Contemporary Research on Pavlovian Conditioning

A "New" Functional Analysis

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Recently, the study of biological function has been reac-
tected as a legitimate focus of research in the field of
animal learning. This "new" functionalism suffuses 2
distinct perspectives with which researchers approach
the study of Pavlovian conditioning. Those who adopt
the ecological perspective explore the role of conditioning
within functional, naturally occurring categories of be-
havior, for example, intraspecific defense, reproduction,
or food recognition. From this perspective, the central
question is, In what ways does conditioning contribute
to animals' ability to survive and reproduce? For those
researchers who explore the cause rather than the func-
tion of conditioning, the central question is, How, and
under what circumstances, does conditioning occur? Al-
though, historically, those who studied causal mech-

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1 I join Shettleworth (1993) in the use of the descriptor "ecologi-
cal" to describe a program of research that focuses on the natural
environment of animals. Although Shettleworth used that adjective to
identify a particular approach within the field of comparative cognition,
rather than Pavlovian conditioning, readers of both literatures will rec-
ognize the commonalities.

Despite the inseparable connection in Pavlov's
(1927) own thinking between causal and func-
tional approaches to behavior—that is, between
the underlying mechanisms of behavior and its adaptive
value—only recently have functional analyses been re-
garded as a legitimate focus of research. Although a few
early American psychologists, such as Margaret Floy
Washburn (1926) and Elmer A. Culler (1938), also re-
garded the study of function as an integral part of their
thinking, the importance of function clearly began to
recede by the late 1940s and became almost a verboten
concept in animal learning theory during the 1950s and
the early 1960s (see Hollis, 1990, for further discussion).

Several historical forces conspired to suppress ex-
perimential consideration of adaptive value. Undoubtedly,
the simplest was the early success of the behaviorist tradi-
tion within psychology, a school of thought that was very
much attracted to Pavlov's methodology (Watson, 1925)
but philosophically was wedded more to proximal ques-
tions than to functional ones (Boring, 1957). Less benign
a force was the open antagonism with which the behav-
iorists of the 1950s regarded early ethological thinking:
Any idea, like adaptive value, that found itself juxtaposed
with the study of instinctive behavior was rejected
automatically.

Two forces were influential in the recent reversal of
this trend. First, beginning in the late 1960s, researchers
were obliged to confront numerous examples of biological
constraints on animals' learning abilities (Hinde &
Stevenson-Hinde, 1973; Shettleworth, 1972). Suddenly,
behaviorists' disregard for the ways in which animals
were adapted to their environments became a limiting
factor, if not an embarrassment. Second, the formal recog-
nition of ethologists Niko Tinbergen, Konrad Lorenz,
and Karl von Frisch with a Nobel prize in 1973, together
with the enviable success of neo-Darwinian evolutionary
analyses in the newly emerging field of behavioral ecol-
ogy, finally removed all traces of tarnish that had marred
the image of functional analyses. Indeed, pioneered by
Tinbergen's (1951) use of creative yet simple exper-
iments, the field of behavioral ecology helped to provide
the experimental methodology for investigations of bio-
logical function. Thus, although a burgeoning con-
straints-on-learning literature might be said to have pro-
vided animal learning psychologists with the impetus to
explore functional questions, the field of behavioral ecol-
ogy contributed the techniques to do so. Not surprisingly
then, a large body of research in contemporary Pavlovian
conditioning, which embodies what I call the ecological
perspective, has as its goal the integration of causal and
functional analyses of conditioned behavior.

But what has become of causal analysis, the ap-
proach that dominated the field of animal learning for so
long? Although a few researchers who study the underly-
ing mechanisms of learned behavior continue to ignore biological function, many more embrace it as an important heuristic. Slowly but inexorably, a decidedly functional motif has been restored to animal learning theory. Because this new approach to the study of causal mechanisms has revealed numerous links to cognitive psychology—links, for example, to the acquisition of causal relations by humans (Denniston, Miller, & Matute, 1996; Wasserman, 1993) or to cognitive problems dealing with event, space, and time correlation (Gallistel, 1990)—I follow Dickinson (1980) in calling it the cognitive perspective.

In this article, I briefly describe some of the exciting new discoveries originating from each of these perspectives. Although a comprehensive review is beyond the scope of this article, the research that I have chosen to highlight nonetheless illustrates the conceptual reorganization that has taken place in contemporary research on Pavlovian conditioning—the "new" functional analysis.2

The Ecological Perspective

How does Pavlovian conditioning increase an animal's ability to secure food, to defeat its rivals, to avoid predators, or to locate mates? What advantage does an animal gain by responding to cues that precede biologically important events? Biological function was a recurrent theme in Pavlov's (1927) writing: An animal's conditional response (CR) was "directed towards the preservation of its existence" (p. 8). Although one would recognize today that adaptive behavior preserves copies of an animal's genes, rather than its existence per se, this translation into neo-Darwinian terminology still reflects very well Pavlov's own conception of tselesoobraznost, or the "purposiveness" of behavior (see Dewsbury, 1997, this issue). Indeed, Pavlov's functional explanation of food CRs, an example of anticipatory responding that Pavlov employed frequently to illustrate tselesoobraznost, predated much modern thinking (Pavlov, 1982; Woods & Strubbe, 1994). Not surprisingly then, as the sections that follow make clear, researchers who approach conditioning from an ecological perspective are concerned with how Pavlovian signaling of biologically important events enables animals to adopt adaptive responses to those events.

Intraspecific Defense: Male-Male Competition

Following a spate of studies in the late 1960s and the 1970s demonstrating that aggressive behavior could be classically conditioned in mammals, birds, and fish (reviewed in Hollis, 1982), the obvious next step was to show that these responses could be adaptive. In an article subtitled "The Best Defense Is a Good Offense" (Hollis, 1984), I reported that Pavlovian signaling of an aggressive encounter enables male blue gourami fish to defend their territories more aggressively than males that do not have the benefit of a signal. Moreover, conditional stimuli (CSs) that predict the absence of a rival for a period of time produce a substantial decrease in territorial aggression (Hollis, Martin, Cadieux, & Colbert, 1984). These cues, called CS's because they predict the absence of an unconditional stimulus (US), probably enable males to relax their territorial defense at times when or in places where an intrusion is unlikely to occur.

Recent work in my lab (Hollis, Dumas, Singh, & Packelman, 1995) has demonstrated that the competitive advantage provided by Pavlovian signaling persists longer than I previously suspected. Following an encounter that was signaled for some males but not for their opponents, each winner and each loser were forced to defend their territory against a novel male in an unsignaled encounter three days later. Classically conditioned males, for which the first fight was signaled, not only were more likely to defeat their rivals than were control males but, having won that encounter, also were more likely to win their second fight than were males that had lost their first encounter. All losers lost their second fight.

These outcomes, which my students and I labeled "winners become winners and losers stay losers," are consistent with well-known neuroendocrinological changes associated with winning and losing aggressive contests in many species of territorial males, including rats, mice, birds, lizards, monkeys, and humans (reviewed in Hollis et al., 1995). In short, that neuroendocrinological research demonstrates that winners exhibit lower levels of corticoids and higher levels of androgens than do their unsuccessful opponents (Hannes, Franck, & Liebmann, 1984). In contrast, males that lose aggressive contests suffer from what might be called an aggressive stress syndrome (Bronson, 1973).

Perhaps because most researchers who study the winners-losers phenomenon are not learning psychologists, they do not seem to recognize the obvious Pavlovian contingencies in their experimental designs (such as arranging successive contests in the same arena). However, Williams and his colleagues have examined directly the role of conditioning in defeated rats. They found that odor cues associated with defeat elicit a variety of highly adaptive responses in losers, including conditioned freezing (Williams & Scott, 1989) and submissive behavior (Williams & Lierle, 1988; see also Williams, 1991). Although no one has looked directly at how Pavlovian cues might affect the subsequent behavior of former winners to produce the "winners become winners" phenomenon, a study of territorial male Siamese fighting fish, Betta splendens (Bronstein, 1986), revealed that males patrol sites where they have had previous encounters with rivals, occasionally exhibiting "keep out" displays.

In addition to warding off rivals and defending themselves against dominant conspecifics, some animals are

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2 As the functionalist Elmer Culler (1938) remarked when he, too, was asked to provide a snapshot of contemporary research on conditioning, "So meager a selection from so extensive a material is hard to justify. . . Every expert will recognize that many of the best contributions are not mentioned" (p. 134).
capable of avoiding dangerous inanimate objects that threaten themselves and their offspring. Here, too, the study of CRs to this type of stressor reveals a highly adaptive behavioral pattern, which consists of approaching the object in a stereotyped "stretched-attention" posture, sniffing the object, and finally burying it (Pinel & Treit, 1978; see Pinel & Mana, 1989, for a review).

As this section on defensive behavior makes clear, animals are forced to cope with a panoply of stressors in their natural environments. Although researchers tend to study separately these different defense systems, the recognition that stressors of all kinds invariably evoke fear and that fear is easily conditioned to a wide variety of available cues has prompted several researchers to explore other theoretically important commonalities. For example, a reanalysis of the learned helplessness effect—the disruption of animals' escape learning following exposure to inescapable shock (Overmier & Seligman, 1967)—reveals that odor cues, which mediate many of the behavior patterns that characterize conspecific defense, are also critical to the expression of learned helplessness (Minor, Dess, & Overmier, 1991). Similarly, both the submissive behavior and the hypolgesia that characterize learned helplessness in rats bear a marked resemblance to defeat by a conspecific (Minor et al., 1991). Finally, Williams (1987) has proposed a model in which he attempts to encompass multiple expressions of defensive behavior, not only conditioned burying behavior and submission resulting from conspecific defeat but also interspecific (antipredator) defense, which I review below. Further elaboration of these multifactor models (e.g., Overmier, 1988; Williams, 1987) is certain to provide an important heuristic for the study of Pavlovian conditioning in general, and defensive behavior in particular.

**Interspecific (Antipredator) Defense**

Probably no one was more influential in creating the right climate for the ecological perspective to take hold than was Bolles (1970, 1975), who emphasized that learned behavior was highly influenced, if not completely constrained, by animals' innate reactions to significant environmental events. For example, rats possess species-specific defense reactions (SSDRs), such as freezing, fighting, and fleeing, and when they are confronted by a threatening situation or by signals predicting a threat, their behavioral repertoire necessarily is restricted to those SSDRs. Taking Bolles's SSDR theory as a starting point, Fanselow (1989, 1994) has adopted a "behavior system" approach to aversively motivated behavior. That is, in much the same way as early ethologists (e.g., Tinbergen, 1951) analyzed reproductive behavior in terms of a hierarchically integrated sequence of responses, each of which has its own eliciting stimulus and control mechanism, Fanselow has shown that the imminence of a predator mobilizes different modes of defense, each of which has its own activating stimuli. For example, as the risk of encountering a predator while foraging increases, rats eat fewer, but larger, meals (Fanselow, 1989); at the other end of the predatory imminence continuum, rats engage in more active defense, which includes biting, jumping, and vocalizing (Fanselow, 1994).

Thus, the behavior system approach serves to highlight the fact that defense is not a single isolated behavior but in fact involves a variety of activities arranged hierarchically. In addition to enhancing our understanding of the conditions under which fear may or may not be classically conditioned to a particular environment and how that fear is expressed (Fanselow, 1990), Fanselow (1994) has been highly successful in mapping some aspects of the neural circuitry mediating defensive behavior. As I show in later sections of this article, the behavior system approach has provided researchers with a very effective heuristic for the study of conditioning.

**Courtship and Reproduction**

As early as 1964, Farris demonstrated that compared with males that did not have the benefit of a signal predicting a female's appearance, Pavlovian signaling of a mate greatly shortened the latency to ejaculate in male Japanese quail. Unfortunately, Farris's data on latency to ejaculate were omitted in his published article on conditioned courtship behavior in the Journal of the Experimental Analysis of Behavior (1967), an omission that reflected, perhaps, the lingering antifunctional Zeitgeist. Nevertheless, in the past 12 years, similar findings have been reported in birds (Domjan, Lyons, North, & Bruell, 1986), rats (Zamble, Hadad, Mitchell, & Cutmore, 1985), and fish (Hollis, Pharr, Dumas, Britton, & Field, 1997). Notwithstanding the importance of these demonstrations per se, the study of conditioned reproductive behavior has moved far beyond simple demonstrations of reproductive efficiency.

Two research programs encompass much of the current work on sexual conditioning. One is Domjan's (1994, 1997) "behavior system" approach to sexual behavior in male Japanese quail. Analogous to Fanselow's (1989, 1994) investigation of defensive behavior, discussed above, Domjan and his colleagues have described the way in which Pavlovian conditioning shapes and modulates both the effective stimuli for sexual behavior in quail and the resulting responses. For example, sexual conditioning increases the range of stimuli that control sexual behavior: Although male Japanese quail initially are unresponsive to certain plumage characteristics of females, they become quite aroused by these visual cues after they are paired with sexual experience (Domjan, Greene, & North, 1989). Likewise, contextual cues, those that arise from the physical environment in which males find females, increase the effectiveness of species-specific stimuli following conditioning (Domjan et al., 1989). Viewed from the ecological perspective, sexual behavior in quail forms a framework in which to understand the function of basic Pavlovian conditioning phenomena, such as blocking (Köksal, Domjan, & Weisman,
conditioned inhibition (Crawford & Domjan, 1996), and sign tracking (Burns & Domjan, 1996).

With a slightly different goal in mind, namely to elucidate the specific reproductive benefits that accrue to males and females as a result of conditioning, my students and I have been exploring sexual conditioning in blue gouramis. Our studies have revealed, for example, that Pavlovian signaling of female accessibility enables territorial males to attenuate their initial aggressive response to arriving females (Holliis, Cadieux, & Colbert, 1989), a well-recognized cost of territorial behavior in many species. Females, too, are able to anticipate the arrival of mates (Holliis et al., 1989), but unlike female quail (Gutiérrez & Domjan, 1997), the CR is similar in male and female gouramis, which is not surprising given that both males and females seek multiple mates.

Recently, my students and I (Holliis et al., 1997) provided the first demonstration of direct reproductive benefits resulting from classical conditioning: Not only does signaling of a mate enable males to attenuate their aggressive response to females, thus permitting them to spawn with females sooner, but classically conditioned males spend more time nestbuilding; they clasp females more often; and, most important, they produce significantly more young than do males that do not have the benefit of a signal.

Our findings, taken together with a report by Graham and Desjardins (1980) demonstrating that reproductive hormone secretion can be classically conditioned, suggest that sexual conditioning may enable animals both to decrease the latency and to increase the efficiency of attempted matings. This hypothesis generates an interesting prediction for behavioral ecologists’ study of extrapair copulations, matings outside the pair bond: Individuals that engage in successful extrapair copulations (reviewed in Alcock, 1993) may be relying on Pavlovian signals to increase the benefits of this reproductive strategy.

Ontogeny of Food Recognition

From honeybees to humans, Pavlovian conditioning plays an important role in the foraging behavior of a wide variety of animals. In some species, that role extends to food recognition, the process wherein the young learn to recognize what is edible and what is not. The associative basis of food recognition has been explored systematically in several species, most notably in chicks (e.g., Hogan, 1984) and in ring doves (e.g., Balsam, Graf, & Silver, 1992; Graf, Balsam, & Silver, 1985). Although food recognition seems rather straightforward in precocial chicks, requiring only that they associate pecking with ingestion (Hogan, 1984), in ring doves the transition from dependent to independent feeding demands an elaborate interplay between a squab and its parents.

For the first 13 days of life, squab are fed regurgitated “crop milk,” sloughed off cells of the esophageal walls, by both parents. Beginning on about Day 3, however, those feedings consist of an increasing quantity of grain and seeds mixed in with a decreasing quantity of crop milk. Although feedings are parent-initiated at first, squab begin to beg for food from their parents at about 9–10 days of age, when the parents begin to leave the young alone in the nest for the first time. Pecking does not emerge until 13–15 days of age and is coincident with parents’ rejection of their squab’s begging attempts. Squab are weaned completely by about 21 days of age.

Balsam and his colleagues (e.g., Balsam et al., 1992; Graf et al., 1985) demonstrated that the transition from dependent to independent feeding is mediated by the behavior of the parents. That is, parental regurgitation of crop milk mixed with seed provides squab with the opportunity to experience both the sensory qualities and the postigestional consequences of seed prior to their own self-initiated experience with it. In addition, parents’ increasing rejection of begging forces squab to peck for themselves. In turn, that pecking permits young squab to experience a Pavlovian association between the sight of grain and positive ingestional consequences. Although, as Balsam et al. (1992) noted, Pavlovian conditioning is not the only experiential mechanism that plays a role in food recognition, it nonetheless serves a critical function in squab’s ability to determine what is and is not edible.

Psychoneuroimmunology

The serendipitous origin of psychoneuroimmunology has become a textbook classic. In 1974, Ader was studying conditioned nausea, a problematic side effect of cyclophosphamide administration. Although cyclophosphamide is a powerful immunosuppressant that has a wide variety of human clinical applications, such as treatment of autoimmune diseases and organ transplant, it produces nausea that is easily conditioned to a host of cues that happen to be coincident with drug administration. One problem with Ader’s study was that to extinguish rats’ conditioned aversion to a taste cue, saccharin-flavored water, he had to force them to drink it. But what was worse, his subjects kept dying. The explanation was simple: As a result of the taste-drug pairings, saccharin became a highly effective immunosuppressant on its own (Ader & Cohen, 1975). The rest, as they say, is history.

Following up on their initial discovery, Ader and Cohen (1982; see review by Ader & Cohen, 1993) demonstrated that the same taste CS could extend the immunosuppressive effects of cyclophosphamide, warding off a lethal autoimmune disease, lupus erythematosus, to which their mouse subjects previously had been exposed. These and other demonstrations of conditioned immunosuppression led Ader (1985) to speculate about the use of conditioning procedures to improve the action of immunosuppressants, drugs that often have a number of debilitating side effects.

In addition to immunosuppression, immunofacilitation also is capable of being conditioned. The activity of natural killer cells, which are thought to play a pivotal role in the body’s defense against cancer, is greatly enhanced in the presence of CSs that have been paired with...
poly I:C, a drug that enhances killer cell activity (Spector, 1987). Finally, Russell et al. (1984) were able to demonstrate the conditioned release of histamine, an outcome, they noted, that bears resemblance to a medical case reported in 1886 by an American physician whose patient sneezed when presented with a plastic rose.

**Drug Tolerance and Addiction**

Although Pavlov (1927) noted that drug-related CRs could be elicited by cues that preceded drug injection (the US), the manner in which these CRs contribute to the phenomena of drug tolerance and addiction has been elaborated most fully by Siegel (see Siegel, 1991, for a review). In short, reliable cues associated with the ingestion or injection of a variety of drugs—including opiates, alcohol, benzodiazepines, phencyclidine, haloperidol, and caffeine—elicit a battery of CRs that, together, oppose the physiological and behavioral reactions to the drug itself. This compensatory CR is, in effect, a drug preparation syndrome that ameliorates the effect of the toxin, preserving physiological homeostasis, and results in what is otherwise known as drug tolerance, the decreasing effect of a drug over repeated administrations. As a conditioning model necessarily would predict, (a) drug tolerance is situation-specific (Dyck, Driedger, Nemeth, Oaschuk, & Greenberg, 1987; Lé, Poulos, & Cappell, 1979); (b) tolerance can be greatly retarded by first habituating subjects to the cues that later will be paired with the drug (Siegel, 1977); (c) tolerance can be extinguished by presenting subjects with only the cues themselves on a few occasions (Siegel, 1978); and (d) tolerance can suddenly “disappear” when a novel stimulus, like a burst of noise, is presented along with the usual cues (Siegel & Larson, 1996), a phenomenon that Pavlov called “external inhibition.”

The Pavlovian conditioning model provides a cogent explanation for a variety of phenomena associated with drug abuse (Siegel, 1991). For example, withdrawal occurs whenever drug-related cues are present but the drug US is not taken; in this instance, the addict feels the full force of the compensatory CR. Addiction to a drug occurs because the only substance that can reduce those symptoms of withdrawal is none other than the drug itself. Finally, enigmatic overdose—that is, an overdose reaction to a drug that had been tolerated in the same amount by the same individual on an earlier occasion—may be the result of alterations in the context of drug administration. That is, as the situation specificity of the model would predict, any change in the context of drug administration would substantially reduce an individual’s compensatory CR and, thus, the individual’s protection from the lethal effects of that drug. Changing the context of drug administration has been shown to increase the lethality of several drugs, including heroin (Siegel, Hinson, Krank, & McCully, 1982), pentobarbital (Vila, 1989), alcohol (Melchior, 1990), and morphine (Siegel & Ellisworth, 1986). Obviously, the protection that the drug CR offers is but one side of a two-edged sword, with addiction as the other; nonetheless, in perhaps no other case has the adaptive value of the CR been demonstrated so dramatically.

**The Cognitive Perspective**

In the 1950s and the 1960s, animal learning psychologists searched for general rules of behavior, principles that would transcend both the confines of particular species and highly controlled laboratory conditions. Although this approach can be credited with helping researchers to establish an encyclopedic catalog of conditioning phenomena (Mackintosh, 1974), what it lacked was an overarching theme, beyond generality, per se, that would bind together that catalog of facts. However, beginning with two experiments in the late 1960s (Kamin, 1968; Rescorla, 1968), a would-be theme began to emerge, namely that Pavlovian conditioning is a means by which animals determine the predictability of events. In other words, the function of conditioning is to decipher cause and effect. Although that description would hardly seem earthshaking now, at the time it was a clear departure from a tradition that had stood firm in rejecting even words like predictability as too mentalistic. Nonetheless, it was a foot in the door, so to speak, that over the years has transformed the field from a collection of isolated principles into a coherent study of cognitive processes.

Adoption of this new cognitive perspective has been anything but fast-paced: It wasn’t until the early 1980s that the transformation was finally provided with both a name, the cognitive perspective, and a prescription for study (Dickinson, 1980; Mackintosh, 1983). Moreover, although Dickinson had noted that significant changes in our understanding of Pavlovian conditioning still were unknown outside the field, Rescorla made the same, still legitimate, complaint in 1988.

Increasingly, however, as I hope to make clear with a few highlights of that research, the cognitive perspective has provided important insights to previously intractable problems. It has done so, from my viewpoint, precisely because it has forced animal learning researchers to ac-

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3 Although learning psychologists generally accept the view that drug tolerance and addiction are products of classical conditioning, a few researchers question the centrality of the compensatory response (e.g., Paletta & Wagner, 1986), that is, the way in which conditioning suberves tolerance and addiction is debated.

4 A few psychologists still object to this type of language because it seems to imply that conditioning requires animals to be capable of complex reasoning. However, like behavioral ecologists who study the conditions under which animals behave optimally in a given situation, learning theorists need not assume that animals are either logicians or mathematicians. As Dawkins (1979) countered when charged with the same criticism, "A snail shell is an exquisite logarithmic spiral, but where does the snail keep its log tables [and] how indeed does it read them?" (p. 188). How do bees measure each angle of their hexagonal honeycombs? To paraphrase Dawkins, the biological machinery that constructs snail shells, builds honeycombs, and determines the predictability of events evolved by natural selection to operate automatically, in the absence of complex feats of reasoning.
knowledge the function of conditioning. That is, one cannot ask how animals discern "logical relations among events" (Rescorla, 1988, p. 153) without, at least implicitly, recognizing that the benchmark of that logic is natural selection. The questions that I pose below to organize this section are similar to rubrics used many years ago by Mackintosh (1974); however, the cognitive perspective, with its recognition of function, has provided new and far-reaching answers.

**How Do Conditional and Unconditional Stimuli Become Associated?**

Two studies provided the watershed for the modern era of Pavlovian conditioning theory. Rescorla (1968) demonstrated that simple temporal contiguity, or proximity, between the CS and the US is not sufficient for producing an association between them. Rather, animals seem to be learning about the probability of an event both in the presence and in the absence of its supposed signal. In other words, a particular sound is not a very good signal for, say, a predator unless the predator is encountered more often in the presence of that sound than in its absence. Similarly, another study by Kamin (1968) demonstrated that a CS could be blocked from becoming associated with a US if it were simply added to another already powerful signal that predicted the US. Together, these studies were interpreted to mean that conditioning involves learning the logical relations among events.

Widespread adoption by animal learning theorists of this conceptualization of conditioning quickly led to new theories of how logical relations are coded by animals (Mackintosh, 1975; Pearce & Hall, 1980; Rescorla & Wagner, 1972). In addition, a plethora of studies attempted to determine just what is being learned when animals are presented with CSs and USs. For example, animals learn about the context in which both CSs and USs appear, and this context itself can exert powerful control over behavior (Balsam & Tomie, 1985; Bouton, 1993). Also, animals form highly specific expectancies of what the CS signals (e.g., Kruse, Overmier, Konz, & Rokke, 1983)—expectancies, some have argued (Hollis, 1982), that function to optimize animals' interaction with the US. Finally, an especially intriguing idea that has attracted much recent research is that animals are capable of learning about the complex hierarchical structure of signaling events in their environment.

A striking illustration of this hierarchical learning is that of occasion setting, or facilitation (Holland, 1983; Rescorla, 1985), in which a CS acts to signal not a single US event but a relation between two other stimuli. For example, a tone CS can be used to indicate that another different CS, say a light, signals food; in the absence of the tone, the light is not followed by food. Investigations of this relatively new phenomenon already have suggested that occasion setting may play a much larger role in conditioning than was previously thought. For example, some researchers have noted the similarity between the control that occasion setters and contextual cues exert on behavior, forcing a reevaluation of contextual control (e.g., Bouton, 1984; Grahame, Hallam, Geier, & Miller, 1990; see Holland, 1992, for a review). Other researchers (e.g., Rescorla, 1991) have argued that occasion setting underlies basic inhibitory conditioning procedures in which one CS is followed by the US, except when it appears together with another different CS, the CS'. If this characterization is accurate, current assumptions about how animals code relations among events need to be overhauled completely. Whatever the outcome of these potentially paradigm-shifting analyses, the study of occasion setting will have changed substantially our understanding of what is learned and how CSs and USs become associated.

To address this same question of how CSs and USs become associated, many investigators have turned to the study of learning in invertebrates. However, these programs of research approach the question from two very different levels of analysis. On the one hand, several researchers, working with a variety of invertebrates—including planarian flatworms, fruit flies, leeches, and slugs, to name a few—are attempting to describe the cellular and molecular events that mediate associative learning (see Byrne, 1990; Sahley, 1995, for reviews). A major finding, from several laboratories, is that Pavlovian conditioning results in modifications of neural circuits, for example, activity-dependent presynaptic facilitation (Hawkins, Abrams, Carew, & Kandel, 1983). In turn, these findings have been a driving force in the field of connectionist modeling, in which computer simulations of neural network models are used both to explain and to predict the vagaries and variety of Pavlovian conditioning phenomena (e.g., Barto & Sutton, 1985; Schmajuk & DiCarlo, 1992).

A different approach to invertebrate conditioning is exemplified by Bitterman and Couvillon (1991). Their goal is to investigate a variety of Pavlovian conditioning phenomena, specifically in honeybees, in an attempt to reveal similarities in and differences between vertebrate and invertebrate learning. Surprisingly, the similarities far outnumber what seem to be a few relatively minor differences (Bitterman & Couvillon, 1991). Leaving aside the fascinating question of behavioral homology, that is, whether the mechanisms of conditioning are similar because of common evolutionary descent, the study of these similarities and differences is likely to shed much light on underlying mechanisms of how CSs and USs become associated.

**What Determines the Nature of the Conditional Response?**

Pavlov (1927) believed that the CS becomes a surrogate US, a substitute for it, and therefore the general nature and form of the CR and the unconditional response should be similar. However, in nature, biologically significant events often are signaled by very different kinds...
of cues, and animals should be predisposed to treat those cues differently. For example, food might be brought back to the burrow by a conspecific, it might be found underneat a dead log, or it might be detected by the sounds it makes rustling in the brush; each signal for food requires a different response. In rats, visual and auditory CSs evoke distinct behavior patterns (Holland, 1977, 1984): Rats startle when the CS, the food predictor, is an auditory cue but rise on their hind legs when it is a localized visual cue above their heads. In contrast, when the CS is a conspecific, rats approach it, sniff it, and make social contact (Timberlake & Grant, 1975); in other words, they perform the kind of social behavior exhibited by rats in response to returning conspecific foragers (Galet, 1990).

Perhaps the most extensively developed answer to the question of what determines the nature of the CR comes from Timberlake’s (1983, 1994; Timberlake & Lucas, 1989) behavior system approach to rat feeding. To give just a few examples, not only do rats respond differently to different cues predicting the appearance of food (reviewed in Timberlake, 1994), but the same CS-US combination evokes different CRs depending on how far apart in time the CS and the US are presented. For example, handling and food consumption are readily conditioned at short intervals, when CSs predict that food is imminent, whereas localized search and general search are conditioned at increasingly longer intervals (Timberlake, 1994). These results contradict the long-held view that longer CS-US intervals necessarily produce weaker associations, demonstrating once again the value of reexamining “general rules” within a functional context.5

What Makes Effective Conditional Stimuli and Unconditional Stimuli?

First, both the CS and the US must be novel with respect to one another. That is, the CS cannot have been presented by itself before it was paired with the US (Albert & Ayres, 1989), nor can the US have been presented by itself before the CS was paired with it (Randich & LoLordo, 1979). Animals that receive either CS preexposures or US preexposures, as these procedures are called, are usually slower to learn the CR. These results are readily incorporated into a cognitive perspective: If Pavlovian conditioning is a mechanism with which animals decipher cause and effect, then it should contain safeguards for effacing spurious signals; in nature, causes and effects co-occur reliably.

Second, learning is enhanced if CSs and USs “belong” together, a phenomenon that was first demonstrated by Garcia and Koelling (1966). In their classic experiment, rats were presented with two cues—a taste CS and an audiovisual CS—and immediately thereafter either were shocked or were made sick. Rats that received shock tended to ignore the taste cue, preferentially associating shock with the audiovisual cue, whereas rats that were made sick tended to ignore the audiovisual cue, preferentially associating malaise with the taste cue. A functional interpretation of this phenomenon is that for animals with a highly developed sense of taste, like rats and humans, tastes are better cues for food toxicity than are external events; avoidance of physical pain, however, is better accomplished by paying close attention to the external physical environment. This functional interpretation makes an interesting comparative prediction of animals that do not rely on taste to select food. For example, because most birds have a poorly developed gustatory system and thus rely more on vision than on taste to select food, they should preferentially form aversions to visual cues rather than gustatory or auditory CSs, just the reverse of rats. Studies of chicks (Gillette, Martin, & Bellingham, 1980) and quail (Wilcoxon, Dragoin, & Kral, 1971) have confirmed this prediction. Moreover, in a long series of experiments designed to explore the role of biological relevance in conditioning, LoLordo and his colleagues demonstrated that in pigeons, not only do visual stimuli predominate in situations involving food (e.g., Shapiro, Jacobs, & LoLordo, 1980) but also visual cues cannot be blocked (LoLordo, Jacobs, & Forere, 1982). That is, biologically relevant visual cues can control feeding behavior even under conditions when other cues are made more reliable predictors of food. These and other studies of belongingness, as the phenomenon sometimes is called, illustrate well the fruitful role that functional considerations have played in the study of causal mechanisms.

Conclusions

Space limitations have prevented me from addressing many other equally important areas of research. Nonetheless, I hope to have shown how an appreciation of biological function—a concept that was important in Pavlov’s thinking, then was discarded as being irrelevant (or, worse, unscientific), and finally was readopted in recent years—has transformed psychologists’ thinking about the process of Pavlovian conditioning. In Rescorla’s (1988) Eastern Psychological Association address entitled “Pavlovian Conditioning: It’s Not What You Think It Is,” he documented the significant changes that have taken place in the field over the past 20 years. The point that I have tried to make is that not only did those changes originate in a new era of functionalist thinking but the future growth of animal learning psychology depends on continued integration of causal and functional analyses.

5 In an earlier review of the Pavlovian conditioning literature in which I described the adaptive value of CRs across a broad range of contexts (Holts, 1982), I noted the distinction between appetitive and consummatory responses but attributed the different forms of the CR to the differing degree to which the CS was localizable. Although this parameter may be important, too, Timberlake’s (1994) demonstration that the CS-US interval can, in itself, influence the CR is an elegant example of using function to make new predictions about mechanism.
REFERENCES


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