “imagine” a sequence of arousing and aversive images as they are described to him/her by a therapist. Maletzky (1980; 1991) extended this procedure by pairing the foul odor of valeric acid or of rotting tissue with the description of a noxious scene associated with a sexually deviant act and referred to this procedure as “assisted” covert sensitization because the noxious scene was accompanied by a noxious agent to increase aversiveness. The procedure resulted in exceptionally good long-term effects in laboratory-controlled studies with large samples of sex offenders as well as uncontrolled case studies. However, because some participants were receiving multiple types of treatments, it is not clear whether the long-term effects were solely the result of assisted covert sensitization, some other treatment, or a combination.

Although most behavior-therapy techniques have focused mainly on Pavlovian conditioning, some techniques have been operant based. Fading or shaping (Quinn, Harbison, & McAllister, 1970; Barlow & Argras, 1973; Bancroft, 1971) has been used to increase sexual arousal to nondeviant stimuli. During fading or shaping, a deviant stimulus is gradually changed to a more conventional

stimulus. For example, Barlow and Argras (1973) used slides showing attractive men that were gradually faded and replaced by those of women. This approach has also been based on imagery by instructing an individual to gradually change the nature of his erotic fantasies (Bancroft, 1971).

In a review of clinical conditioning studies of behavioral reorientation of pedophiles, Kelly (1982) found that several clinical techniques were used in both uncontrolled case studies and experimental designs. These techniques included aversive conditioning, masturbatory reconditioning, and covert sensitization methods. Kelly (1982) found that 75% of the 32 studies he reviewed used some form of aversive conditioning. He also found that 79% of the subjects studied in the review responded favorably to behavioral reorientation treatments of varying kinds. However, problems with these studies such as an overrepresentation of published positive results, lack of control procedures, and problems with assessment make this statistic difficult to interpret.

Broader-based treatment programs that incorporate cognitive mediation processes (i.e., perceptions, attitudes, beliefs), social skills, and other nonconditioning approaches have been in existence since the 1970's (e.g., Marshall & Williams, 1975; Abel, Blanchard, & Becker, 1978). Some contemporary treatment programs for sex offenders continue to use masturbatory reconditioning and covert sensitization procedures, but in the context of more comprehensive therapy programs that address cognitive and social processes (Marshall, Jones, Ward, Johnston, & Barbaree, 1991).

Empirical Studies of Human Sexual Arousal

More than two decades ago, Langevin and Martin (1975) cautioned that "there have been few empirical demonstrations that Pavlovian conditioning procedures can be used to elicit penile tumescence" (p. 350). In a more recent review of the empirical literature, O'Donohue and Plaud (1994) concluded that the question of whether sexual arousal could be conditioned was still open for debate. They argued that, although the current literature was replete with case studies demonstrating the effectiveness of various techniques involving conditioning, there was little empirical evidence for its role in sexual arousal.

Empirical research of this nature began shortly after the development of a method employed by Freund (1963) to measure penile volume change. Shortly afterwards, Rachman (1966) conducted one of the earliest studies on the Pavlovian conditioning of sexual arousal. In his study, a photographic slide of a pair of black boots (CS) was paired with a slide of an attractive nude woman (US). After numerous pairings, a conditioned penile arousal response developed to the slide of the boots, essentially resulting in what might be termed a "sexual fetish." Consistent with behavioral accounts of sexual deviation, it was concluded that sexual arousal could be conditioned to previously neutral stimuli. Further, this research provided support that sexual deviations could result from the pairing of sexual arousal and previously neutral stimuli.

Much of the early empirical research on human sexual arousal, such as Rachman's (1966), was plagued by lack of proper control procedures, participant awareness, small sample sizes, and voluntary control of the penile tumescence or cognitive ability to inhibit erections (Laws & Rubin, 1969; Henson & Rubin, 1971). Langevin and Martin (1975) followed up previous experiments with two Pavlovian conditioning experiments designed to control for prior methodological

flaws. They presented slides taken from non-erotic material (CS) to assess baseline responding as well as probe trials to assess adaptation of the CS. Sexually explicit slides served as the US. Several CS and US pairings resulted in penile tumescence to the conditioned stimuli, and the conditioned response extinguished when the CS was presented alone for 10 trials. However, the researchers did not include a backward or a random control procedure to rule out non-associative effects, nor did they pretest the US with a physiological measure but rather relied on subjective ratings of level of arousal.

To date, only one laboratory experiment of human male sexual arousal that includes appropriate control conditions has been reported. In this experiment, Plaud and Martini (1999) conditioned male sexual arousal across 3 sessions with 9 subjects. Each session was composed of 15 stimulus periods and 15 detumescence periods. Three subjects participated in each of the three experimental conditioning procedures. Sexually explicit visual stimuli preselected by each subject were utilized as the US, and a slide of a penny jar was employed as the CS. In the first procedure, short delay conditioning, the CS was presented for 15 s, followed immediately by the US for 30 s (with a CS/US overlap of 1 s). Interspersed in the 15 trials were 5 probe trials in which the CS was presented alone. Following each trial, a 2 min detumescence period permitted a return to baseline of the response. The second procedure was a backward conditioning procedure that was identical to the conditioning procedure except that the US was presented before the CS. In the third procedure, a random control condition, the presentation of the CS and US was determined randomly to test for non-associative effects. Results indicated that participants showed systematic increases in penile tumescence from baseline in the short delay condition procedure but not during either of the control conditions.

One problem with empirical studies with humans may be with using penile plethysmography to measure sexual arousal. Some findings suggest that sexual arousal may be voluntarily controlled. For example, in one experiment (Laws & Rubin, 1969), when participants were asked to inhibit their erections while exposed to erotic motion pictures that previously resulted in full erections, they showed a 50% reduction in their erections. In addition, when asked to develop an erection in the absence of erotic stimuli, every participant was able to do so. Thus, it is unclear whether the ability of participants to voluntarily control their sexual arousal response plays a role in human empirical research and to what degree.

To date, only two studies have been conducted to examine the role of conditioning in female sexual arousal in humans. Speculations for this relatively small amount of research include explanations such as: learning is less likely to be heavily involved in female sexual arousal (e.g., Domjan & Hollis, 1988) or that the conditioned stimuli used to condition sexual arousal might be biased in their effectiveness toward males compared to females in that males may be more sensitive to visual stimuli in these paradigms (e.g., Murnen & Stockton, 1997). Whatever the reason(s), determining the optimal parameters that facilitate a conditioned response may contribute to the difficulty of conducting conditioned sexual arousal studies in females. In one experiment (Letourneau & O'Donohue, 1997), subjects were given an amber light for between 30 and 130 s followed by a 1 or 10 s interstimulus interval and an erotic video. Control subjects were given the same stimuli except in an explicitly unpaired fashion. Fifty conditioning trials were conducted and 15 probe trials consisted of the 30 or 130 s CS presented alone. Subjective levels of arousal and vaginal pulse amplitude (VPA) were measured during probe trials. Both, experimental and control subjects showed an increase in

subjective ratings of arousal and VPA during exposure to the erotic video from resting. However, no group differences in either measure were found during CS probe trials. It is unclear why no differences were found in the present experiment but there are several possibilities: the USs were too weak, the CS may not have been salient enough, too few participants, extinction of the probe CSs during testing, or other insufficient parameters.

A more recent experiment (Hoffman, Janssen, & Turner, 2004) explored conditioning of the sexual arousal of women by measuring VPA in a more complex experimental design. First, they compared genital sexual arousal between males and females using the same experimental paradigm. Second, they tested for the presence of selective associations, that is whether some CSs become more readily associated with some USs, by presenting photographs of either a sexually relevant CS (abdomen of the opposite sex) or a sexually irrelevant one (gun). Third, they varied participant awareness by varying the time duration of the CSs between very brief and long. Eleven different 30 s videos of explicit heterosexual activity were used as USs. Each participant was exposed to both CS types but only one of them was paired with a US (the "CS+"). A CS that was not paired with a US (CS-) was included in 11 conditioning trials. Thus, during each trial, participants in the paired conditions received a CS- for either 30 ms or 10 s, a 40 s ISI, and a CS+ for 30 ms or 10 s immediately followed by a 30 s US. Eleven trials were conducted with an ITI of about 2 min. An unpaired control group was given a 10 s CS+, a 10 s CS-, and a 30 s US in an explicitly unpaired fashion. Results demonstrated that when the CSs were presented subliminally, both men and women showed more conditioned arousal to the sexually relevant CS (abdomen) than the nonsexually relevant CS (gun). However, when the CS was consciously perceived, men showed the same response, but women showed conditioned arousal to the sexually irrelevant CS compared with the relevant one. The latter was suggested to have been due to an increase in autonomic nervous system responding such that women showed greater general arousal (as indicated by skin conductance responses) to the gun than to the male abdomen.

The findings of Hoffman et al. (2004) are important for several reasons. First, this is the first experiment to demonstrate conditioned sexual arousal in women. This may have been due to the use of more effective parameters in eliciting conditioned sexual arousal. Second, the findings support the notion that awareness of the CS-US contingency may not be necessary for the occurrence of classical conditioning in humans as has been suggested by others (e.g., Lovibond & Shanks, 2002). Third, that women showed more conditioned sexual arousal to the gun than to the abdomen may indicate that sexually irrelevant stimuli might be as effective at conditioning sexual arousal as irrelevant ones; although, as mentioned, this may have been due to general arousal rather than sex-specific arousal.

In sum, empirical evidence for conditioning in human sexual arousal is scant. The interpretation of the results from existing studies is limited as a result of procedural problems and confounds. It should also be mentioned that there is still some uncertainty as to whether the human laboratory model of sexual arousal is an appropriate analogue to human sexual deviance in the real world.

Research with Nonhuman Animals

In contrast to the literature on human sexual arousal and Pavlovian conditioning, empirical research with nonhuman animals has predominated the literature in this area. Traditional learning theory has been used in a post hoc manner in an attempt to explain certain phenomena or findings generated from this empirical research. However, the theories that have driven the empirical research on sexual arousal in animals have not been traditional learning theories, such as the Rescorla and Wagner model (1972), that address trial-by-trial acquisition of conditioned sexual behaviors. Rather, they have typically been theories focused on stimulus control issues, how some cues are more effective than others in controlling various aspects of sexual behavior, on the role of functionality, and how learning elicits the emergence of new responses or changes the topography of the response.

Nature of the Conditioned Stimulus (CS)

The nature of the CS is an important theoretical issue with regard to Pavlovian conditioning and sexual behavior because it may, in part, determine the conditions under which learning occurs and the topography of the conditioned response that is elicited as a result of learning (Holland, 1984). In the tradition of laboratory studies of learning, early sexual learning studies employed arbitrary auditory and visual cues as CSs. For example, Farris (1967) presented a buzzer to male Japanese quail just before permitting them to copulate with a female. Within 20 trials, males were observed to perform conditioned courtship responses to the sound of the buzzer. In a similar experiment but using a small red light as a CS, male quail demonstrated conditioned approach behavior to the light when it was presented prior to copulation with a female quail (Domjan, Lyons, North, & Bruell, 1986). In another experiment with quail, Domjan, O'Vary, and Greene (1988) used two different CSs, a small yellow stuffed toy dog (Pound Puppy) and female quail whose appearance had been altered, by attaching two bright orange feathers to her shoulders. (The feathers reduced the likelihood of males to show unconditioned copulatory behavior toward the females). Male subjects acquired conditioned approach behavior to both types of stimuli. However, only the embellished female elicited conditioned copulatory responses such as mounting and cloacal contact attempts. Cusato and Domjan (1998) later found that development of conditioned copulatory responding requires both the presence of some of the head features of a female bird (species-specific cues) and pairing of those cues with sexual reinforcement. Thus, although arbitrary CSs such as lights and tones seem to serve as effective CSs, they appear to elicit different conditioned responses than those elicited by more female-like conditioned stimuli.

“Places” and “odors” that have been paired with copulation have also been shown to serve as effective conditioned stimuli. For example, Kippin and associates (Kippin et al., 1998; Kippin & Pfaus, 2001; Kippin et al., 2001) found that neutral odors (almond, lemon) previously paired with copulation resulted in male rats ejaculating preferentially with females that bear those odors. In other research, neutral odors paired with copulation have been shown to increase serum testosterone and luteinizing hormone levels in rats (Graham & Desjardins, 1980).

Places that serve as conditioned stimuli may become predictors of sexual activity during Pavlovian conditioning that later elicit anticipatory and/or

appetitive responses. For example, male rats learn to run from level to level in bilevel chambers in anticipation of receiving access to a sexually receptive female rat (Mendelson & Pfaus, 1989; Pfaus, Mendelson, & Phillips, 1990). This level-changing behavior can be enhanced by unconditioned olfactory cues present in the chamber, although in some strains of rats (e.g., Wistar rats) olfactory cues are necessary for the expression of the appetitive level changing (van Furth & van Ree, 1996). Male rats also develop a conditioned place preference for an environment associated with copulation with a receptive female (Agmo & Berenfeld, 1990; Hughes, Everitt, & Herbert, 1990; Mehrara & Baum, 1990; Miller & Baum, 1987; Paredes & Alonso, 1997). Similar to male rats, male quail develop both increased locomotor activity in anticipation of the introduction of a female bird into a chamber that contains a distinct context; and a conditioned place preference for a distinct chamber in which they copulated with the female quail (Akins, 1998).

There is evidence that places that become associated with sexual encounters may also increase conditioned copulatory responses in animals. For example, placing male rats in a chamber in which copulation has previously occurred results in a dramatic decreased latency to display penile erections (Sachs & Garinello, 1978). In contrast, Zamble and his associates demonstrated the difficulty of identifying which experimentally programmed cues and background cues served as the conditioned stimuli that came to be associated with sexual arousal. In several reports (Zamble, Hadad, & Mitchell, 1985; Zamble et al., 1985; Zamble, Mitchell, & Findlay, 1986), they used a procedure in which male rats were carried from a holding room and placed into a plastic tub for 10 min (the programmed cues). The rats were then transported to an adjacent room and placed on the opposite side of a conditioning arena where a receptive female rat could be seen, heard, and smelled, but not touched by the male. After several conditioning trials, males were presented with the programmed cues followed by unrestricted access to a receptive female rat. The experimenters found no differences in sexual arousal in the absence or presence of the programmed cues. They also found that extinction of the conditioned response (mean ejaculatory latency) occurred similarly in the absence or presence of the programmed cues, suggesting that the background cues present during conditioning (e.g., removal from the animal room, transport, the arena, the experimenter) also served as effective conditioned stimuli. One explanation for this may involve “overshadowing” (Pavlov, 1927); when two types of stimuli are presented at around the same time, the presence of one type, that might be more easily trained, may hinder learning about the other type. In the current experiment, the background cues may have overshadowed learning about the programmed cues. However, in another experiment, Zamble et al. (1986) demonstrated that only background cues that were novel during conditioning served as effective conditioned stimuli, whereas those that were familiar, perhaps through latent inhibition were less effective.

CS-US Relevance and Selective Associations

Seligman (1970) and Garcia and Koelling (1966) have suggested that associations between certain kinds of stimuli and responses are more readily acquired, often referred to as “selective associations.” The literature on selective associations has demonstrated that the relevance of the CS to the US influences the acquisition and maintenance of associative learning (see Domjan, 1983 for review). In animal research, a variety of conditioned stimuli may serve as effective

conditioned stimuli that later come to evoke sexual responding. However, very few conditioned stimuli seem particularly effective at eliciting consummatory aspects of responding (completing a behavior such as copulating) compared with appetitive ones (those that bring an organism into contact with a stimulus such as approach). There is some evidence that species-specific cues may be more effective than arbitrary cues in eliciting conditioned copulatory responses when the US is sex related. For example, Cusato and Domjan (1998) found that the conditioning of copulatory responses of male quail occurred when the CS contained species-specific cues (small amount of female head cues) and the US was sexual reinforcement, but not when the US was food. Prior to conditioning, the CS did not evoke an unconditioned response. Cusato and Domjan (1998) proposed that facilitation of copulatory responses by female cues may be an adaptive specialization, such that the presence of the species-specific cues represents a predisposition for males to learn to respond to cues that predict copulatory opportunity.

Stimulus relevance has been shown to influence sexual responding in a “blocking” paradigm. According to the blocking effect (Kamin, 1969), an association between a CS (stimulus A) and US is first established. Once stimulus A is well conditioned, a second stimulus (stimulus B) is presented with stimulus A during conditioning trials. If responding to stimulus B is then tested alone, prior conditioning of stimulus A may block the development of conditioned responding to stimulus B. With regard to stimulus relevance, one might predict that conditioned responding to a stimulus that is more relevant to the US may be less easily blocked by the presence of a previously conditioned stimulus. In one experiment, Koksals, Domjan, and Weisman, (1994; Experiment 1) pretrained male Japanese quail with an audiovisual stimulus that consisted of a buzzer and flashing green light (CS1), followed by copulatory opportunity with a female bird (US). Once they demonstrated asymptotic conditioned approach behavior to the CS1, a wood block (CS2) that had no resemblance to a female bird was added to the CS1 on conditioning trials. As a result, approach responding to the CS2 alone during testing was blocked or decreased compared to control groups.

In another experiment (Koksals et al., 1994; Experiment 2), the CS2 was no longer a wood block but rather a soft terrycloth object that consisted of a vertical and a horizontal cylinder that allowed for mounting and cloacal thrusts. The CS1 (buzzer and flashing green lights) was paired with copulatory opportunity with a female quail until responding occurred. Subsequently the CS1 was paired with the CS2 as in the previous experiment and the CS2 object was tested. Male quail responded with little conditioned approach to the object compared to control groups, indicating that blocking had again occurred. In contrast, when the CS2 was a similar terrycloth object that contained a taxidermically-prepared female head (species-specific cues) on top of the vertical cylinder (Koksals et al., 1994; Experiment 3), male quail responded with as much conditioned responding as control groups. The present findings may be a result of the female head CS2 being more salient, and thereby attracting more attention and more readily forming an association with the US (Lolordo, Jacobs, & Foree, 1982). Alternatively, the findings may be attributed to explanations such as Pearce’s (1987) notion that blocking might be due to a stimulus generalization decrement from the conditioning of the CS1-CS2 compound stimulus to the testing of the CS2 alone. That is, the female head CS2 may have been more similar to the CS1-CS2

combination at test compared to the wood block and terrycloth model without the female head cues.

Behavior Systems Approach

The behavior systems approach was developed in an attempt to combine concerns about control of functional behavior with concerns about the role of learning on eliciting new responses and stimulus control (Timberlake, 1993, 1994; Fanselow, 1994; Hogan, 1994; Shettleworth, 1994). According to this approach, presentations of a US in a conditioning procedure activate the behavior system relevant to that US. Behavior systems are assumed to consist of a series of modules organized in a temporal spatial sequence, with general search behavior at one end of the continuum and focal search behavior and consummatory behaviors at the other end. During Pavlovian conditioning, a CS becomes integrated into the system that is activated by the US. The conditioned response that becomes elicited by the CS depends on the nature and the timing of the predictive stimuli.

The behavior systems approach provides a framework for organizing the diverse sexual conditioning effects. In a formulation of a behavior system for sexual conditioning in male Japanese quail, Domjan (1994) described how learning about various types of cues come to control different aspects of the sexual response. As previously discussed, successful conditioning of copulatory responses appears to occur only in the presence of some plumage and other features of a female quail (Domjan, et al., 1986; Domjan et al., 1988; Akins, 2000). In addition, local cues (arbitrary CSs) that have been paired with copulation elicit focal search or conditioned approach behavior (Domjan, et al., 1986). However, if local cues are first presented with species-specific cues that are gradually removed, they can come to elicit conditioned copulatory responses (Domjan, Huber-McDonald, & Holloway, 1992). (The authors' explanation for this finding was an associative mediational interpretation—Holland, 1981. The interpretation proposes that two associations were formed; one between the species-specific cues and the terrycloth used to gradually cover it; the other between species-specific cues of the live female with copulatory reinforcement. The species-specific cues of the object and those of the live female served to mediate an association between the terrycloth covering and sexual reinforcement.) Contextual cues or "places" may serve as modulators or occasion setters to facilitate copulatory responding elicited by the shape and plumage of a female's head and neck (Domjan, Greene, & North, 1989), and to facilitate approach behavior elicited by conditioned local cues (Domjan, Akins, & Vandergriff, 1992). A more recent experiment has also demonstrated that contextual cues presented alone may elicit what might be characterized as general search behavior in the form of increased locomotor activity (Akins, 1998).

According to the behavior systems approach, the topography or form of the conditioned response is not only dependent on the nature of the CS but also on the time interval between the CS and the US (CS-US interval). Recall that a behavior system consists of a sequence of responses that range from appetitive to consummatory responses. The CS-US interval is assumed to determine where the CS becomes integrated into that sequence of responses. In the sexual behavior system, a CS is introduced shortly before access to a female if the CS-US interval is short. This CS should elicit focal search or approach behavior. If the CS-US interval is long and the CS is introduced early in the sequence, it may elicit general search behavior. These predictions were tested in an experiment in which large

rectangular experimental chambers were used (Akins, Domjan, & Gutierrez, 1994; see also Akins, 2000). Male quail were presented with a small wood block (CS) for either 1 or 20 min, followed by copulation with a receptive female bird. Male quail that received the 1 min CS-US interval demonstrated approach behavior to the block (akin to focal search behavior), whereas those that received the CS for 20 min demonstrated increased locomotor activity throughout the large chamber (akin to general search behavior). The results support the predictions made by the behavior systems approach.

Incentive Sequence Model

The “Incentive Sequence Model” recently proposed by Pfaus (1996; see also Pfaus, 1999; Pfaus, Kippin, & Centeno, 2001) is a cross-species comparative model that addresses how both Pavlovian and instrumental conditioning direct sexual responding in males. The model accommodates a range of sexual responses and categorizes them into general subclasses of appetitive and consummatory behaviors. Pfaus and his colleagues propose that behavioral responses occur sequentially from appetitive to consummatory phases. The appetitive phase consists of preparatory and anticipatory responses, both of which are said to be learned but differ based on whether they need to be made to obtain the incentive. Preparatory responses need to be made to acquire the incentive whereas anticipatory responses do not. The consummatory phase consists of species-specific responses made in direct contact with the partner. A typical incentive sequence for a rat might begin with an anticipatory response such as motor activation and when contact with a female rat has been made, the male may mount and attempt to copulate with the female. Similarly, the human male might show excitement in anticipation of a sexual encounter and once he has made contact with a female, genital stimulation might occur. Thus, the model allows for comparisons of incentive sequences between animals and humans. The strength of the model is that it allows for species-specific behaviors within the same subclass of appetitive and consummatory behaviors to be compared between species.

Adaptive Value of Pavlovian Conditioning in Sexual Behavior

One theme that has been emphasized in the nonhuman animal literature on learning and sexual behavior is that of “adaptive value” or “biological function”. Adaptive value refers to the way in which a behavior contributes to an animal’s reproductive success or to their ability to survive and reproduce (Williams, 1966). There is a wide range of nonhuman animal species and situations in which Pavlovian conditioning occurs that suggests that this type of learning has adaptive value (for review see Hollis, 1997).

Pavlovian conditioning may contribute to the reproductive fitness of organisms both by facilitating behavioral interactions between males and females and by stimulating critical aspects of reproductive physiology. In one experiment, male rats ejaculated more quickly than control rats when the presentation of a female rat was signaled (Zamble, et al., 1985). Similarly, when the availability of a female quail was preceded by an auditory signal, males that had previously learned that the auditory cue signaled access to a female, mounted the female more quickly than males that received a different auditory signal presented with that female (Gutierrez & Domjan, 1996). In another study, male blue gourami fish attenuated

their territorial aggression and began courtship sooner with female conspecifics in response to learned signals of a female's appearance (Hollis, Cadieux, & Colbert, 1989).

Pavlovian conditioning may also serve to stimulate the critical physiology necessary for reproduction. Male rats presented with a CS that reliably preceded access to a receptive female rat showed increased serum levels of testosterone and luteinizing hormone (LH) after CS presentation (Graham & Desjardins, 1980). More recently, it has been found that male quail that were classically conditioned to a CS that was paired with sexual reinforcement with a female quail (the US) released greater volumes of semen and greater numbers of spermatozoa than control group subjects that received the CS and US in an unpaired fashion (Domjan, Blesbois, & Williams, 1998).

There is little evidence that Pavlovian conditioning contributes to direct reproductive fitness when fitness is defined as the number of offspring produced. In one experiment, blue gourami fish produced more offspring if access to a sexual partner was signaled by a CS than if the sexual partner was unannounced (Hollis et al., 1997). Classically conditioned blue gourami males not only spawned with females sooner and clasped them more often but produced significantly more young than male gouramis that did not have the benefit of the signal. Although there may be more direct measures of fitness relative to others (such as number of surviving offspring that reproduce), these findings provides some indication for the role of conditioning in reproductive fitness.

Although, unfortunately not well studied, Pavlovian conditioning may also contribute to the reproductive fitness of females. Female blue gouramis that receive a signal of the presentation of a male prior to a mating encounter stay close to their appeasement-displaying male partners and are more easily led to the nest (Hollis, et al., 1989). Female quail that are provided a signal for the presentation of a male prior to a mating episode demonstrate increased squatting behavior toward the signal in the presence of the male partner (Gutierrez & Domjan, 1997). Thus, learning may serve to enhance the mating interactions of females thereby increasing the likelihood of successful reproduction.

Parallels Between Human and Nonhuman Animal Research

Theoretical Issues

There are several problems that make it difficult to draw parallels between the human and animal literature on sexual arousal. First, as Pfaus has often pointed out (e.g., Pfaus, 1996), theoretical models of animal and human sexual behavior have evolved from two very different bodies of literature. Models of human sexual behavior have been derived from clinical case studies of sexual deviancy, anecdotal stories, and the outcome of behavior therapy techniques. In contrast, animal models of sexual behavior have been based primarily on observations and controlled experimentation in the laboratory. Despite the difference in the divergent paths of animal and clinical models of sexual arousal, clinical theories may have evolved in parallel with learning theory. Some early investigators of learning have traditionally followed the general process approach (e.g., Thorndike, 1911), in which universal laws or rules are used to organize and explain the diversity of events across different species. More contemporary investigators have abandoned this approach for approaches that may allow for more comprehensive

explanations and the study of naturalistic behaviors (e.g., Timberlake, 1990). Other modern learning theorists (e.g., Mackintosh, 1983; Rescorla, 1988) have developed more cognitive models of Pavlovian conditioning. For example, Rescorla (1988) argues that Pavlovian conditioning is a more complex process than the simple formation of an association between two stimuli. He suggests that “organisms are information seekers that use logic and perceptual relations among events, as well as preconceptions to form a sophisticated representation of the world.” In a similar manner, clinical theories have moved away from the emphasis of Pavlovian conditioning as a factor in the development and maintenance of sexual deviations, and toward multifactorial theories that include learning but that are more comprehensive and that emphasize cognitive, social, and biological components, and their interactions with learning.

The behavior therapy literature is thought to have evolved from a traditional Pavlovian conditioning view such that the acquisition of sexually deviant behaviors is under relatively limited voluntary control and is thought to be beyond conscious awareness. Zinbarg (1990) has argued that current thinking in behavioral therapy is outdated and needs to be revised, especially in light of the development of more cognitive models of Pavlovian conditioning (e.g., Mackintosh, 1983; Rescorla, 1988). There is also some suggestion that the lack of empirical support for Pavlovian conditioning in sexual arousal may be a result of the narrow conditioning view that behavior therapists have held over the years (Marshall & Eccles, 1993).

In addition to more cognitive models of Pavlovian conditioning, other approaches have been developed to address how conditioning influences sexual responding. As previously discussed, the behavior systems approach (e.g., Timberlake, 1993) takes into account the various systems that have evolved to enable animals to accomplish tasks necessary for survival, such as feeding. It assumes that presentation of a US such as food activates the behavior system relevant to that US. Later, the CS becomes incorporated into the sequence of responses that make up the behavior system. A similar approach, the incentive sequence model (e.g., Pfaus, 1996) categorizes a wide range of sexual responses into general subclasses of appetitive and consummatory phases, some that involve learning. This categorization allows for a comparison of species-specific behaviors within general subclasses. Both approaches include a continuum ranging from appetitive to consummatory responses, with organisms moving from one phase to another along the continuum. Both approaches focus on species-specific repertoires, and the behavior systems approach additionally focuses on the kinds of conditioned stimuli, or the nature of the CS, that might be effective in eliciting a conditioned response. Thus, the two approaches appear to be compatible and, if integrated with what is known about physiology such as the involvement of hormones, may be useful in making predictions about some aspects of human sexual arousal. Unfortunately, however, researchers continue to be limited in testing these predictions because of the inability to measure a variety of appetitive and copulatory behaviors in humans. This is because, although sexual arousal in humans can be assessed by measuring the amount of blood flow in the genitalia, the closest one can get to measuring sexual motivation in humans is to ask questions related to levels of desire, frequency of thoughts, etc. Therefore, it is difficult to make comparisons between sexual responses of humans and animals, and thereby to use the two models to make predictions about sexual behavior.

Empirical Issues

Sexual behavior studies with animals have not been very effective in providing valuable information to clinical researchers because the focus on these studies has been on specific questions with regard to mechanism and function. In addition, sexual behavior studies with animals have been focused on providing demonstrations of learning/conditioning phenomena, such as blocking (Koksal et al., 1994), occasion setting (e.g., Domjan et al., 1992), contextual cue learning (e.g., Zamble et al., 1986), and long-delay learning (Akins et al., 1994). With the exception of second order conditioning, there has been no mention of learning phenomena that resemble these in the human literature.

In second order conditioning, a previously conditioned CS (CS1) is used in the role of a US to produce conditioning to a new stimulus (CS2). Zamble et al. (1985) exposed rats to a second order stimulus that had been paired with a visual CS1 that had been previously paired with copulation (US). These rats demonstrated shorter ejaculation latencies to the second order stimulus compared with unpaired control groups that received either unpaired second order trials after paired first order trials, or those that received unpaired first order trials but had paired second order trials. In a similar experiment, Japanese male quail were given a second order stimulus that had been paired with a visual/auditory stimulus (CS1) that had been previously paired with visual access to a female quail (Crawford and Domjan, 1995). Male quail showed more approach behavior to the second order stimulus relative to a control group that were given paired first order but unpaired second order trials, and one that was given paired second order but paired first order trials.

In humans, as previously described, it has been suggested that pairing a CS with tactile-induced sexual arousal results in first order conditioning in which the CS is a first order stimulus. However, when pairing a CS with a nontactile stimulus that was previously paired with sexual arousal, the CS serves as a second-order stimulus (Marshall & Eccles, 1993). The methodology used in most empirical studies with humans has involved pairing a CS with a nontactile stimulus, a second order CS. Thus, second order conditioning has been tested and observed in both animals and humans, but is less commonplace in animal studies of sexual arousal because of experimenters' ability to use copulation as the reinforcer in these studies. It should be noted that, as previously mentioned, there have been clinical treatments based on the notion of pairing a CS with masturbation to enhance responding to normative sexual stimuli, but with little long-term success (for review see Laws & Marshall, 1991b).

With regard to the role of the nature of the CS or stimulus relevance in eliciting sexual arousal, human experiments may link more closely with animal experiments than perhaps thought. For example, Rachman (1966) and Rachman and Hodgson (1968) demonstrated sexual arousal in human participants to a pair of black boots (CS). Similarly, Gosselin and Wilson (1980) found that in male fetishists, sexual arousal occurred mainly to stimuli that were pink, black, smooth, silky, and shiny. According to McConaghy (1987), objects such as black boots and those that contained the aforementioned stimulus characteristics (as described by Gosselin & Wilson, 1980) were effectively associated with sexual arousal because they have similar properties to that of the female vulva. Furthermore, Langevin and Martin (1975) failed to find evidence of conditioning when they used randomly presented geometrical patterns as CSs that were paired with sexual arousal.

Perhaps the arbitrary nature of the latter CSs to sexual arousal or the lack of CS-US relevance prevented an association from occurring. A recent experiment conducted by Hoffman et al. (2004) further supports the notion of stimulus relevance in humans, although its findings suggest a more complicated scenario. Both men and women showed greater sexual responding when a subliminal CS was more sexually relevant (the abdomen of an individual of the opposite gender) than when it was less relevant (a gun). The results were different, however, when the CS was consciously perceived. Nevertheless, similar to what has been found in animal studies, empirical studies with humans seem to also support the notion of constraints on learning.

In contrast to the findings on the adaptive value of sexual learning in animals, there is no direct evidence that learning is adaptive in human sexual arousal. There is speculation that, similar to other species of animals, sexual experience may result in improved reproductive performance (see Woodson, 2002 for review) but this is not specific to Pavlovian conditioning. Indeed, much of the literature on human sexual arousal suggests that sexual arousal that results from learning may be maladaptive as opposed to adaptive. For example, Money (1987) describes a letter from a male subject explaining the development of a fetish for caning that presumably resulted from disciplinary beatings received in school. This emphasis on the maladaptiveness of sexual learning is clearly a function of the concentrated focus of human literature on clinical treatment and behavior therapy techniques for deviant sexual behavior.

One theme that has been neglected by both human and nonhuman animal studies is the role of learning in female sexual behavior and arousal. This is in spite of evidence that in nonhuman animals, females appear to control many aspects of sexual interaction, and in humans, sexual learning may contribute to the etiological mechanisms of sexual dysfunction. In animals, female sexual conditioning has been most evident in conditioned place preference experiments. For example, female rats demonstrate a place preference for a distinct context that is paired with copulation (Oldenburger, Everitt, de Jonge, 1992). Additionally, female rats show a more robust place preference where they were allowed to pace the rate of copulation by controlling the speed and frequency at which copulation occurred compared with a place where they were not allowed to pace the rate of copulation (Paredes & Alonso, 1997; Paredes & Vazquez, 1999). Similarly, female hamsters demonstrate a copulatory-induced conditioned place preference though it is unclear whether aggression plays a role in these results since female hamsters also display a place preference for compartments paired with aggressive encounters (Meisel & Joppa, 1994). Until recently, it was unknown whether female sexual arousal in humans was susceptible to conditioning. The first experiment conducted to investigate this (Letourneau & O'Donohue, 1997) failed to reveal sexual conditioning in women. In contrast, Hoffman et al. (2004) found evidence for conditioning of sexual arousal in women. Thus, although there have been difficulties in conducting animal and human studies on female sexual arousal and conditioning, there is growing support to suggest that female sexual arousal can be conditioned. However, whether one successful demonstration of conditioned sexual arousal in women is sufficient evidence for its existence may be debatable.

Finally, a phenomenon referred to as "human evaluative conditioning" may be relevant to the investigation of conditioned sexual arousal in humans. In human evaluative conditioning (e.g., Hammerl & Grabitz, 1996), the contingent presentation of neutral stimuli with liked or disliked stimuli is sufficient for

changing the evaluative tone of the neutral stimuli in a positive or negative direction. Successful evaluative conditioning seems to be independent from awareness of the stimulus pairings arranged by the experimenter (Baeyens, Eelen, & Van den Bergh, 1990). It also appears to be highly resistant to extinction, that is, unreinforced presentations of the CS do not change the previously acquired value of the stimulus (Baeyens, Eelen, Van den Bergh, & Crombez, 1989); sensitive to US-preexposure effects (Hammerl, Bloch, & Silverthorne, 1997); and can be used in a sensory preconditioning procedure (Hammerl & Grabitz, 1996). Future sexual arousal experiments with humans may attempt to address whether the factors that influence human evaluative conditioning also influence conditioning of sexual arousal.

In summary, in spite of major differences in the divergent paths of the literature on animal and human sexual arousal and conditioning, some overlap does exist. For example, it is clear from both bodies of literature that secondary stimuli associated with sexual arousal may become conditioned, and more recent evidence suggests that female sexual arousal may be susceptible to conditioning. Empirical studies on both animals and humans have led to some similar conclusions about the importance of stimulus relevance or the nature of the CS in conditioning sexual arousal. In addition, whereas the reinforcer used in animal studies has usually been copulation, the reinforcer in human studies has typically been photographs or slides of sexually arousing stimuli. Even with regard to human studies, it is questionable as to how effective these stimuli are, and therefore how adequately the human laboratory model represents human sexual deviance in the real world. In contrast to human research, the adaptive value of conditioning and sexual behavior has been well studied in animal research. This research has provided evidence that conditioning may serve to guide behavior toward stimuli that are predictive of reproductive success and that this may have fitness consequences. One can only speculate as to whether this is true with regard for humans. Finally, clinical theories and treatments have been derived from studies on sexual deviance. Just as the conceptualization of learning has been broadened to include more cognitive mediation in animals, clinical theories have evolved to focus more on cognitively mediated theories of human sexual deviance.

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