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PAVLOVIAN CONDITIONING: A Functional Perspective

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■ **Abstract** From a functional perspective, Pavlovian conditioning involves learning about conditioned stimuli (CSs) that have a pre-existing relation to an unconditioned stimulus (US) rather than learning about arbitrary or neutral CSs. In addition, the most important product of learning involves changes in how the organism responds to the US, not in how it responds to the CS, because the US is the more biologically relevant stimulus. These concepts are illustrated using examples from a variety of behavioral and physiological situations including caloric intake and digestion, breast feeding, poison-avoidance learning, eyeblink conditioning, sexual conditioning, fear conditioning, aggression, and drug tolerance and sensitization.

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INTRODUCTION

Pavlovian conditioning is one of the oldest and most extensively studied learning paradigms. The paradigm basically involves two stimuli. The unconditioned stimulus (US) elicits vigorous responding without any special prior training, or unconditionally. Because of that, the US originally was labeled the unconditional stimulus (Gantt 1966). In contrast, the conditioned stimulus (CS) elicits little more than an orienting response at first. The effectiveness of the CS depends, or is conditional, upon its pairings with the unconditioned stimulus. Hence, the CS originally was called the conditional stimulus. Learning is identified by the emergence of new responses to the CS, called conditioned responses or CRs. Because the development of conditioned responding depends on the pairing of the CS and US, the learning is considered to involve the establishment of an association between the CS and the US. This has made Pavlovian conditioning a favorite paradigm for the study of associative learning. Staddon (1983), for example, characterized Pavlovian conditioning as "the prototype for all signal learning" (p. 103).

The associative tradition encouraged investigators to use conditioned stimuli that are initially unrelated to, or arbitrary, with respect to the US. In fact, the initial independence of the CS and US has been incorporated into the definition of Pavlovian conditioning. Authors have characterized the CS as "arbitrary" (Bower & Hilgard 1981, p. 49) or "neutral" (Anderson 1995, p. 10; Papini 2002, p. 491; Shettleworth 1998, p. 109; Staddon 1983, p. 102) with respect to the US.

The view that Pavlovian conditioning involves learning about neutral or arbitrary cues that come to elicit conditioned behavior has provided a great deal of information about associative mechanisms. Parallel to, but in the shadows of, the associative tradition, a functional perspective on Pavlovian conditioning also has been developed (Domjan et al. 2000; Hollis 1982, 1997). The functional perspective is encouraged by the fact that Pavlovian conditioning has been demonstrated in a wide range of species and response systems (Turkkan 1989). The prevalence of Pavlovian conditioning suggests it is an adaptive trait that readily occurs under natural circumstances and serves to promote reproductive fitness, directly and/or indirectly. These are the key assumptions of a functional perspective (Dukas 1998; Hollis 1982, 1997; Shettleworth 1983, 1994).

Natural Learning Paradigms

If Pavlovian conditioning is an adaptive trait, it presumably occurs under natural circumstances. However, outside the laboratory, the hand of an experimenter is not available to make sure that occurrences of a conditioned stimulus are reliably paired with presentations of a US. Rather, the CS-US pairings that are necessary for Pavlovian conditioning have to be features of the natural environment. For that to be the case, the CS has to be naturally related to the US instead of being an arbitrary cue or a neutral stimulus. An arbitrary CS may coincide with a US occasionally under natural circumstances, but such accidental pairings are bound to be rare. In addition, an accidental pairing will be preceded and followed by unpaired CS and US encounters, which will undermine the development of conditioned responding (e.g., Benedict & Ayres 1971, Rescorla 2000). Thus, although CS-US associations reside in the nervous system, they no doubt reflect physical relationships between conditioned and unconditioned stimuli that exist in the natural environment of the organism.

A pre-existing relation between the CS and the US can take several different forms. One possibility is that the CS is a stimulus early in the causal chain of events that leads to the US (Dickinson 1980, Staddon 1988). Another possibility is that the CS is a feature of the US that initially does not elicit the unconditioned response but comes to do so after repeated encounters with the US. This was the case in the first documented demonstration of Pavlovian conditioning, which was conducted by S.G. Vul'fson in Pavlov's laboratory (Boakes 1984, Todes 1997). Vul'fson repeatedly presented various substances to dogs (sand, dry food, wet food, or sour water) and measured the quantity and quality of saliva elicited by each. After one of these substances had been placed in the dog's mouth several times, Vul'fson noticed that the dog would salivate when it was "teased" by having the substance presented at a distance.

In Vul'fson's demonstration, the US was the sand or dry food in the mouth. The CS was the sight and/or smell of the US at a distance. Notice that the CS was not unrelated to the CS at the outset of training. Rather, the CS and the US were different features of the same object (sand, for example).

In the absence of experimental intervention, having a CS and a US that are different features of the same object helps to make sure that the CS will occur with the kind of contingent and temporal relation to the US that will result in the establishment of an association. This type of pre-existing relation between the CS and US is probably a feature of most naturally occurring instances of Pavlovian conditioning and therefore has to be carefully considered in a functional analysis. Therefore, I review instances in which the CS is a natural precursor of the US, to see whether these examples of Pavlovian conditioning have any unique properties.

Conditioned Modifications of the Unconditioned Response

In addition to fashioning laboratory experiments that better mimic natural conditions, a functional approach requires focusing on aspects of behavior that are of potential adaptive significance. From a functional perspective, the important task for the organism is to interact effectively with the unconditioned stimuli it encounters. By definition, USs are of great biological significance (Pavlov 1927). In contrast, conditioned stimuli are important only because of their relation to a US. If the US does not occur, a response to the CS is a useless "false start."

Conditioned responses are functionally significant only to the extent that they facilitate the subject's interactions with the US.

The significance of conditioned responses in facilitating the subject's interactions with a US was brought into focus in several important papers by Hollis (1982, 1990, 1997). However, the implications of this claim have not been fully appreciated. If the primary function of Pavlovian conditioning is to improve how an organism interacts with the US, then the critical behavioral consequence that one should measure in studies of classical conditioning is how responses to the US change as a function of learning. Accordingly, I review various lines of evidence showing how Pavlovian conditioning can modify responses to unconditioned stimuli.

LEARNING WITH ECOLOGICALLY RELEVANT CONDITIONED STIMULI

Definitions of classical conditioning that call for selecting a conditioned stimulus that is "neutral" or "arbitrary" imply that the choice of a CS is of little consequence for the outcome of conditioning experiments. That is hardly the case. The choice of the CS can make a big difference. One prominent parameter is CS intensity. Generally, more intense conditioned stimuli produce faster learning and more vigorous conditioned responding (e.g., Kamin 1965). The conditioned stimulus can also determine the nature of the conditioned response (Holland 1984). In this section, I review evidence that conditioning effects also vary as a function of the ecological relevance of the CS.

Poison-Avoidance Learning

One of the most dramatic examples of learning influenced by the conditioned stimulus was discovered in the course of research on poison-avoidance learning. The ingestion of a poisonous food involves first tasting the food and then swallowing and digesting it. The poisonous effects become prominent as the food becomes absorbed in the body. This sequence of events results in the learning of an aversion to the taste of the food (Garcia et al. 1974, Rozin & Kalat 1971, Rzoska 1953). Taste-aversion learning has been modeled in the laboratory by permitting rats to drink an innocuous flavored solution (e.g., saccharin) and then injecting them with something that makes them sick (e.g., lithium chloride). By experimentally controlling the exposure to the CS and the US, investigators have been able to examine how the learning is influenced by the nature of the CS and the effects of the CS-US interval.

Taste aversion learning can occur in a single trial, even if the US is delayed several hours after the CS (Garcia et al. 1966, Smith & Roll 1967). However, the aversion learning occurs much more readily if the CS is a novel taste than if the CS is an auditory and/or visual cue (Domjan & Wilson 1972, Garcia & Koelling 1966). Furthermore, the long-delay learning of taste aversions is at least in part due to the specificity of the learning to taste cues (Revusky 1977).

For organisms that hold food in their front paws, the aversive consequence of eating poisonous food is reliably preceded not only by taste cues but also by the olfactory and tactile cues of the poisonous food as it is held in preparation for eating. Aversions also can develop to these tactile and olfactory features of the food (Domjan 1973, Domjan & Hanlon 1982). However, food-related tactile and olfactory cues have to be distinguished from the tactile and olfactory cues that are encountered during the course of locomotion or other noningestive activities. Studies have shown that at least in the case of odor aversion learning, the sensations provided by the motor movements involved in eating and drinking facilitate this discrimination (Domjan 1973).

Taste-Odor Potentiation and Contrablocking

The taste and odor features of ingested food are closely related because as one gets close enough to a food to taste it, one invariably encounters the food's odor. This relationship appears to result in some unusual learning effects.

When two conditioned stimuli are presented simultaneously and paired with a US, the typical outcome (called overshadowing) is that the presence of one CS interferes with the conditioning of the other (e.g., Kamin 1969). In contrast to overshadowing, when a taste and an odor are presented together prior to illness, the presence of the taste sometimes facilitates rather than interferes with the conditioning of the odor (Bouton et al. 1986; Rusiniak et al. 1982a,b). This phenomenon is called potentiation.

Another important compound cue effect is "blocking." In the blocking design, subjects are conditioned first to asymptote with one CS. A second CS is then added to the first one, as conditioning trials are continued. The interesting result is that the presence of the initially conditioned CS interferes with (or blocks) the conditioning of the added CS. The blocking effect was demonstrated initially in fear conditioning in rats with light and noise conditioned stimuli (Kamin 1969) and became a keystone phenomenon that inspired numerous major theories of learning. However, an effect opposite blocking (contrablocking) occurs if taste and odor cues are used. When an odor cue is added to a previously conditioned taste stimulus (or a taste cue is added to a previously conditioned odor), aversion conditioning of the added stimulus is facilitated rather than blocked (Batsell et al. 2001, Batson & Batsell 2000).

Caloric Conditioning

Nutritious foods provide caloric repletion rather than poisoning as the postingestive consequence. Tastes can become associated with caloric repletion, with the outcome that subjects increase their preference for the associated flavor (Fedorchak 1997, Sclafani 1997). The caloric substances may be mixed with the CS flavor or intubated directly into the stomach. The resultant flavor preferences have been characterized as highly resistant to extinction (Fedorchak 1997, Mehiel 1991), but it is not clear to what the resistance to extinction was compared. Interestingly, a caloric conditioned preference is sensitive to changes in hunger, with higher preferences evident when the subject is food deprived as compared with being nondeprived (e.g., Capaldi et al. 1994). This latter finding suggests that stimulus-stimulus, or S-S, learning mechanisms mediate caloric conditioning.

Sexual Conditioning

The effects of environmental regularities have been also examined in sexual conditioning with male Japanese quail (Domjan et al. 2004). Sexual conditioning is conducted by presenting a CS shortly before providing the male with access to a female. If a localized stimulus (e.g., a light) serves as the CS, the male quickly comes to approach the CS as the conditioned response (Domjan et al. 1986).

Japanese quail are ground birds that live in grassy areas (Schwartz & Schwartz 1949). When a male initially detects a female, he is likely to see just a part of her body, perhaps her head sticking up through the grass. By approaching these limited visual cues, the male will get close to the female and may get a chance to copulate with her. This sequence of events may be modeled in the laboratory by presenting a CS that includes the taxidermically prepared head of a female (see Cusato & Domjan 1998, Figure 1), and following that with access to a live female with whom the male may copulate.

Studies have shown that such a naturalistic CS elicits only modest approach behavior unconditionally. However, if the CS is paired with access to a live female, conditioned approach behavior significantly increases (Köksal et al. 1994). In addition, the males also come to grab and attempt copulations with the naturalistic CS (Cusato & Domjan 1998). Such conditioned copulatory responses did not develop in subjects that were conditioned with an arbitrary CS that had the same size and shape but lacked female head cues. Additional comparisons revealed a constellation of learning effects that differentiated the naturalistic CS from the more conventional arbitrary CS. The naturalistic CS was resistant to blocking (Köksal et al. 1994) and failed to show extinction (Krause et al. 2003). It was also resistant to increases in the CS-US interval (Akins 2000), resulted in stronger second-order conditioning (Cusato & Domjan 2001), and showed a sensitization rather than a habituation effect with repeated unreinforced exposures (Cusato & Domjan 1998).

Fear Conditioning

Fear conditioning typically is investigated using experimental procedures in which an auditory or visual CS is presented to laboratory rats shortly before a brief foot shock. Outside the laboratory, however, fear conditioning is likely to cues that are natural precursors of an aversive event. Such precursors are easy to identify in predator-prey interactions. For example, the sight and sound of a rattlesnake preying on a rabbit is a natural precursor of the biting attack. An extensive series of experiments have examined the conditioning of fear to the sight of a snake in monkeys and people (Öhman & Mineka 2001, 2003). In both species, stronger fear conditioning was found when the CS was provided by visual cues of a snake rather than visual cues of flowers or mushrooms. However, the flower and mushroom stimuli were just as effective as the sight of a snake in appetitive conditioning procedures (EW Cook et al. 1986, M Cook & Mineka 1990). This selective advantage of the snake stimuli in fear conditioning was also evident when the stimuli were presented to human participants without their conscious awareness (Öhman & Soares 1998). The evolutionary basis of selective conditioning of snake stimuli is further supported by evidence that snake cues are more effective in human fear conditioning than are visual cues provided by a gun (EW Cook et al. 1986).

Selective associations in fear conditioning also have been demonstrated in pigeons, where auditory cues have been found to be more effective as a CS for shock, whereas visual cues are more effective as a signal for food (LoLordo 1979). In addition, auditory-shock associations are resistant to the blocking effect (LoLordo et al. 1982). The presentation of a previously conditioned CS does not interfere with the development of a tone-shock association. Thus, as in sexual conditioning (Köksal et al. 1994), a naturalistic CS is less susceptible to blocking.

Maternal Nursing and Infant Suckling

Another situation in which the natural course of events results in the reliable pairing of conditioned and unconditioned stimuli is provided by the interactions between mother and infant that occur during the course of nursing. The unconditioned stimulus for the milk letdown and milk ejection reflex is suckling stimulation of the breast. Olfactory and other cues from the infant typically precede suckling stimulation, and these cues can become conditioned to elicit the release of oxytocin and prolactin, hormones that stimulate milk letdown and ejection (Fuchs et al. 1987; Grosvenor & Mena 1972, 1974; McNeilly et al. 1983). Correspondingly, various exteroceptive cues provided by the mother before a nursing episode can become conditioned to elicit suckling on the part of the infant (Blass 1990, Blass et al. 1984). Research has clearly demonstrated that such conditioned endocrine and suckling responses can develop. However, in this line of research specific experiments have not been conducted to see if naturalistic conditioned stimuli are more effective than arbitrary cues.

Discussion

The evidence reviewed above suggests that learning with ecologically relevant stimuli often proceeds differently from learning with arbitrary cues. In food-aversion learning, sexual conditioning, and fear conditioning, the use of an ecologically relevant CS resulted in acquisition that was more robust and was resistant to the blocking effect. In food aversion learning and sexual conditioning, the learning also occurred over longer CS-US delays. These and the other contrasts with conventional conditioning phenomena that were described suggest that efforts to understand how Pavlovian conditioning occurs in the natural environment have to consider the role of pre-existing relations between CSs and USs.

CONDITIONED STIMULUS INTENSITY, SALIENCE, AND BIOLOGICAL SIGNIFICANCE One possible explanation for the more robust learning effects that were observed when an ecologically relevant CS was used in food-aversion learning, sexual conditioning, and fear conditioning is that the naturalistic CSs were more intense or salient than the corresponding arbitrary cues. Consistent with this possibility, several investigators have reported that a target CS is less likely to be blocked by a previously conditioned cue if the target CS is of higher intensity (Feldman 1975, Hall et al. 1997, Miller & Matute 1996). However, stimulus salience or intensity is not likely to be the primary dimension that distinguishes naturalistic CSs from arbitrary cues. In studies of food aversion learning, taste cues were more effective than audiovisual cues only if poisoning was used as the US. When shock served as the US, the relative effectiveness of taste versus audiovisual cues was reversed (Domjan & Wilson 1972, Garcia & Koelling 1966). Similarly, in studies of fear conditioning in pigeons, auditory cues were more effective than visual cues only if the US was shock—not if the US was food (LoLordo 1979). In studies with monkeys and people, the flower and mushroom stimuli that were not effective in fear conditioning worked well when appetitive conditioning was conducted (EW Cook et al. 1986, M Cook & Mineka 1990).

Another way to characterize the difference between a naturalistic CS and an arbitrary cue is that the former is of greater biological significance. Gunther et al. (1997) defined biological significance by the vigor of responding (conditioned or unconditioned) that is elicited by a stimulus at the outset of a training procedure. Consistent with this interpretation, the naturalistic CS used in the sexual conditioning experiments elicited more responding even in the absence of conditioning than did the arbitrary CS (Cusato & Domjan 1998, Köksal et al. 1994), and this may have been responsible for the resistance to blocking, extinction, and increases in the CS-US interval that was observed. Stimuli of greater biological significance also have been shown to be more resistant to blocking, overshadowing, relative validity, and degraded contingency manipulations in fear conditioning (Miller & Matute 1996, Oberling et al. 2000).

OBJECT LEARNING In many of the examples described above, the pre-existing relation between CS and US was provided by the fact that the stimuli were different features of the same object. Food-aversion learning and caloric conditioning involve learning about different features of ingested food. The CS feature is the taste of the food, and the US feature is its aversive or caloric postingestional consequence. One may also conceptualize the sexual conditioning with a naturalistic CS as an instance of object learning. The naturalistic CS included the taxidermically prepared head of a female quail, whereas the US was copulatory access to a live female. The partial female visual cues that were provided by the CS were just one feature of the US, which included additional visual, auditory, and tactile stimuli, as well as movement cues produced by the female's behavior.

In fear conditioning, visual cues provided by a snake were paired with an aversive US. In the laboratory experiments (Öhman & Mineka 2001, 2003), the aversive US was not a snakebite but a shock or the sight of a demonstrator monkey behaving fearfully. However, the laboratory procedures presumably activated processes that evolved to deal with encounters with dangerous snakes.

In the conditioning of oxytocin and prolactin release, the CS and US were both provided by the infant. Suckling on the part of the infant provided the US, and cues provided by the infant before nipple attachment served as the CS. Correspondingly, different features of the mother provided the CS and the US in conditioning infant suckling. In this case, orosensory stimuli of the nipple served as the US and maternal cues preceding access to the nipple served as the CS.

Object learning or part-whole associations also have been examined in the context of drug conditioning (Cepeda-Benito & Short 1997, Greeley et al. 1984, Kim et al. 1999) In these experiments, a small dose of a drug was given as a CS for a larger subsequent dose. For control subjects, the two drug doses were administered in an unpaired fashion. Test trials revealed that the small drug dose came to activate a conditioned compensatory response (see Conditioning and Drug Tolerance section below). However, further research is required to determine whether such drug CSs have properties different from more arbitrary CSs in these situations.

Learning that involves associating different features of an object is no doubt widespread. Organisms have to learn about all sorts of objects to successfully navigate their environment. We can recognize something as being a chair even if we only see a small part of it because we have learned a constellation of associations involving different features of chairs. The prevalence of object learning makes object learning a useful heuristic for identifying CS-US pairings in the natural environment. If a US object has multiple features, only some of which elicit behavior unconditionally, the initially ineffective features of the object may come to elicit responding as well through Pavlovian conditioning.

Whether the concept of object learning helps to explain some of the special properties of learning with ecologically relevant stimuli remains to be seen. The more rapid and robust learning that was observed with ecologically relevant stimuli in food-aversion learning, sexual conditioning, and fear conditioning is yet to be satisfactorily explained. Öhman & Mineka (2001, 2003) favor an evolutionary account of the special efficacy of snake cues in fear conditioning. An evolutionary explanation also was offered for the special efficacy of taste cues in food aversion learning (Garcia et al. 1974). Evolutionary explanations leave open the question of proximate mechanism. Both Öhman & Mineka (2001) and Garcia et al. (1974) offered neurophysiological proximate hypotheses. Behavioral mechanisms may also promote object learning. When the CS and the US are different features of the same object, the two events are likely to covary more closely and may have more stimulus elements in common. Stricter covariation and greater similarity can both promote CS-US associations (e.g., Rescorla & Furrow 1977, Testa 1975).

CONDITIONED MODIFICATIONS OF RESPONSES TO THE UNCONDITIONED STIMULUS

An associationist approach to classical conditioning emphasizes the learning of an association between the CS and the US. Once this association has been learned, presentation of the CS activates a representation of the US (Rescorla 1988) or a representation of *what* significant biological event is about to occur. However, it was clear even from the research in Pavlov's laboratory that subjects learn not only what will occur but also when it will happen. Pavlov (1927) noted that when an extended CS-US interval is used, the CR becomes delayed as training progresses, until it occurs close to the actual time of US delivery. (This phenomenon was termed "inhibition of delay.") Subsequent research has confirmed that subjects encode not only CS-US associations but also precise information about the temporal relation between the CS and the US (Blaisdell et al. 1998, Denniston et al. 1998, Savastano et al. 1998), and that conditioned responses can be timed beautifully to occur just when the US is about to be presented (Kehoe et al. 1989).

If subjects timed their CRs perfectly, the CR would occur exactly when the US was delivered, and no behavior would be evident during the CS-US interval. This has encouraged the use of test trials to measure conditioned behavior. However, such test trials miss the critical function of Pavlovian conditioning, which is to permit the subject to respond to the US more effectively. From a functional perspective, the most important consequence of learning is how the subject's interactions with the US change as a function of having that US preceded or signaled by a conditioned stimulus. Such conditioned modifications of the UR have been documented in several situations.

Conditioned Modification of the Eyeblink Response

Irritation of the eye elicits a blink unconditionally. The eyeblink reflex has been a popular response system for the study of classical conditioning (Gormezano et al. 1983). Furthermore, one of the first demonstrations of conditioned modification of the UR was in eyeblink conditioning. Testing human participants, Kimble & Ost (1961) found that a CS that had been paired with an airpuff US not only elicits a blink as a conditioned response, but the magnitude of the blink response to the airpuff is attenuated by prior presentation of the CS. This phenomenon was called "conditioned diminution of the UR." Subsequent investigators did not always replicate the conditioned diminution effect and also reported enhanced responding to the US following exposure to a CS on occasion. A more systematic examination of the parameters of the conditioned diminution effect suggested that a critical variable is the intensity of the US. Conditioned facilitation of the UR is more likely with low US intensities, and conditioned diminution of the UR is likely with higher US intensities (Donegan & Wagner 1987). Thus, a CS may attenuate or enhance unconditioned responding under different parametric conditions.

Contrasting conditioned modifications of the UR also have been observed in conditioning with pharmacological unconditioned stimuli (see below).

Sexual Behavior and Reproductive Success

As is the case in other domains of Pavlovian conditioning, the emphasis in studies of sexual conditioning has been on conditioned responses that develop to cues that are predictive of sexual reinforcement (Domjan & Holloway 1998). However, a growing body of evidence indicates that a sexually conditioned CS can also facilitate responding to the US in a sexual situation. Exposure to a sexually conditioned stimulus decreases the latency of rats to ejaculate during copulations with a female (Zamble et al. 1985), and decreases the latency of male quail to initiate copulation with a female (Domjan et al. 1986). Furthermore, this decrease in copulatory latency helps to determine the outcome of sexual competition. When two male quail receive access to a single female, the male that is able to predict the sexual encounter because of a CS is able to copulate with the female first (Gutiérrez & Domjan 1996).

In studies with the blue gourami fish (*Trichogaster trichopterus*), males that encountered a female after exposure to a sexually conditioned light stimulus showed reduced levels of aggression and more frequent courtship appeasement action patterns in response to the female (Hollis et al. 1989). In other studies, male quail were found to be more responsive to minimal female cues if these cues were presented in a context that was previously paired with access to a female (Hilliard et al. 1997). Other evidence of conditioned modifications of unconditioned behavior is evident in female quail presented with a conditioned stimulus that signals the impending introduction of a male (Gutiérrez & Domjan 1997). The females show no response to a sexually conditioned stimulus but the CS makes them more receptive once they encounter a male.

The ultimate standard for evidence of functional significance is reproductive success. If a behavioral trait is of adaptive significance, individuals with that behavioral trait should produce greater numbers of offspring. Sexual behavior is one of the few systems in which the contributions of learning to reproductive outcomes can be measured directly. In the first study involving direct measurement of reproductive outcome, Hollis et al. (1997) permitted male blue gourami to copulate and tend eggs after exposure to a sexually conditioned stimulus. Males that encountered a female after exposure to a sexually conditioned stimulus showed less aggression toward the female, more nest-building behavior, more clasping behavior, and shorter latencies to spawn. Most importantly, sexual encounters that were preceded by a conditioned stimulus yielded more than 10 times as many offspring as unsignaled encounters.

Sexual conditioning has been also found to increase reproductive parameters in quail. Male quail release greater numbers of sperm following exposure to a sexually conditioned stimulus as compared with a control condition (Domjan et al. 1998). More recently, Adkins-Regan & MacKillolp (2003) found that the sexual conditioning of either the male or the female increases the number of fertilized eggs that are produced following a copulatory interaction. Increased numbers of fertilized eggs also were found in a subsequent study (Mahometa & Domjan 2004), but only when both the male and the female were able to anticipate a sexual encounter. In addition, Mahometa & Domjan (2004) showed that as with the blue gourami, the greater fertilization success is correlated with changes in how the males and females react to each other. Exposure to a sexually conditioned stimulus increases the female's receptivity and the efficiency of the male's copulatory behavior.

Aggression

Agonistic behavior contributes to reproductive success through the defense of important resources, such as food, territory, nesting sites, or potential mates (Poole 1985). The unconditioned stimulus for aggression is the presence of a rival or intruder male. In many studies of the conditioning of agonistic behavior, the emphasis has been on the development of aggressive responses to a conditioned stimulus that was paired with a territorial intruder (e.g., Jenkins & Rowland 1996, Thompson & Sturm 1965). However, Hollis (1984, 1990) found that such Pavlovian conditioning also increases the effectiveness with which a territorial male fights with an intruder. Male blue gourami for which an aggressive encounter was preceded by a previously conditioned light CS made significantly more bite and tail-beating responses than did subjects in a control group that previously had the CS unpaired with the US. Interestingly, the success that paired subjects experienced in their test encounter with the intruder also made these males more effective combatants in an unsignaled fight conducted two weeks later (Hollis et al. 1995). Thus, the increase in US effectiveness that was initially stimulated by the presentation of the CS was long-lasting and persisted when the US subsequently was presented in the absence of the CS.

Maternal Nursing and Infant Suckling

As described above, another social situation that readily lends itself to conditioning effects involves the interactions between mother and infant that occur during the course of nursing. Although the emphasis in this area of research has been on the development of conditioned endocrine and suckling responses to conditioned stimuli, these conditioned stimuli may also enhance the effectiveness of an unconditioned stimulus. Typically, the unconditioned stimulus for oxytocin secretion and milk letdown is suckling stimulation provided by the infant. However, other aspects of the infant can serve as CSs and elicit these as conditioned responses (Fuchs et al. 1987; Grosvenor & Mena 1972, 1974; McNeilly et al. 1983). Furthermore, the CS cues provided by the infant may also enhance responses to the suckling US. In a recent study involving dairy cows, for example, Tancin et al. (2001) found that the presence of a mother's calf can increase oxytocin release and milk yield in response to standard unconditioned stimulation of the teats by a milking machine. These effects were more prominent in multiparous cows that presumably had a more extensive conditioning history involving the pairing of a calf with tactile stimulation of the teats.

Fear-Potentiated Startle

One paradigm in which the focus has always been how the conditioned stimulus modifies responses to an unconditioned stimulus is knows as the fear-potentiated startle. The startle response is a defensive response that can be readily elicited in the laboratory by a brief loud noise (Hoffman & Ison 1980). In this system, the brief loud noise is the unconditioned stimulus and the startle response is the unconditioned response. Brown et al. (1951) demonstrated that conditioned fear elicited by an audiovisual stimulus enhances the startle response elicited by a brief loud noise in rats. The parameters of this fear-potentiated startle procedure have since been examined in detail (e.g., Walker & Davis 2002) and the paradigm has become a highly productive technique for investigating the neural and pharmacological mechanisms of fear and defensive behavior (Davis 1997, Fendt & Fanselow 1999, Hijzen et al. 1995). Most of the research on fear-potentiated startle has been conducted with laboratory rats. However, the procedure has been also extended to rhesus monkeys (Winslow et al. 2002). Fear-potentiated startle has been also studied with human participants, using the eye-blink response as an index of startle, and shock or the threat of shock paired with a CS to elicit fear (Ameli et al. 2001, Grillon & Davis 1997, Riba et al. 2001).

Conditioned Hypoalgesia

Aversive conditioning can also lead to changes in pain elicited by an aversive unconditioned stimulus. This phenomenon was initially labeled "conditioned analgesia," but because one cannot be certain that pain is eliminated entirely by exposure to a conditioned stimulus, a more conservative term for the effect is "conditioned hypoalgesia." In one study (Fanselow & Baackes 1982), for example, rats received shock in a distinctive experimental chamber and were then tested for conditioned fear and pain sensitivity either in the same context or in a different context that had not been paired with shock. Conditioned fear was measured in terms of time spent freezing, and pain sensitivity was measured by recording recuperative responses to having an irritant (a small dose of formalin) injected into one of the hind paws. Subjects tested in the shock chamber showed extensive freezing but little reactivity to the painful formalin injection. In contrast, subjects tested in the alternative context showed very little freezing and substantial levels of recuperative behavior induced by the formalin injections. Similar context-elicited hypoalgesia has been obtained with cold-water swimming and exposure to carbon dioxide as the aversive US (Blustein et al. 1997, Mongeluzi et al. 1996). Conditioned hypoalgesia also has been observed with discrete conditioned stimuli (Illich & Grau 1991, Matzel & Miller 1987).

Conditioned hypoalgesia exhibits many of the properties of other conditioning effects, including extinction (Fanselow 1984, Matzel et al. 1988), blocking (Ross 1985), latent inhibition (Maier & Watkins 1991), conditioned inhibition (Wiertelak et al. 1992), and second-order conditioning (Ross 1986).

The hypoalgesia elicited by the shock-associated context in the study by Fanselow & Baackes (1982) was reversed by treatment with the opiate antagonist naltrexone, suggesting that the reaction was mediated by the release of endogenous opiates (Matzel & Miller 1987). The conditioned hypoalgesia and conditioned freezing are also attenuated by benzodiazepines (Fanselow & Helstetter 1988).

Conditioned hypoalgesia has important implications for the mechanisms of aversive conditioning. As Fanselow (1991) noted, "analgesia may act as a negative feedback loop that regulates conditioning" (p. 79). During the course of acquisition, the development of conditioned hypoalgesia will reduce the effectiveness of the US and thereby limit the development of conditioned fear. Conditioned hypoalgesia may also be responsible for the blocking effect (Fanselow 1998). Consistent with these predictions, treatment with naloxone increases fear conditioning (Fanselow 1981, Westbrook et al. 1991), reduces the blocking effect (Schull 1979), and also attenuates the US pre-exposure effect, which is a form of blocking in which the context serves as the previously conditioned stimulus (Matzel et al. 1988).

Digestion and Feeding

The first unconditioned stimulus used in studies of Pavlovian conditioning was food. If an important function of Pavlovian conditioning is to modify how the organism interacts with the unconditioned stimulus, evidence of this should be available with food USs. It was recognized early on that the conditioned salivation that occurred in anticipation of dry meat powder can be helpful in digesting the food, and salivation in anticipation of an irritant in the mouth (e.g., a weak acidic solution) can serve to dilute the aversive stimulus. More recently, Woods and his colleagues have argued that such anticipatory responses are critical for the efficient digestion of large meals (Woods 1991, Woods & Ramsay 2000, Woods & Seeley 2002, Woods & Strubbe 1994).

Food intake triggers major physiological adjustments involved in the digestion, absorption, and storage of the energy source. Woods has compared eating a large meal to suffering a major physiological assault (Woods 1991). In addition to stimulating the secretion of digestive hormones and enzymes, eating causes the release of a cascade of stress hormones, including adrenocorticotropic hormone, epinephrine, and norepinephrine. Pavlovian conditioning serves to mitigate the disruptive effects of eating by mobilizing the secretion of digestive hormones and enzymes before the food reaches the gut. As Woods noted, "by successfully anticipating the ingestion of food, animals can make appropriate compensatory responses and hence lessen the impact of eating upon the body" (Woods 1991, p. 492).

The importance of Pavlovian processes in digestion is clearly illustrated by how insulin secretion is regulated. Insulin is required for the transfer of nutrients from the blood to target tissues and is released by the pancreas in response to elevated serum levels of carbohydrates, fats, and proteins. However, insulin is often released before ingested nutrients are absorbed into the circulatory system.

The taste or smell of food can trigger the release of insulin long before the food is digested and enters the bloodstream. This has been labeled "cephalic insulin" because it is mediated by brain mechanisms rather than signals originating in the gut. Cephalic insulin secretions also occur in anticipation of predictable large meals and in response to conditioned stimuli that precede meals (Woods et al. 1977). Anticipatory insulin secretion also can be conditioned with injections of insulin rather than meals serving as the US (Woods & Kulkosky 1976).

Cephalic insulin and conditioned insulin secretions are responses to cues that precede the gut stimuli that ordinarily serve as the US for insulin secretion. Hence, these are conditioned responses rather than modified unconditioned responses. However, as Woods & Strubbe (1994) have pointed out, "the increment in cephalic insulin coming when it does circumvents the need for a much greater postprandial insulin response" (p. 149). Measurements of the insulin response consequent to the ingestion of a meal would provide decisive evidence on this point.

One interesting implication of these mechanisms is that subjects who are able to anticipate a meal should be able to tolerate the stresses of eating more effectively. Consistent with this prediction, rats eat more following a signal for feeding (Zamble 1973). In the study by Zamble, visual and auditory stimuli served as the conditioned stimulus predictive of a meal. Temporal cues can also serve as conditioned stimuli if meals are provided at fixed intervals (e.g., once a day). Interestingly, rats fed at the same time each day eat less if their usual feeding is delayed so that it does not occur in conjunction with the usual temporal CSs (Bousfield & Elliott 1934). This is a remarkable finding because delaying a feeding increases food deprivation.

As Woods and his colleagues have pointed out, the Pavlovian approach to the analysis of eating provides a perspective that contrasts with more traditional negative feedback models. Both approaches start with the axiom that ingestion serves to provide needed nutrients and is part of a homeostatic regulatory system. According to classic negative feedback models, organisms monitor an aspect of energy balance (levels of glucose or lipids, for example), and ingestion is initiated when a physiological index of energy balance indicates a deficit. Food intake then rectifies this deficit. The Pavlovian approach suggests that physiological antecedents of meals such as a drop in blood sugar or a decrease in metabolic rate do not trigger eating but help to process the impending meal more effectively (Woods & Seeley 2002, Woods & Strubbe 1994).

Conditioning and Drug Tolerance

The administration of a psychoactive drug also may be viewed as creating a major physiological disturbance, whose anticipation may permit the recruitment of processes to deal more effectively with the drug insult. Thus, the types of conditioning mechanisms that facilitate the digestion of food are potentially also relevant to coping with drug experiences (Woods & Ramsay 2000). That drugs may act as unconditioned stimuli was evident to Pavlov, whose associates observed salivation and other conditioned responses in dogs that were exposed to cues that reliably preceded the administration of morphine and apomorphine (Pavlov 1927, pp. 35–37). However, as in his studies with food, Pavlov emphasized the development of responses to conditioned stimuli that did not have much impact before being paired with the drug administrations. How the presentation of a drug-conditioned stimulus may alter the organism's reactions to the drug itself was not considered until later in the twentieth century, when investigators became interested in the role of Pavlovian conditioning in drug tolerance and sensitization (Eikelboom & Stewart 1982; Siegel 1989, 1991; Siegel et al. 2000; Woods & Ramsay 2000; Young & Goudie 1994).

Drug tolerance refers to a decrease in a measured drug effect that is frequently observed with repeated administrations of the drug. Learning has been implicated in drug tolerance in part because drug tolerance can last as long as a year (Cochin & Kornetsky 1964). However, the most significant feature of drug tolerance that has encouraged a learning interpretation is its situation specificity. Drug tolerance is most readily observed when the circumstances of drug administration during a test trial are the same as the circumstances that existed during prior drug treatments. If the context or cues in the presence of which the drug was previously administered are altered, drug tolerance is reduced or abolished. The situation specificity of drug tolerance has been demonstrated with a variety of drugs, including opiates (Siegel 1991), ethanol (Lê et al. 1979), nicotine (Cepeda-Benito et al. 2000), pentobarbital (Cappell et al. 1981), haloperidol (Poulos & Hinson 1982), and benzodiazepines (King et al. 1987). Other features of learning evident in drug tolerance include extinction (Siegel et al. 1980); external inhibition (Poulos et al. 1988); latent inhibition (Goodison & Siegel 1995); inhibitory conditioning (Fanselow & German 1982); stimulus generalization and loss of stimulus control over time (Feinberg & Riccio 1990); and sensory preconditioning, blocking, and overshadowing (Dafters & Bach 1985, Dafters et al. 1983).

Pavlovian analyses of drug tolerance have emphasized how physiological and behavioral responses to a drug are attenuated by the presence of drug-predictive cues that become conditioned by repeated drug administrations. Efforts to understand why a drug-conditioned stimulus contributes to tolerance have involved examining conditioned responses elicited by the CS in the absence of the drug itself. For drugs that show the development of tolerance, the CS generally elicits physiological and behavioral changes that are opposite to or compensate for the drug effects. Such drug-compensatory CRs have been observed with a variety of drugs, including opiates (Grisel et al. 1994, Krank et al. 1981), ethanol (Larson & Siegel 1998), and caffeine (Andrews et al. 1998, Rozin et al. 1984).

The Pavlovian analysis of drug tolerance is based on homeostatic regulatory concepts. It assumes that the administration of a drug creates physiological disturbances that in turn activate compensatory changes that serve to attenuate those perturbations. Initially, the compensatory adjustments occur only as delayed unconditioned responses to the drug. However, as conditioning proceeds, the unconditioned compensatory responses also come to be activated by the drug-predictive CSs and thereby contribute to the attenuated drug effects that are observed (Dworkin 1993, Eikelboom & Stewart 1982).

The Pavlovian analysis of drug tolerance is well supported by a large body of evidence and has been extended to analyses of drug abuse and treatment (Siegel et al. 2000, Siegel & Ramos 2002). When originally formulated, the model focused on exteroceptive drug-predictive cues. More recently, the model has been extended to also incorporate internal cues involved in the initiation of an episode of drug self-administration (Donny et al. 1995) as well as internal cues characteristic of the onset of a drug experience (Kim et al. 1999). These extensions help explain why drug tolerance is more evident if the drug is self-administered and why some cases of long-term tolerance are not context specific (Siegel et al. 2000, Siegel & Ramos 2002).

Drug Conditioning and Sensitization

Although the Pavlovian model of drug tolerance has enjoyed wide success, it is limited to physiological systems that involve some form of homeostatic regulation. Systems in which the physiological changes induced by a drug do not activate compensatory unconditioned adjustments are not predicted to show conditioned tolerance. Such systems may in fact show the opposite outcome, namely sensitization. Sensitization is an increase in the impact of a drug that occurs with repeated drug administrations. Although research on the contributions of Pavlovian conditioning to drug sensitization is not as extensive as research on conditioned drug tolerance, Pavlovian processes have been implicated in drug sensitization as well (Stewart 1992). Furthermore, Pavlovian sensitization is assumed to play an important role in models of drug abuse. In particular, the development of drug craving has been attributed to a context-specific drug sensitization process (Robinson & Berridge 1993, 2000).

Anagnostaras & Robinson (1996), for example, demonstrated sensitization of locomotor behavior in rats elicited by amphetamine. The rats were first given 10 injections of a fairly high dose of amphetamine (3 mg/kg) before being tested with one of several amphetamine doses. Sensitization developed in the context in which the drug was administered but was not observed if the subjects were tested with amphetamine in a different context. Furthermore, extinction of the contextual cues attenuated the drug sensitization effect (see also Drew & Glick 1988, Hinson & Poulos 1981, Post et al. 1981, Terelli & Terry 1999).

Discussion

The emphasis on research concerned with CS-induced modifications of responding to the unconditioned stimulus has been on documenting such effects and building a case that such effects obey conventional laws of associative learning. The mechanisms of such effects have garnered much less attention. Perhaps the simplest way to explain such effects is in terms of the summation of responses to the CS and the US. According to the summation model, certain conditioned responses come to be elicited by the CS. If the US is presented right after the CS, the responses observed during the US period represent the summation of delayed CRs and responses directly elicited by the US.

The summation model has been used to explain conditioned drug tolerance (e.g., Siegel 1989). In this explanation, the CS is presumed to elicit a drug-compensatory conditioned response, which serves to attenuate the effects of the drug that is administered in the CS context. Consistent with this interpretation, in many instances of conditioned tolerance, the response elicited by the drug-conditioned CS is opposite the initial physiological disturbance caused by the drug itself. The summation model has also been used to explain conditioned modifications of eyeblink responding to a US (Donegan & Wagner 1987), and the model readily lends itself to explanations of UR modification in nursing, suckling, and feeding, although it has not been precisely tested in those situations.

Although the summation model may explain some instances of conditioned modifications of responding to the US, it cannot serve as a general account of such effects. In particular, the summation model is not readily applicable to instances in which responses to the CS are qualitatively different from the responses that are elicited by the US. The fear-potentiated startle paradigm is a case in point. Here the conditioned response is a conditioned suppression or freezing response to a relatively long CS. In contrast, the startle US is a much shorter (e.g., 500 msec) stimulus that elicits a vigorous startle reaction. The summation model is also difficult to reconcile with instances of enhanced sexual and aggressive behavior. Many of the sexual and aggressive responses that occur in the presence of a conspecific sexual partner or intruder are not observed when a conditioned stimulus is presented because the CS typically does not provide supportive stimulation needed for various copulatory and combative action patterns.

A simple summative model has also been brought into question by evidence that conditioned modifications of unconditioned behavior do not always correspond to conditioned responses elicited by a CS. In their studies of conditioned amphetamine sensitization, for example, Anagnostaras & Robinson (1996) observed increased locomotion as a CR when they administered saline in the amphetamine-paired context. However, the size and timing of this CR was not adequate to fully account for the sensitized amphetamine response that was observed in the same context.

As an alternative to the summation model, Anagnostaras & Robinson (1996) proposed that conditioned stimuli modify unconditioned responding through an occasion-setting mechanism whereby the CS sets the occasion for the US (Holland 1992, Rescorla 1985, Schmajuk & Holland 1998). However, it is unclear how occasion setting might account for CS-induced modifications of responding to the US, since this mechanism deals with interactions between target and modulating CSs rather than interactions between conditioned and unconditioned stimuli.

A more promising alternative to the summation model rests on the common observation that the fundamental outcome of Pavlovian conditioning is that the CS comes to activate a representation of the US (Rescorla 1988). This activation of the

US representation prior to the occurrence of the US presumably allows for more effective interactions with the US once the US arrives. Hollis (1982) referred to this kind of process as "prefiguring." Prefiguring or anticipatory activation of the US representation may alter responses to the US in different ways in different response systems. Possible mechanisms include reductions in the threshold for eliciting unconditioned behavior and/or changes in the perception of the US. Additional research is required to document how these mechanisms might operate.

SUMMARY AND CONCLUSION

Pavlovian conditioning is typically described as a form of learning in which a neutral or arbitrary CS becomes associated with US, and as a consequence the CS comes to elicit a conditioned response. This description emphasizes that the CS is unrelated to the US at the outset of conditioning and that learning is best measured by the development of new responses to the CS. These features accurately characterize many laboratory studies of Pavlovian conditioning (especially those conducted in the associationist tradition) but fail to capture the critical features of Pavlovian conditioning from a functional perspective.

A functional perspective assumes that Pavlovian conditioning is an adaptive trait that occurs under natural circumstances. This simple claim has two important implications, one relevant to the conditioned stimulus, and the other relevant to the conditioned response.

For Pavlovian conditioning to occur in the ecological niche of an organism, CS-US pairings must be a feature of that environment. For that to be the case, the CS cannot be unrelated or arbitrary with respect to that US. Rather, there must be a pre-existing ecological relation between the CS and the US. Thus, a functional approach to Pavlovian conditioning rejects the common characterization that Pavlovian conditioning involves learning to associate a neutral or arbitrary CS with a US.

In addition to focusing on how learning might occur in the natural environment, a functional approach directs us to focus on behavioral consequences of Pavlovian conditioning that are of adaptive significance. The common characterization of Pavlovian conditioning emphasizes how organisms learn new responses to the CS. However, starting with Pavlov himself, researchers have widely acknowledged that conditioned stimuli are not particularly important in their own right. Therefore, the adaptive significance of Pavlovian conditioning probably does not rest with how an organism's interactions with the CS are improved by learning. From a functional perspective, the critical task for the organism is to cope with the unconditioned stimulus, which is of much greater biological import. Therefore, a functional perspective directs our attention to how an organism's responses to the US are changed by Pavlovian conditioning.

Evidence of learning with conditioned stimuli that are natural precursors of the US is available from studies of poison avoidance, food intake, sexual behavior, fear and defensive behavior, and maternal nursing and infant suckling. Although the details have not been documented in all of these learning situations, the studies have provided provocative evidence that learning with naturalistic stimuli proceeds differently from learning with arbitrary cues. In particular, learning with naturalistic stimuli is more rapid, more resistant to increases in the CS-US interval, and more resistant to the blocking effect. These findings suggest that the phenomena of Pavlovian conditioning may differ for naturalistic as contrasted with arbitrary conditioned stimuli. The mechanisms mediating these learning effects may not be distinctive, but considerable additional research is required to understand how conventional learning mechanisms may produce some of the special learning effects that have been documented with naturalistic CSs.

Although conventional descriptions of Pavlovian conditioning emphasize the development of conditioned responses to the CS, numerous studies have shown that conditioning also alters how organisms react to, and interact with, the unconditioned stimulus. Evidence of conditioned modifications of responding to the US is available from studies of eyeblink conditioning; sexual, aggressive, and maternal behavior; fear conditioning; feeding and digestion; and drug conditioning. These conditioned modifications of responding to the US improve the efficacy of the organism's interactions with the US and reduce the disruptive effects of encountering the US. If these changes in responding to the US are of adaptive significance, they should also be correlated with increased reproductive fitness. In most of the behavior systems examined, adaptive significance is inferred from parameters that are presumed to be related to reproductive fitness. Adaptive significance can be demonstrated more explicitly in the sexual behavior system, which permits direct measurement of reproductive fitness. Consistent with a functional perspective, recent studies have shown that Pavlovian conditioning enhances sperm output and various aspects of sexual behavior, and increases the number of offspring that result from a sexual interaction.

Breland & Breland (1961) warned more than 40 years ago that common laboratory paradigms for the study of learning might not accurately reflect learning in natural ecosystems. Although this warning was voiced in relation to operant and instrumental conditioning, it was soon generalized to include Pavlovian and other forms of learning (Hinde & Stevenson-Hinde 1973, Seligman & Hager 1972). Initially the development of a vibrant functional approach to the study of Pavlovian conditioning was hampered by inadequate and difficult methods of discovery (Domjan & Galef 1983). The behavior systems approach developed by Timberlake and his associates (e.g., Timberlake 2001) represents a promising solution to these difficulties. The issues reviewed in the present chapter are theoretically agnostic and complementary to the behavior systems approach. They emphasize two important factors that are central to a functional approach to Pavlovian conditioning: (*a*) the use of conditioned stimuli that are natural precursors of a US, and (*b*) the measurement of changes in behavior directed toward the US rather than the CS as the primary behavioral manifestation of Pavlovian conditioning.

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