Part I
Basic Classical Conditioning
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Principles of Pavlovian Conditioning

Description, Content, Function

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Although both early human memory researchers and behaviorists studied processes that today would be considered Pavlovian, Ivan Pavlov is credited with discovering classical conditioning and first officially describing the process to an English-speaking audience with the publication of *Conditioned reflexes* in 1927. Pavlov’s systematic investigation of Pavlovian conditioning uncovered most of the primary phenomena, and his sharp and nuanced discussions are still relevant today.

Gottlieb (2011) defined Pavlovian, or classical, conditioning as the “adjustments organisms make in response to observing the temporal relations among environmental or proprioceptive stimuli.” The most well-known form involves pairing a neutral conditioned stimulus (CS) with a biologically relevant unconditioned stimulus (US) that automatically elicits an unconditioned response (UR), leading the CS to elicit a conditioned response (CR) qualitatively similar to the UR. Pavlov’s first reported example used dogs as subjects, a metronome CS, food as the US, and salivation as the UR and CR (Pavlov, 1927, p. 26).

Pavlovian conditioning is most clearly defined and constrained by its method, which involves maintaining strict control over the presentation of stimuli. There appear to be few clear principles that distinguish Pavlovian conditioning from other forms of associative learning, such as instrumental learning and human associative memory, and we agree with Rescorla and Solomon (1967)’s conclusion the Pavlovian conditioning is most distinct in how determined the form of the learned response is by the choice of US. Pavlovian responding is also characteristically resistant to instrumental contingencies. For example, it is difficult to prevent a pigeon from pecking (CR) at a discrete key light (CS) paired with food (US), even if pecking prevents the delivery of food (Williams & Williams, 1969).
Overview

Basic Excitatory Phenomena

Acquisition is the primary phenomenon of Pavlovian conditioning and refers to the growth in conditioned responding resulting from pairing a CS and US over time (Pavlov, 1927, p. 26). A CS that produces conditioned responding is sometimes referred to as an excitor. An example of an excitor is a brief tone that, due to repeated pairings with an air puff to the eye, elicits anticipatory eyeblinking.

An animal that has learned to blink to a tone may also blink when presented with a novel auditory stimulus. The magnitude of this generalized responding is a function of the similarity of the new stimulus to the originally trained CS (Pavlov, 1927, p. 111). Generalization functions can be modified by discrimination learning, in which some stimuli are reinforced while others are nonreinforced. For example, the generalized responding from a tone to a burst of white noise can be reduced by interspersing presentations of the noise alone.

A tone paired with an air puff to the eye gains more than the ability to elicit anticipatory blinking. It also develops the ability to serve as a conditioned reinforcer for another, second-order, CS (Pavlov, 1927, p. 33). Second-order conditioning tends to lead to lower levels of responding than does first-order conditioning. Thus, a light paired with a tone excitor will likely elicit less conditioned eyeblinking than will the tone itself. Conditioned reinforcers are contrasted with primary reinforcers that do not need prior training to be able to establish conditioned responding. Unlike in instrumental conditioning, Pavlovian reinforcers refer to stimuli that may be appetitive or aversive.

Basic Inhibitory Phenomena

Inhibitory phenomena are those that manifest in opposition to conditioned responding. When stimuli both reduce responding to simultaneously presented excitors and are slow to become excitors themselves, as compared to neutral stimuli, they are called inhibitors (Rescorla, 1969a). This type of inhibition is sometimes referred to as operational inhibition. It is contrasted with the theoretical inhibition that is used as an explanation for transient decreases in excitatory responding.

Extinction refers to the loss in conditioned responding that occurs when an excitor is subsequently presented in a manner that breaks the CS-US relationship (Pavlov, 1927, p. 49). For example, our tone excitor will stop eliciting conditioned eye-blanks if it is repeatedly presented alone. Although extinction is explained by appeal to inhibitory mechanisms, extinguished stimuli do not typically become operational inhibitors (Rescorla, 1969a).

Suppression of responding may also be observed when a nonreinforced stimulus is interspersed among the reinforced trials of another CS and a US. For example, if noise alone presentations are interspersed among tone-air puff pairings, generalized responding to the noise will be reduced. The suppression of responding observed in a discrimination procedure is referred to as differential inhibition. Unlike extinguished stimuli, differentially conditioned stimuli may become operational inhibitors (Pavlov, 1927, p. 120).
A particularly powerful form of differential inhibition results from a conditioned inhibition procedure in which a stimulus is nonreinforced in the presence of an excitor that is reinforced when presented alone. For example, if our tone signals an air puff except when it is presented together with a light, the light will become a conditioned inhibitor capable of passing the operational tests for inhibition (Pavlov, 1927, p. 68).

Perhaps it is not surprising that with extended training, organisms may come to withhold responding to a CS until closer to the time of the US. The decrease in responding to early parts of a CS that may result from extended training is referred to as inhibition of delay (Pavlov, 1927, p. 88).

Basic Framework

Early theorists most often adopted a contiguity view of learning, in which the pairing of stimuli in time and space was the necessary and sufficient condition for generating conditioned responding. Although Hull (1943) expanded on this view in arguing that drive reduction was also necessary for learning, it is his other contributions that have made him central to contemporary understandings of Pavlovian processes.

Hull (1943) adopted the view of Pavlovian conditioning as an associative process by which the magnitude of the association determined the magnitude of conditioned responding. He presented a simple mathematical learning rule that specified the change in associative (habit) strength that resulted from the pairing of a CS and a US. The vast majority of subsequent quantitative models developed within the associative framework contain Hull’s simple learning algorithm (Mackintosh, 1975; Pearce, 1987; Rescorla & Wagner, 1972; Wagner, 1981).

Hull (1943) helped to cement a view of Pavlovian conditioning as an incremental trial-based process involving changes in the associative strength between stimuli. The parameters of his model are what were originally thought to be the determinants of Pavlovian learning. Primary was the number of trials. Secondary included three durations related to the CS-US interval: the length of the CS, the temporal gap between the CS and US, and the extension of the CS past the US; as well as two salience parameters, one for the CS and one for the US.

Hull’s Choices

CS-US Interval

**Delay Conditioning.** Most demonstrations of acquisition use a delay conditioning procedure where CS offset coincides with US onset. As such, CS duration is the only determinant of the CS-US interval in delay conditioning. There appear to be two conflicting ideas related to effects of CS duration. The first is that there is an optimal CS-US interval that is highly procedure-dependent. For skeletal muscle CRs, like eyeblink conditioning, the optimal CS-US interval is often a fraction of a second (Gormezano & Kehoe, 1981), but for other types of CRs, such as sign-tracking and conditioned fear, the optimal interval may be multiple seconds (Gibbon, Baldock, Locurto, Gold, & Terrace, 1977; Yeo, 1974).
That there is an optimal CS-US interval conflicts with the other main idea about CS duration, that shortening it promotes acquisition (Lattal, 1999). This conflict is likely a result of optimal durations being at the low end of the range of durations that can establish conditioned responding. What appears most relevant is that certain procedures allow for conditioning with CS-US intervals much longer than others. In fear conditioning, CS durations of several minutes can be effective (Kamin, 1965), and in conditioned taste aversion, CS-US trace intervals of up to 24 hours can establish conditioned aversions (Etscorn & Stephens, 1973).

Trace Conditioning. When the CS terminates prior to US onset, acquisition of conditioned responding may be strongly impaired (Ellison, 1964). This procedure is known as trace conditioning, referring to one explanation for the conditioned responding that does occur: A memory trace of the CS is contiguously paired with the US. Although a gap between CS offset and US onset impairs conditioned responding, the impairment does not necessarily reflect a failure to learn. Trace conditioning can lead a CS to become inhibitory (LoLordo & Fairliss, 1985). It also may lead to increasing levels of responding during the time between CS offset and US onset (Marlin, 1981).

Simultaneous Conditioning. Early research suggested that simultaneous CS-US presentation did not lead to conditioned responding (Kimble, 1961), but it is clear that in many cases it does (Heth & Rescorla, 1973). Simultaneous conditioning may lead to different forms of learning than does forward conditioning. For example, in flavor conditioning, simultaneous, but not delay, conditioning prevents the reacquisition of an extinguished preference (Higgins & Rescorla, 2004).

Backward Conditioning. Backward conditioning refers to presenting the US prior to presenting the CS. Typically, US offset and CS onset coincide. After a small number of trials, it is not uncommon to observe excitatory conditioned responding, but after further trials, the responding diminishes and the CS may become an inhibitor (Heth, 1976). One complexity is that a backward CS may pass an operational test for inhibition while at the same time establishing excitatory second-order conditioning to another CS (Barnet & Miller, 1996). Romaniuk and Williams (2000) provided an explanation for this by demonstrating that the initial 3 s of a 30 s backwards CS was excitatory while the remaining 27 s was inhibitory. Adding a 3 s gap between US offset and CS onset eliminated excitatory responding, strengthened inhibition, and prevented second-order conditioning.

Stimulus Intensity

US Magnitude. Some argue that acquisition of conditioned responding should be broken down into components that include the point of acquisition and the asymptotic magnitude of responding (Gallistel, Fairhurst, & Gibbon, 2004). In general, increasing US intensity or number tends to increase the magnitude of conditioned responding (Mackintosh, 1974, pp. 70–71); however, although Morris and Bouton (2006) detected effects of US magnitude on the point of acquisition in aversive and appetitive procedures with rats, how strongly US magnitude influences the point of acquisition is still not clear. Unlike US intensity, the effects of increasing US duration are not consistent across procedures (Mackintosh, 1974).
CS Intensity. Razran (1957), in summarizing 161 Russian studies relevant to effects of CS intensity, concluded that there was abundant evidence that increasing CS intensity increased both the rate of acquisition and the asymptotic magnitude of performance. A caveat was that when CS intensity was very high, performance was sometimes impaired. Outside of Russia, results of varying CS intensity have been more equivocal (Mackintosh, 1974, pp. 41–45).

Mackintosh (1974) suggests that effects of CS intensity, like those of US duration, are more likely to be observed in within-subject than in between-subject experiments, perhaps explaining some of the earlier Russian findings. This explanation is consistent with findings showing that when stimuli are presented in a way in which they are available for comparison, higher valued ones are augmented (positive contrast) while lower valued ones are diminished (negative contrast) (Flaherty, 1996).

Form of Acquisition

A second aspect of Hull’s (1943) model was that it predicted a particular geometric form of growth. Explicit is the mathematical form. Implicit is the gradual and increasingly slow progression of learning. The left side of Figure 1.1 shows a group-averaged learning curve for 16 pigeons in a 32 trials/day autoshaping procedure. Plotted is the rate/min of keypecking to a 5 s keylight CS that immediately preceded a 5 s access to grain US. The right side of Figure 1.1 shows a learning curve for one of the 16 pigeons. Both the learning curves start with a period characterized by the absence of conditioned responding, followed by a growth in conditioned responding until an asymptotic level is reached. The curves differ in that the individual curve shows a longer latency before conditioned responding emerges and a steeper rise. Gallistel et al. (2004) demonstrated that over a wide range of Pavlovian procedures,

![Figure 1.1](image_url)  
**Figure 1.1** Left: group-averaged learning curve for 16 pigeons in a 32 trials/day autoshaping procedure. Right: learning curve for 1 of the 16 pigeons.
group-averaged learning curves obscure the relative abruptness of individual learning curves. This abruptness suggests that two separate components of the learning curve can be meaningfully distinguished, the point of acquisition and the asymptotic magnitude of conditioned responding.

Trial Repetition

Repeatedly pairing a CS and a US leads to acquisition of conditioned responding. This does not mean that the number of repetitions is a primary determinant; increasing the number of trials is almost always accompanied by a corresponding increase in cumulative training time and number of sessions. It is reasonable to ask what is known about each of these factors in isolation.

Training Time. It is well established that increasing training time by lengthening the intertrial interval (ITI) increases the likelihood that an animal will develop conditioned responding, speeds acquisition, and promotes higher levels of conditioned responding. A particularly striking example is a quantitative analysis of the effects of ITI on pigeon autoshaping (Gibbon et al., 1977), replotted in Figure 1.2. The left side shows trials to criterion as a function of ITI. The right side shows hours of cumulative ITI to criterion. Cumulative ITI more strongly predicted rate of acquisition than did number of trials.

Number of Sessions. Kehoe and Macrae (1994) presented the most impressive evidence that increasing the number of sessions independently promotes acquisition. Their analysis of the literature that showed that rabbit eyeblink conditioning could be either fast or slow to develop depending on the number of trials per session. The left panel of Figure 1.3 replots their best-fitting function relating trials per session to trials to acquisition along with a new curve relating trials per session to sessions to criterion. As with cumulative ITI, number of sessions more strongly predicted rate of acquisition than did number of trials.

Number of Trials. Gottlieb (2008) assessed for the effects of number of trials on acquisition of conditioned approach behavior in mice and rats by varying the number of trials animals received in daily sessions of the same duration. In between-subject experiments, there was little evidence that up to 16-fold differences in the number

![Figure 1.2](image_url) Replot of pigeon autoshaping data from Gibbon et al. (1977), Experiment 1. Left: # trials to criterion as a function of ITI. Right: # cumulative training hours to criterion as a function of ITI. Groups differed in CS duration (4–32 s).
of trials per session promoted acquisition, although some impairment has been observed in the case of animals receiving only a single trial per session (Gottlieb & Prince, 2012). Gottlieb and Prince (2012) concluded that within a session, adding trials between any pair has little effect. As with US magnitude and CS intensity, within-subject effects of number of trials appear more readily obtainable than do between-subject effects (Gottlieb & Rescorla, 2010).

Figures 1.2 and 1.3 clearly point to repetitions over time being more important than number of repetitions in establishing conditioned responding. Figure 1.1 illustrates that the gradual nature of learning is still being called into question. Hull’s (1943) choices may have been reasonable, but only those relating to the CS-US interval have received unequivocal support. Even there, Hull did not have a mechanism by which trace and backward conditioning could lead to inhibition.

Content of Learning

The simplest framework for understanding what is learned in Pavlovian conditioning is the Stimulus-Response (S-R) framework of behaviorism that pre-dated the first unambiguous reports of Pavlovian conditioning (Guthrie, 1935; Hull, 1943; Thorndike, 1911). Within this framework, animals come to reflexively respond to a CS that has been contiguously paired with a UR.

Pavlov (1927) envisioned learning as a process by which CS and US neural centers become linked through asynchronous mutual activation. As a result, the CS comes to activate the US center, leading to responding. This reflects a view from within the Stimulus-Stimulus (S-S) framework, in which learning results in representations of the CS and US becoming linked. From an S-S view, a tone activates the idea of shock, and so the rabbit blinks. From an S-R view, a tone elicits a blink. The idea of shock is a mental event that is not directly observable, and so S-S theories are inherently cognitive in nature, early attempts to model the mind to explain behavior. Even so, like the early behaviorists, Pavlov considered the CR to be automatic and identical to the UR in form.

Two strategies have been used to try to show evidence of S-S learning. The first attempted to demonstrate learning in the absence of a UR. For instance, Brogden
(1939), showed learning in a sensory preconditioning procedure that involved first pairing two neutral CSs before pairing one with the US and showing that the other also came to elicit conditioned responding. A more recent strategy has been to modify the value of the US after it has been used to train a CS. Any post-conditioning influence on the CS would be evidence for S-S learning.

One way to accomplish this is to use second-order conditioning and to modify the first-order stimulus through extinction. For example, one might first pair a tone with an air puff, then a light with the tone. The key question is whether the conditioned eyeblinking to the light is then affected by extinction of the tone. Supporting an S-R view, in a number of appetitive and aversive procedures and species, extinguishing the first-order stimulus has little effect on responding to the second-order stimulus and so provides no evidence of S-S learning (Rizley & Rescorla, 1972).

A second way to assess for S-S learning is to directly modify the primary reinforcer in a first-order conditioning experiment. Often, this is done by pairing a food reinforcer with illness (Holland & Straub, 1979). The results of primary reinforcer devaluation studies show decreased conditioned responding due to US devaluation and so provide evidence for S-S learning.

A way to reconcile these findings can be found in the few second-order conditioning studies that have devalued the primary reinforcer and assessed for effects on the second-order CS. Devaluation both through poisoning and motivational shifts has been found to reduce responding to a second-order CS (Ross, 1986; Winterbauer & Balleine, 2005). This suggests that in some cases the failure to adjust conditioned responding of a second-order CS after extinction of the first-order CS may not be due to exclusive S-R learning. Rather, organisms may have formed a direct association between the second-order CS and the primary US, despite those stimuli not having been contiguously paired.

Tolman (1932) adopted an S-S framework but rejected Pavlov’s (1927) notion of stimulus substitution. He held instead that a CS predicts US occurrence and so leads to preparatory responding. One distinction between Pavlov’s view and Tolman’s is that for Pavlov the key element that determines behavior is the UR, while for Tolman it is the US. This allows Tolman to accommodate CRs that appear qualitatively different from URs. Although Mackintosh (1974) points out that most CRs look like URs, and that the exceptions may not prove fatal to the idea of CR-UR identity, there are a number of cases where the measured CR is either unrelated or superficially opposite to the UR. For example, the CR to shock is often freezing, whereas the UR involves vigorous motor activity. In conditioned tolerance procedures, the CR is may be exactly the opposite of the UR, as in the case of cues paired with morphine that lead to hyperalgesia and not analgesia (Siegel, 1983).

Contingency

Degraded Contingency

Partial Reinforcement. A major change in thinking about Pavlovian conditioning came about from studies that varied the proportion of trials in which the CS and US were paired. One way to vary this is to intersperse nonreinforced presentations of
the CS. This has the effect of reducing the probability that the US will follow the CS and is referred to as partial reinforcement (Gottlieb, 2005).

Although the results from studies of partial reinforcement are not entirely consistent, reducing probability of reinforcement most often impairs acquisition of conditioned responding (Mackintosh, 1974). When the number of reinforced trials and the time between CS presentations are held constant, continuous reinforcement more often leads to higher levels of asymptotic responding than does partial reinforcement, though it has relatively little influence on the number of reinforced trials before conditioned responding emerges. There is also some evidence that deleterious effects of reducing the probability of reinforcement might manifest most strongly in whether organisms acquire the conditioned response at all and not in how rapidly it emerges or how vigorous it becomes (Gottlieb, 2005).

**Intertrial USs and Explicit Unpairing.** The effects on acquisition of presenting USs that are not preceded by CSs (unsigned USs) are less ambiguous than the effects of partial reinforcement: Unsigned USs strongly impair conditioned responding. This impairment is graded such that when sufficient USs are presented during the ITI to equate reinforcement rate during the CS and in its absence, a CS will not come to elicit conditioned responding (Rescorla, 1966, 1968). Furthermore, when the ITI reinforcement rate exceeds that during the CS, the CS will develop inhibitory properties (Rescorla, 1969b). This means that CS-US contiguity is not sufficient to generate conditioned responding. Nor may contiguity in the operational sense be necessary for learning. The explicitly unpaired condition, where USs are only delivered during the ITI, leads to inhibitory learning even though the CS and US are never contiguously paired. It appears that what most predicts conditioned responding is the relative likelihood of the US in the presence and absence of the CS, a quantity referred to as CS-US contingency.

**Content: Additions to Associative Structure**

It appears that what is essential in acquiring conditioned responding is discriminating the predictive value of the CS from that of the background. These findings necessitated that the associative structure expand to include associations between the background (context) and discrete stimuli, associations that either interfere with the acquisition or the expression of conditioned responding (Bouton, 1993; Gibbon & Balsam, 1981; Miller & Schachtman, 1985; Rescorla & Wagner, 1972).

**Relative Contingency: Cue Competition Phenomena**

**Stimulus Compounds**

Stimuli are never presented in isolation. When the experimenter lacks control over other stimuli in the environment, those stimuli are referred to as background or contextual stimuli. When the experimenter creates complexes of stimuli from individual elements, those stimuli are referred to as compounds. The study of compound conditioning reflects the understanding that organisms face the problem of discriminating stimuli that are informative from all the others that may be co-occurring.
When an excitor is first presented in compound with a neutral CS, it is not uncommon for there to be less responding than to the excitor alone. This is referred to as external inhibition, as the neutral stimulus appears to be inhibiting the conditioned response (Pavlov, 1927, p. 44). Alternatively, the decrement can be thought of as a result of the stimulus compound being represented as its own holistic stimulus that only partially generalizes to the excitor (Pearce, 1987). This distinction reflects two distinct views of Pavlovian processes. In one, stimuli can be reduced to elements that, when combined, maintain all their essential properties (Rescorla & Wagner, 1972). In the other, every stimulus, compound or not, is a distinct element (Guthrie, 1935; Pearce, 1987). Although this conceptual distinction is nontrivial, the quantitative realization of it appears to rely largely on the degree to which the predictive values of simultaneously presented stimuli are summed or averaged (Wagner, 2003). Reports of excitatory summation are common (Pavlov, 1927; Wagner, 1971), but less so are accounts that both compare compound responding to the maximal element and that attempt to rule out performance factors relating to greater stimulation when the compound stimulus, and not an element, is presented (Rescorla, 1997).

**Compound Conditioning**

**Overshadowing.** Overshadowing refers to a reduction in conditioned responding when a CS is reinforced in compound compared to if it were reinforced alone. For example, a light paired with an air puff may lead to substantially less anticipatory eyeblinking if it is conditioned in the presence of a tone than if it is conditioned alone. When stimuli differ in salience, one stimulus may completely overshadow the other (Mackintosh, 1971). Although overshadowing may not be complete, reports of mutual overshadowing in which both elements overshadow each other are uncommon (Kehoe, 1982).

**Blocking.** Blocking is one of the most important and well-established contemporary phenomena. It was first demonstrated by Kamin (1968) in a rat fear conditioning procedure. Kamin found that when a compound stimulus made up of a light and a noise was followed by shock, animals came to suppress ongoing bar pressing to the light alone. However, if the noise had previously been paired with shock, the light did not suppress bar pressing. Blocking provides strong evidence that contiguity is insufficient to generate conditioned responding, but it also suggests that contingency is insufficient, as well; in both of Kamin’s groups, the contiguity and contingency between the light and the shock was equivalent.

**Superconditioning.** Blocking is an example of a more general principle by which individual CSs determine the acquisition of conditioned responding to other simultaneously presented stimuli. For example, if a light is established as a conditioned inhibitor of eyeblinking, subsequently conditioning a tone in the presence of the light can facilitate CR acquisition to the tone. This phenomenon is referred to as superconditioning (Williams & McDevitt, 2002; Wagner, 1971). A general principle to emerge is that the acquisition of conditioned responding to a CS trained in compound is an inverse function of the degree to which other simultaneously presented stimuli are predictive.

**Protection from Extinction.** If reinforcing a light in the presence of an excitatory tone can block the light from developing conditioned responding, nonreinforcing
the light-tone compound may lead the light to become inhibitory (Holland, 1988). This phenomenon is referred to as protection from extinction, referring to the target CS preventing the blocking CS from fully extinguishing. When the target CS is an inhibitor, the protective effect may be even greater (Rescorla, 2003a).

**Contingency Becomes Relative Contingency.** Blocking and protection from extinction have their analogs in Rescorla’s (1966, 1968, 1969b) contingency experiments. A random pairing procedure becomes a one-stage blocking procedure with the context playing the role of the blocker. Similarly, including the context as a CS turns the explicitly unpaired procedure into a one-stage protection from extinction procedure (the context is protected from extinction when the CS is present), which is the typical way of generating conditioned inhibition. Rescorla’s contingency experiments, then, can be viewed as special cases of cue competition experiments.

Linear regression is the primary statistic researchers use to determine the relative contributions of predictor variables to particular outcomes. The outputs of regression analyses are measures of predictive strength (beta coefficients) that have been adjusted to take into account correlations amount predictor variables themselves. Cue competition phenomena suggest that in determining the predictive value of a stimulus, organisms take into account the predictive value of other co-present stimuli in a similar way. Indeed, the most influential associative model, the Rescorla-Wagner (R-W) Model (Rescorla & Wagner, 1972), is an algorithm that, when given enough information, asymptotically computes beta coefficients; when given insufficient information to parcel out predictive value to each element, as in the case of overshadowing, the R-W Model splits the difference among possible predictors. A more explicit regression mechanism is incorporated in the modeling of Gallistel and Gibbon (2000). It is informative that Pavlovian processes appear to be serving a similar function as a statistic developed to optimally allocate predictive value.

**Overexpectation.** If organisms are computing something like linear regression coefficients, then a compound made up of two predictors should lead to an expectation of an outcome that is greater than to either predictor alone. Returning to our example preparation, consider the situation in which both a light and a tone are separately trained to elicit conditioned eyeblinking. When they are then presented in compound, there should be a greater air puff expectation than when either CS is presented alone. But the compound is followed by the same air puff used to establish the individual CSs. This conflicting information should lead either to configuring (generation of an interaction term) or to a decrement in predictive value attributed to each element of the compound. Indeed, reinforcing a compound of two excitors can lead to a decrease in responding to either element, a phenomenon known as overexpectation (Lattal & Nakajima, 1998).

**Relative Validity.** Although the R-W Model was developed to account for cue competition, the phenomenon of relative validity poses a unique challenge (Rescorla & Wagner, 1972). Demonstrating relative validity involves comparing conditioned responding to a CS element that has been presented in two different kinds of discriminations. In one, the common element (X) has been reinforced in the presence of one CS and nonreinforced in the presence of another (AX+, BX−). In the other, the element is equally often reinforced and nonreinforced in the presence of the two other stimuli (AX−, BX−). Wagner, Logan, Haberlandt, and Price (1968) found that X leads to greater conditioned responding in the latter discrimination,
demonstrating that the validity of a predictor depends on whether the other stimuli are better or worse predictors. Relative validity is clearly a cue competition phenomenon, but models like the R-W Model accommodate the effect only when the partially reinforced compounds have an asymptotic associative strength closer to that of a continuously reinforced stimulus than to that of a nonreinforced stimulus. However, recent evidence suggests that the associative strength of a partially reinforced stimulus is unbiased (Andrew & Harris, 2011).

**Extinction of Conditioned Inhibition.** The most serious problem from a regression framework is that posed by conditioned inhibition: Nonreinforced presentations of an inhibitor do not extinguish the inhibition (Williams, 1986). Similarly, nonreinforcing a compound of an inhibitor and a neutral CS does not lead the neutral CS to become excitatory (Baker, 1974). Pavlovian theories find this intuitive finding difficult to accommodate.

### Conditional Contingency

#### Occasion Setting

One complexity in viewing regression (or relative contingency) as a normative model of attributing predictive value is that it assumes a particular structure of the world in which the predictive values of stimuli do not systematically vary within a particular stimulus environment; however, it is possible for stimuli to have different predictive value depending on the local context. Consider, for example, a discrimination (A−, AX+) in which a tone-light compound (AX) is followed by air puff while the light (A) is separately nonreinforced. Although the regression solution attributes full predictive power to the tone (X), it is possible instead to frame the problem as one in which the light is predictive conditional on the presence of the tone. That is, instead of signaling the air puff, the tone signals that when the light is present the air puff is likely to occur. From this perspective, it is the light that controls conditioned eyeblinking and the tone that modulates this control.

To distinguish these possibilities, Ross and Holland (1981) took advantage of the fact that visual and auditory CSs paired with food evoke different behaviors in rats. They demonstrated that in an A−, AX+ simultaneous discrimination, the conditioned response was consistent with control by X. However, when X preceded and overlapped with A, the response was consistent with control by A. It appeared that in the serial discrimination, X did not gain the ability to elicit conditioned responding but rather set the occasion for A to elicit conditioned responding. This Pavlovian phenomenon of occasion setting has two common forms, positive and negative, referring to whether the occasion setter signals that a CS otherwise nonreinforced will be reinforced (positive occasion setting) or that a CS otherwise reinforced will be nonreinforced (negative occasion setting).

Holland (1992) distinguished occasion setters from simple CSs in three ways. The first, relating to response form, only applies to positive and not negative occasion setting. The second is that occasion setters do not lose their properties when they are either extinguished or reinforced on their own. The third distinguishing feature of occasion setters is that they tend to modulate responding to a smaller set of stimuli
than do typical CSs. Holland (1992) originally concluded that occasion setters showed CS-US selectivity, as they failed to modulate responding to other CSs paired with the same US or to the original target CS paired with a different US. However, Rescorla (1985) showed that occasion setters can modulate responding to nontarget stimuli that have been targets of different occasion setters. This form of generalization reflects a level of abstraction that is more often associated with inferential accounts of information processing.

**Interference Phenomena**

The existence of occasion setting suggests that in attributing predictive value to stimuli, Pavlovian mechanisms are sensitive not only to relative but also to conditional contingencies. Behavior consistent with computations of conditional contingency can also be observed when the experimentally determined contingencies are solely conditional on time. This is the case when contingency is abruptly changed, for example when a tone signaling an air puff is suddenly presented alone. It is possible that organisms simply update their estimates as new information is acquired, but it is also possible that they maintain some form of conditional knowledge that certain contingencies are in effect at different times. Although there are a number of different treatments that involve abrupt changes in stimulus environment, we have chosen to focus on the three most common ways in which the predictive value of a single CS is abruptly changed.

**CS Preexposure.** Latent inhibition refers to a reduction in conditioned responding that is observed when nonreinforced CS trials are presented prior to conditioning (Lubow, 1973). Despite the name, latent inhibitors are slow to be established as appetitive or aversive excitors or inhibitors (Reiss & Wagner, 1972; Rescorla, 1971). That is, presenting a tone repeatedly without consequence makes it hard to learn anything about that tone. Context plays a large role. Latent inhibition is attenuated when a CS is preexposed in a different context from that of subsequent training and is also attenuated as a direct function of the amount of post-conditioning exposure to the preexposure/training context (Lubow, Ristikin, & Alek, 1976).

**CS Pre-training.** Counterconditioning refers to the procedure by which a CS is first trained with one US and then with another of opposite valence. This form of pre-training typically interferes with the acquisition of new conditioned responding (Konorski & Szwejkowska, 1956). For example, pairing a tone with shock makes it more difficult to then pair the tone with food and vice versa. Aversive-to-appetitive counterconditioning more reliably shows the interference effect than does appetitive-to-aversive counterconditioning (Bouton & Peck, 1992), though an impressive set of experiments by Nasser and McNally (2012) clearly establishes that appetitive-to-aversive interference can be consistently obtained.

**CS Postexposure.** Extinction refers to the procedure by which the contingency of an excitatory CS with a US is abruptly removed. It also refers to the reduction in conditioned responding that results (Vurbic & Bouton (this volume); Urcelay, 2012). Typically, extinction is accomplished by presenting the CS without the US, but it also occurs when the CS-US relationship is degraded in other ways, such as introducing a random relationship between CS and US (Delamater, 1996). Characteristic of extinction is that extinguished conditioned responding is highly
susceptible to recovery, as with the passage of time (spontaneous recovery). An extinguished CS may also show recovery of responding when presented concurrently with a novel stimulus (disinhibition) or in a context in which an animal has had relatively little experience since an unsigned US was last presented (reinstatement). Recent work has focused on the recovery that occurs when animals are tested outside the extinction context (renewal). Renewal is strongest when animals are trained and extinguished in different contexts and are tested in their training context (ABA renewal). It is weaker when training, extinction, and testing are conducted in different contexts (ABC renewal), and it is weakest, though still apparent, when training and extinction are conducted in the same context and testing occurs in a different one (AAB renewal) (Bouton, 2002).

It now appears that extinction is not unique. Whenever a second phase of training involves opposition of a response acquired in the first stage, as with counterconditioning and overexpectation, the first stage response shows recovery (Bouton & Peck, 1992; Peck & Bouton, 1990; Rescorla, 2007). These results strongly argue that excitatory learning is not fully erased but rather that its expression is selectively opposed by the superimposition of new inhibitory learning.

Findings such as these have led to the suggestion that inhibitory processes are particularly sensitive to disruption and may fade in time. Another possibility is that what is learned second is more sensitive to disruption than what is learned first. Distinguishing these possibilities depends on what happens to a stimulus that is first trained as a latent or conditioned inhibitor and then trained as an excitor. Although there is now some evidence for recovery of latent and conditioned inhibition (De La Casa & Lubow, 2002; Nelson, 2002), studies are few and there are notable failures to obtain (Rescorla, 2005).

The study of interference phenomena has shown that new learning does not fully erase old learning and that the subsequent expression of conditioned responding depends on temporal and physical context. Both occasion setting and the interference phenomena suggest that organisms are sensitive to conditional contingencies at different timescales.

Content: Hierarchical Associations

Within associative structure, conditional likelihoods are represented by hierarchical associations between modulators and CS-US associations. In occasion setting, modulators tend to be discrete stimuli, whereas in the interference phenomena, modulators tend to be contextual stimuli that may vary with the passage of time.

Time

Time is of central importance to Pavlovian conditioning, and there is evidence that organisms are not merely sensitive to it but that they encode specific durations. In the peak procedure, in which occasional nonreinforced probe trials with extended duration CSs are interspersed throughout acquisition, what is typically observed is normally distributed responding that peaks at the time of US delivery (Gallistel & Gibbon, 2000; Pavlov, 1927, p. 41). This timed behavior has been observed to
emerge as soon as does conditioned responding (Balsam, Drew, & Yang, 2002) and to maintain throughout extinction (Guilhardi & Church, 2006). There is even evidence that this temporal encoding may precede the emergence of conditioned responding (Ohayama & Mauk, 2001).

In discussing the role of CS duration and ITI on acquisition, we did not mention another important regularity. If both the CS duration and the ITI are proportionately shortened or lengthened, the opposing beneficial and detrimental effects appear to cancel out. The ratio of ITI: CS-US interval (also called the C:T ratio) appears to be a powerful, though not perfect, predictor of the rate and magnitude of conditioned responding (Gibbon et al., 1977; Lattal, 1999).

Content: Addition of US Features

The growing acceptance of the importance of time as both a variable that influences conditioning as well as a variable that may be encoded has led to the most recent expansion of associative structure to include distinct features of the US (Delamater & Oakeshott, 2007). Although the view that USs have distinct sensory and motivational components is not new, that they may also have temporal features that represent when they occur relative to other stimuli, as well as hedonic and other features, marks a further departure from the view first proposed by Hull (1943). At the extreme are those who believe that the features of the US that are encoded include explicit statistical information about rates or probabilities of occurrence (e.g., Gallistel & Gibbon, 2000). From this perspective, associative strength is no longer a necessary construct, as the information provided by variations in associative strength is instead provided by representations of specific environmental quantities.

From Prediction to Performance

How Pavlovian Learning Translates into Conditioned Responding

Associative learning is inferred from amounts of conditioned responding, but how underlying learning manifests in behavior is neither well understood nor well specified. The typical assumption is that increases in responding reflect increases in estimates of associative strength. Unfortunately, the weakness of this assumption has made a number of important questions difficult to address. Recently, Rescorla (2000a) has described a compound testing technique that partially overcomes this limitation. He has used this technique to empirically address a number of important issues for the first time, such as the relative amounts of associative change when stimuli are conditioned in compound (Rescorla 2000a, 2001c), whether the superiority sometimes observed in retraining is due to difference in initial associative strength or difference in learning rate (Rescorla, 2002a), and whether the generalization gradient is broader for inhibition than excitation (Rescorla, 2002b). Although the questions Rescorla addressed are themselves important, it is the methodological advancement that will likely have the widest impact. We see no comparable situation where advancement in the logic of experimental design has allowed such a variety of theoretically important ideas to become testable. A sample of these designs and the first reported results from their use are presented in Table 1.1.
<table>
<thead>
<tr>
<th>Reference</th>
<th>Phase 1</th>
<th>Phase 2</th>
<th>Phase 3</th>
<th>Test/Result</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rescorla (2001a)</td>
<td>A+, C+, B−, D−</td>
<td>A+, B+</td>
<td></td>
<td>BC &gt; AD</td>
<td>More change on early acquisition trials than on later trials</td>
</tr>
<tr>
<td>Rescorla (2001a)</td>
<td>A+, B+, C+, D+</td>
<td>A−, C−</td>
<td>A−, B−</td>
<td>BC &lt; AD</td>
<td>More change on early extinction trials than on later trials</td>
</tr>
<tr>
<td>Rescorla (2002b)</td>
<td>A+, B−, C+, D−</td>
<td>A−, B−, C+, D+(^1)</td>
<td></td>
<td>AD &gt; BC</td>
<td>More change on reinforced trials than on nonreinforced trials</td>
</tr>
<tr>
<td>Rescorla (2002b)</td>
<td>A+, B−, C+, D−</td>
<td>A−, D+(^2)</td>
<td></td>
<td>AD &gt; BC</td>
<td>More inhibitory generalization than excitatory generalization</td>
</tr>
<tr>
<td>Rescorla (2002a)</td>
<td>A−, B−, C−, D−</td>
<td>A−, C−</td>
<td>A+, B+</td>
<td>BC &gt; AD</td>
<td>Slower rate of learning with latent inhibitor than with novel CS</td>
</tr>
<tr>
<td>Rescorla (2002a)</td>
<td>A+, B−, C+, D−</td>
<td>A−, B−, C−, D−</td>
<td>A+, B+</td>
<td>BC &gt; AD</td>
<td>Reacquisition faster due to head start and not faster learning rate</td>
</tr>
<tr>
<td>Rescorla (2003b)</td>
<td>A+, B−, C+, D−</td>
<td>A−, B−, C−, D−</td>
<td>AB+</td>
<td>AD &gt; BC</td>
<td>Reacquisition also faster due to higher learning rate</td>
</tr>
</tbody>
</table>

Note: Letters refer to CSs, + = reinforcement, − = nonreinforcement.

\(^1\) Brief training in Phase 2.

\(^2\) Extended training in Phase 2.
How Pavlovian Learning Motivates Appetitive Instrumental Responding

The interaction of Pavlovian and instrumental processes has been a topic of interest throughout the study of learning and motivation. Although early interest focused on fear conditioning and avoidance learning, recent emphasis has been on the influence of appetitive CSs on instrumentally trained responses; this will be our focus, as well.

**Pavlovian-Instrumental Transfer.** Pavlovian to instrumental transfer (PIT) refers to the augmenting of an instrumentally trained response by a CS that has been separately trained with the same outcome. It is typically studied in rats where lever pressing for food may be increased by presentation of a CS separately paired with food. Appetitive PIT is both outcome specific and nonspecific. Nonspecific PIT refers to the ability of a CS to elicit more instrumental behavior than occurs in its absence. It is dependent on the strength of competing goal-directed responses directly elicited by the appetitive CS. More interesting is outcome-specific PIT, in which a CS acts selectively on instrumental responses trained with the CS’s own US as opposed to responses trained with a different US. For example, a tone paired with a food pellet will lead rats to press a lever rewarded with food pellets more than a lever rewarded with liquid sucrose. Notably, a CS may elicit outcome-specific PIT while still suppressing instrumental responding and so failing to show nonspecific PIT (Holmes, Marchand, & Coutureau, 2010).

The most startling property of outcome-specific PIT is that it does not depend on the current predictive value of the CS, as its magnitude appears unaffected by both extinction and US devaluation (Delamater, 1996; Holland, 2004). Furthermore, Rescorla (2000b) demonstrated outcome-specific transfer to a CS randomly paired with a US, even when the CS did not come to elicit conditioned responding. It appears that outcome-specific transfer is established whenever there are surprising CS-US pairings and, once established, is resistant to change. Indeed, as far as we know, Delamater (2012) has provided the only report of a loss in transfer once the CS-US relationship has been established, the result of extinguishing a CS that had been given a small number of acquisition trials. This pattern of transfer implies that Pavlovian processes function as more than mechanisms of prediction.

If PIT reflects motivational properties of the CS, the motivation appears to be guided by an aspect of the reinforcer that is independent of obtaining and consuming it. This is consistent with a mechanism by which the CS activates a particular feature of the US representation that cannot be devalued and that subsequently activates the responses that brought it about (Balleine & Ostlund, 2007; Holland, 2004; Holmes et al., 2010).

**Behavior Systems Approach to PIT.** Timberlake (1994) promoted a behavior systems approach to conditioning that envisions CSs as eliciting a variety of species- and motivation-specific behaviors that depend on temporal proximity to the US. When food is more temporally distant, a CS elicits in a rat a general search mode characterized by increased attention to environmental stimuli relevant to food. As the US becomes more proximal, the general search mode gives way to a focal search mode which includes more specifically food-directed behavior (Silva & Timberlake, 1997).

It may be the case that outcome-specific PIT is a behavior characteristic of a general reward-directed search mode evoked in times when a proximal reward is not
expected. This would explain why CS extinction may facilitate PIT and why it is easier to detect when the instrumental responses are being extinguished and the reinforcers are not proximal. The simultaneous facilitation of reinforcer-related behaviors and indifference toward the occurrence of the reinforcer suggests to us that the search behavior is not motivated toward directly obtaining reward. Rather, it may be aimed toward investigating which responses are effective in obtaining reward. Such a motivation toward focused exploration is consistent with a view of Pavlovian conditioning summarized by Domjan, Cusato, and Krause (2004, p. 232): an “adaptive process that promotes efficient interactions of the organism with significant biological events in its natural environment.” It is also an adaptive understanding consistent with the mechanistic views of Balleine and Oslund (2007) and Holland (2004).

Summary and Conclusion

Conditioned responding emerges as a function of observing contingent relationships among stimuli over time. It is sensitive to both relative and conditional contingencies. For the simplest form of associative formation, that between a single salient stimulus and a biologically relevant outcome, large numbers of observations are not needed, but observations must be separated in time. Predictive value, once established, is sensitive to changes in contingency. New contingencies are learned, but old ones are not forgotten, and old habits can reemerge in times of uncertainty. Once an association has been formed, it is hard to un-form, and that association will guide instrumental behavior independent of contingency.

Pavlovian processes are most strongly linked to predicting the likelihood that an important event will or will not occur at a certain time, allowing organisms to engage in complicated sequences of preparatory behavior that culminate in appropriately timed conditioned responding. Independent of this, Pavlovian processes may serve a role analogous to the hypothesis generating roles of theories in scientific research: to focus the search for additional control of the environment.

After almost a century of investigation, Pavlovian “simple learning” processes appear more and more like nonverbal analogs of many of the skills we spend countless hours trying to teach in statistics and research methods courses. In that context, we call them critical thinking.

Acknowledgments

We thank Robert Rescorla for advice and discussions as well as for his remarkable contributions to the study of mind and behavior. We also thank Peter Holland for useful discussion.

References


