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Pavlovian Conditioning Mechanisms and Theories

Did you know that

- Pavlovian conditioning can result in the learning of a new conditioned reflex or stimulus–response (S–R) connection as well as a new stimulus–stimulus (S–S) connection?
- conditioned responding can be increased or decreased by changing the value of the unconditioned stimulus (US), which is an intervention that does not involve presenting the conditioned stimulus (CS)?
- according to all contemporary models of learning, what you learn about one stimulus depends on the associative value of other concurrently present stimuli?
- a CS can lose associative strength even though it is paired with a US?
- attentional theories assume that what happens on one trial determines how much attention is devoted to the CS on the next trial?
- although time is a critical factor in conditioning procedures, many major theories of learning do not include time as a major variable?
- the absolute duration of the CS is not as important for conditioned responding as the ratio between the CS duration and the interval between successive US presentations?

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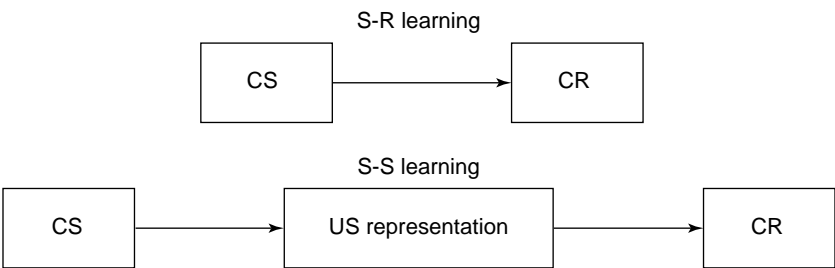
- conditioned responding can depend on the associative value of the CS compared with the associative value of other cues that were present at the time the CS was conditioned?

Originally, Pavlovian conditioning was considered to be a simple form of learning that depended only on pairings of a conditioned stimulus (CS) with an unconditioned stimulus (US) and resulted in the conditioning of a new reflex. This naive perspective has turned out to be incorrect in many ways. Long-delay taste aversion learning, selective associations, the blocking effect, contingency effects, and relative cue validity effects all challenge the view that Pavlovian conditioning is a simple form of learning. In this chapter, we further illustrate the richness and complexity of Pavlovian conditioning by focusing on the underlying mechanisms and theories that address this form of learning. We discuss two major questions: First, what is learned in Pavlovian conditioning? Second, how is it learned?

WHAT IS LEARNED IN PAVLOVIAN CONDITIONING?

The signature outcome of a Pavlovian conditioning procedure is that the participant comes to perform a conditioned response when the CS is presented. What mechanism is responsible for this conditioned response (CR)? There are two prominent alternatives (see Figure 6.1). According to the first mechanism, the CS comes to elicit the CR directly. This is called stimulus–response learning, or **S–R learning**, and is the simpler of the two mechanisms. S–R mechanisms dominated theories of learning up until the “cognitive revolution” that swept over psychology in the 1970s. That revolution encouraged more “cognitive” theories of learning and the possibility that through Pavlovian conditioning, the CS comes to activate a representation of the US. That US representation or memory in turn generates the CR. This second mechanism is called

FIGURE 6.1. Distinction Between S–R and S–S Learning



Note. In S–R learning, a direct connection or association is established between the CS and the CR such that the CR is elicited directly upon presentation of the CS. In S–S learning, the CS activates a representation of the US, which in turn leads to the CR. CR = conditioned response; CS = conditioned stimulus; S–R = stimulus–response; S–S = stimulus–stimulus; US = unconditioned stimulus.

stimulus–stimulus learning, or **S–S learning**. Both S–R and S–S learning mechanisms can generate the conditioned response, so how can we distinguish between them?

S–R Learning

According to the S–R learning mechanism, classical conditioning leads to the formation of an association between the CS and the CR. As a result of this CS–CR association, presentation of the CS activates the conditioned response directly and automatically. Such S–R learning is what is implied by the traditional notion that Pavlovian conditioning results in the learning of a new reflex response to the CS.

S–S Learning

How S–S learning generates conditioned responding is a bit more complicated. According to the S–S learning mechanism, Pavlovian conditioning results in the learning of a CS–US association. Once this association is acquired, presentation of the CS will activate a neural representation of the US (see Figure 6.1). Expressed informally, this means that upon encountering the CS, the participant will start thinking about the US. This activation of the US representation does not generate a response automatically. Rather, what the participant will do will depend on its motivation to respond to the US at that time.

A powerful technique for differentiating between S–R and S–S mechanisms was popularized by Robert Rescorla (1973) and is basically a test of performance used to infer what the organism learned. The test involves evaluating the vigor of conditioned responding after a change in motivation to respond to the US. In one type of experiment, for example, motivation to respond to the US is reduced by decreasing the value of the US following the training phase. This manipulation is called **US devaluation**.

Effects of US Devaluation

Consider, for example, the common experience of getting excited when you get a whiff of your favorite food cooking on the stove. This occurs because you previously ate and enjoyed the food with its distinctive odor. The odor–food pairings result in sign tracking: You will approach the stove where the food is cooking when you encounter the odor. Does this approach CR reflect S–R or S–S learning? Rescorla would recommend testing to see how you respond when you are hungry compared with when you are satiated after the original learning. Eating a large meal should reduce your interest in food and is a form of US devaluation. If your approach CR reflected S–S learning, you will be less likely to approach the stove after having eaten a large meal. With S–S learning, the CS should activate a memory of the US, which now has a reduced value and therefore should be less effective in producing the CR. In contrast, if your approach CR reflected S–R learning, food satiation will not

change your response to the odor CS because the path to the response does not involve the US representation (see Table 6.1).

In a laboratory study of US devaluation, Derman et al. (2018) used a sign-tracking procedure with rats. The experimental chamber was outfitted with two retractable response levers, one on either side of a food cup. Periodically one or the other lever was extended into the chamber. Extensions of one of the levers always ended in the delivery of a food pellet (Lev1+), whereas extensions of the other lever occurred without a US (Lev2−). As you might predict, the rats came to approach and contact Lev1+ much more frequently than Lev2−. After this differential acquisition of sign tracking, a US devaluation procedure was carried out for the experimental group. During this phase, neither response lever was available, and a conditioned aversion was established to the food pellets (by making the rats sick after eating the food pellets). The effects of the US devaluation procedure were tested in the last phase of the experiment in which each response lever was presented periodically without any deliveries of food pellets. A control group did not receive US devaluation. They got similar training but did not learn an aversion to the food pellets.

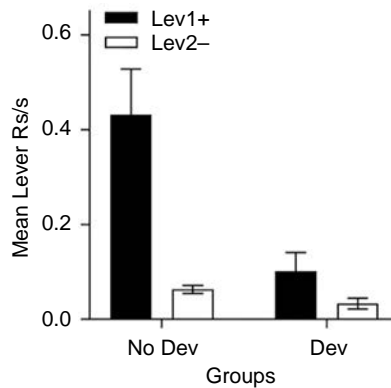
The results of the test sessions are summarized in Figure 6.2. The data for the control group that did not receive US devaluation are shown on the left (NoDev). As expected, these rats approached and contacted the lever that had been paired with food (Lev1+) much more often than the lever that did not end in food deliveries (Lev2−). Results for the experimental group that received aversion conditioning to the food pellets (Dev) are summarized on the right of Figure 6.2. The US devaluation procedure significantly reduced approach and contacts with the food-paired lever (Lev1+). This shows devaluation of the US produced a significant suppression of the conditioned response. Such a US devaluation effect indicates that the CR was mediated primarily by S–S rather than S–R mechanisms. Note, however, that even in rats whose US had been devalued, a small amount of residual conditioned responding was evident. This residual responding might reflect some S–R learning in this situation.

US devaluation has been found to reduce conditioned responding in a variety of conditioning situations and provides solid evidence for S–S learning. For example, in a study of sexual conditioning with male domesticated quail, Holloway and Domjan (1993) first paired presentations of a light CS with sexual access to a female. Initially, the CS did not elicit any significant behavior.

TABLE 6.1. Design and Predictions of US Devaluation Study

Phase 1	Phase 2	S–R prediction	S–S prediction
Experimental group			
Conditioning	US devaluation	No change in CR	Decline in CR
Control group			
Conditioning	No devaluation	No change in CR	No change in CR

Note. CR = conditioned response; S–R = stimulus–response; S–S stimulus–stimulus; US = unconditioned stimulus.

FIGURE 6.2. Effects of Unconditioned Stimulus Devaluation on Sign Tracking in Rats

Note. Two response levers served as conditioned stimuli. Presentation of one lever was paired with food (Lev1+) whereas presentations of the other lever (Lev2-) occurred without food. After responding developed to Lev1+, some of the rats learned an aversion to the food pellets (Dev) whereas the others did not (No Dev). These data show responding to each lever at the end of the experiment. From "Sign-Tracking Is an Expectancy-Mediated Behavior That Relies on Prediction Error Mechanisms," by R. C. Derman, K. Schneider, S. Juarez, and A. R. Delamater, 2018, *Learning and Memory*, 25(10), p. 555 (<https://doi.org/10.1101/Im.047365.118>). Copyright 2018 by R. C. Derman, K. Schneider, S. Juarez, and A. R. Delamater. Reprinted with permission.

However, because the males were sexually motivated, they always readily approached and copulated with the female that was released at the end of each conditioning trial (the US). With repeated conditioning trials, the males also learned to approach the CS. After 10 conditioning trials, the CS elicited a strong approach or sign tracking response, regardless of where the males were at the start of the trial.

After acquisition of the sign tracking response, US devaluation was carried out by reducing the sexual motivation of the birds. Sexual motivation was reduced by changing the light cycle in the laboratory to mimic winter conditions, when the birds do not breed. Subsequent tests of approach responding to the CS indicated a substantial decrease in conditioned responding caused by the drop in sexual motivation. These results indicate that conditioned sexual behavior is also mediated primarily by S–S rather than S–R learning mechanisms. The CS activates a representation of the sexual US. That in turn leads to conditioned responding, but only if the participants are motivated to respond to the sexual US. Sexual conditioning is not limited to quail. Human beings come to respond to various visual, olfactory, and tactile cues associated with sexual activity. The data from the quail study suggest that such sexual conditioned responses will be reduced under conditions of low sexual motivation. (For studies of the neuroscience of S–S learning, see Desgranges et al., 2010; Saddoris et al., 2009.)

A particularly interesting implication of studies of US devaluation is that one can alter responses to a CS using procedures that involve manipulations

that focus on the US rather than the CS itself. Most clinical interventions that seek to reduce maladaptive conditioned responses involve changing the properties of the CS by using something like an extinction procedure (see Chapter 10). US devaluation effects suggest an alternative avenue. Focusing on changing the value of the US may be especially useful in clinical situations where the troublesome CS cannot be easily identified or manipulated.

Sensory Versus Hedonic Properties of the US

Experiments on the effects of US devaluation have told us a great deal about the nature of S–S learning. If decreasing the value of the US after conditioning reduces responding to the CS, we may conclude that the CS activates a representation or memory of the US. This does not tell us what aspect of the US comes to mind to generate the conditioned response when the CS is presented, however.

USs are complex events with multiple features (Konorski, 1967). A savory cookie, for example, has a specific flavor and it evokes pleasure or enjoyment. The flavor of the cookie is a **sensory** feature, or perceived through the senses, and the pleasure the cookie evokes is a **hedonic** feature, experienced through emotions. Through Pavlovian conditioning, a CS can come to activate the sensory features of the US, its hedonic features, or both. Complicated experiments have been carried out to distinguish between sensory and hedonic learning (Delamater, 2012b). The distinction is of considerable interest because these forms of learning are mediated by different neural mechanisms (e.g., Corbit & Balleine, 2011), and learning about the hedonic features of a US helps us better understand how Pavlovian conditioning is involved in the motivation of goal-directed behavior.

HOW ARE PAVLOVIAN ASSOCIATIONS LEARNED?

We next turn to considering possible mechanisms involved in the learning of Pavlovian associations. The modern era in theories of associative learning was launched by the discovery of the blocking effect (reviewed in Chapter 5), which demonstrated that CS–US contiguity is not sufficient for learning. The first highly influential theory that explained the blocking effect was the Rescorla–Wagner model. Other models and theories soon followed. These theories sought to explore alternative ways of characterizing learning and tried to overcome some of the shortcomings of the Rescorla–Wagner model. However, the Rescorla–Wagner model remains the standard against which other theories are often evaluated. Interestingly, this model was silent on the issue of what the organism learns—for example, S–S versus S–R associations. Instead, it attempted to identify the rules by which learning occurs across conditioning trials.

The Rescorla-Wagner Model

Because the blocking effect was critical in shaping the development of contemporary learning theory, the basics of the blocking effect are reviewed in Figure 6.3. Participants first receive one CS (A) paired with the US. After conditioned responding to A is well established, a new stimulus (B) is added, and the AB compound is paired with the US. Blocking is said to occur if the presence of the previously conditioned stimulus A interferes with the conditioning of the new added stimulus B.

Why does the presence of the previously conditioned stimulus A block the acquisition of responding to stimulus B? Kamin (1969), who originally identified the blocking effect, explained the phenomenon by proposing that a US must be surprising to be effective in producing learning. If a CS signals a US that you previously learned about, the US will not be surprising and therefore will not stimulate the “mental effort” needed for the formation of an association. Expected events are things individuals have already learned about. Hence expected events will not activate processes leading to new learning. To be effective, the US must be unexpected or surprising.

To navigate efficiently in our world, we are constantly making predictions about what will happen next. If we are surprised by something (e.g., a US), it is because we made a prediction error. The idea that the effectiveness of a US is determined by how surprising it is formed the basis of the **Rescorla-Wagner model** (Rescorla & Wagner, 1972; Wagner & Rescorla, 1972). The model has enabled investigators to explore the role of prediction error and US surprisingness in a wide variety of conditioning phenomena. The Rescorla-Wagner model had a huge impact on the field of conditioning and learning (S. Siegel & Allan, 1996) and continues to be employed in a variety of areas of psychology, computer science, and neuroscience. We now know a great deal about how prediction error is represented in the nervous system and how it determines learning (Kim et al., 1998; Waelti et al., 2001).

FIGURE 6.3. Review of the Design of a Blocking Experiment

	Phase 1	Phase 2	Test
<i>Experimental Group</i>	A → US	A + B → US	B
<i>Control Group</i>		A + B → US	B

Note. In Phase 1, the experimental group gets stimulus A conditioned to asymptote. In Phase 2, both the experimental and the control group get stimuli A and B presented simultaneously and paired with the unconditioned stimulus. Finally, both groups are tested for responding to stimulus B.

If you expect a small gift for your birthday but a rich uncle gives you a car, you will have made a large prediction error and will be very (pleasantly) surprised. This is analogous to getting an unexpectedly large US. If you expect to get a car but receive a box of candy, you will also be surprised (but in this case unsurprisingly so). This is analogous to an unexpectedly small US. According to the Rescorla–Wagner model, an unexpectedly large US is the basis for excitatory conditioning or increases in associative value. In contrast, an unexpectedly small US is the basis for inhibitory conditioning or decreases in associative value. A critical component of the model is the assumption that predictions of the US (and prediction errors) are calculated based on all the cues present on a conditioning trial.

Strong conditioned responding indicates a strong expectation that the US will occur, whereas weak conditioned responding indicates a low expectation of the US. Using the magnitude of the CR as a proxy for US expectancy, we can infer that the US is highly surprising at the beginning of training and not at all surprising by the end when conditioned responding has reached an **asymptote**, or limit. Thus, distance from the asymptote of learning may be used as a measure of US surprise.

The basic ideas of the Rescorla–Wagner model are expressed mathematically by using λ to represent the asymptote of learning possible with the US that is being used and V to represent the associative value of the stimuli that precede the US. The surprisingness of the US (or the size of the prediction error) will then be $(\lambda - V)$. According to the Rescorla–Wagner model, the amount of learning on a given trial is assumed to be proportional to $(\lambda - V)$, or US surprisingness. The value of $(\lambda - V)$ is large at the start of learning because V (the associative value of the stimuli preceding the US) is close to zero at this point. Hence, substantial increments in associative strength occur during early conditioning trials. Because the associative value of the cues that precede the US increases, the difference term $(\lambda - V)$ will get smaller, and less additional learning will occur.

Learning on a given conditioning trial is the change in the associative value of a stimulus. This change can be represented as ΔV . Using these symbols, the idea that learning depends on the surprisingness of the US (or the magnitude of a prediction error) can be expressed as follows:

$$\Delta V = k(\lambda - V)$$

In this equation, k is a constant related to the salience of the CS and US. **Salience** reflects the perceived intensity of the CS and US and is assumed to be fixed throughout conditioning. The term $(\lambda - V)$ represents the surprisingness of the US. Putting all this together, $\Delta V = k(\lambda - V)$ is the fundamental equation of the Rescorla–Wagner model.

Application to the Blocking Effect

The basic ideas of the Rescorla–Wagner model clearly predict the blocking effect. In applying the model, it is important to keep in mind that expectations

of the US are based on all the cues available during a conditioning trial. As illustrated in Figure 6.3, the blocking design first involves extensive conditioning of stimulus A so that the participants acquire a perfect expectation that the US will occur based on the presentation of stimulus A. Therefore, at the end of Phase 1, V_A equals the asymptote of learning ($V_A = \lambda$). In Phase 2, stimulus B is presented together with stimulus A, and the two CSs are followed by the US. According to the Rescorla–Wagner model, no conditioning of stimulus B will occur in Phase 2 because the US is now perfectly predicted by the presence of stimulus A: $(\lambda - V_{AB}) = 0$.

The control group receives the identical training in Phase 2, but for them the presence of stimulus A does not lead to an expectation of the US. Therefore, the US is surprising for the control group in Phase 2 and produces new learning to the added B stimulus.

Loss of Associative Value Despite Pairings With the US

The Rescorla–Wagner model is consistent with such fundamental facts of classical conditioning as acquisition and the blocking effect. However, much of the importance of the model has come from its unusual predictions. One such prediction is that under certain circumstances the conditioned properties of stimuli will decline despite continued pairings with the US. That is highly counterintuitive. Why should a CS lose associative value if it continues to be paired with the US? The Rescorla–Wagner model predicts that stimuli will lose associative value when they are paired with the US if there is an overexpectation of that US.

The design of a US overexpectation experiment is outlined in Figure 6.4. In Phase 1, stimuli A and B are paired with the same US (e.g., one pellet of food) on separate trials. This continues until each of stimuli A and B predict perfectly the one food pellet US, or $V_A = V_B = \lambda$. Phase 2 is then initiated. In Phase 2, stimuli A and B are presented simultaneously for the first time, and the AB stimulus compound is followed by the original single food pellet US.

When stimuli A and B are presented simultaneously at the start of Phase 2, the expectations based on the individual stimuli are assumed to add together, with the result that two food pellets are predicted as the US ($V_{AB} = V_A + V_B = 2\lambda$).

FIGURE 6.4. Design of the Overexpectation Experiment

Phase 1	Phase 2	Test
A → US B → US	A + B → US	A, B

Note. In Phase 1, participants receive stimuli A and B, each paired with the unconditioned stimulus (US; i.e., one food pellet). In Phase 2, stimuli A and B are presented together, creating an expectation of more than the one-pellet US. As a consequence, the associative values of stimuli A and B each decrease in Phase 2.

This is an overexpectation because the US remains only one food pellet. Thus, there is a discrepancy between what is expected (two pellets) and what occurs (one pellet).

At the start of Phase 2, the participants find the US surprisingly small. This is analogous to our earlier example when you expected to receive a car for your birthday but were given a box of candy instead. To bring expectations of the US in line with what actually happens in Phase 2, the model assumes that participants have to decrease their expectancy of the US based on the individual stimuli A and B. Thus, stimuli A and B are predicted to lose associative value despite continued presentations of the same US. The loss of associative value is predicted to continue until the sum of the expectancies based on A plus B equals one food pellet. The predicted loss of conditioned response to the individual stimuli A and B in the overexpectation experiment is highly counterintuitive but has been verified repeatedly (e.g., Kehoe & White, 2004; Lattal & Nakajima, 1998; Sissons & Miller, 2009). (For a study of the neural mechanisms of the overexpectation effect, see Rasmussen et al., 2015.)

Conditioned Inhibition

The Rescorla–Wagner model treats the development of conditioned inhibition as another illustration of the consequences of US overexpectation. Consider, for example, the standard inhibitory conditioning procedure (see Figure 5.5). This procedure involves trials when the US is presented (reinforced trials) and trials when the US is omitted (nonreinforced trials). On reinforced trials, a conditioned excitatory stimulus (CS^+) is paired with the US. On nonreinforced trials, the CS^+ is presented together with the conditioned inhibitory stimulus, CS^- .

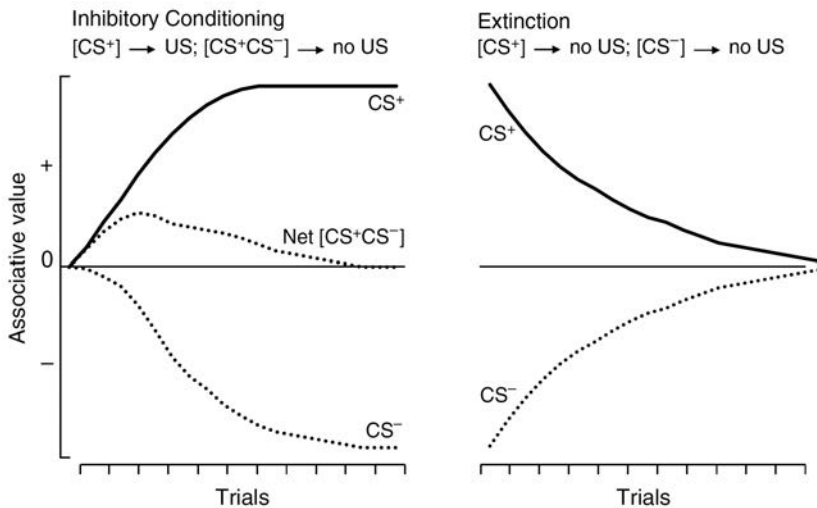
To apply the Rescorla–Wagner model to the conditioned inhibition procedure, it is helpful to consider reinforced and nonreinforced trials separately. To anticipate the US on reinforced trials accurately, the CS^+ has to gain conditioned excitatory properties. Excitatory conditioning involves the acquisition of positive associative value and ceases once the organism predicts the US perfectly on each reinforced trial. This is illustrated in the left panel of Figure 6.5.

On nonreinforced trials, both the CS^+ and CS^- occur. Once the CS^+ has acquired some degree of conditioned excitation (because of its pairings with the US on reinforced trials), the organism will expect the US whenever the CS^+ occurs, even on nonreinforced trials. However, the US does not happen on nonreinforced trials. This creates overexpectation of the US, similar to the example in Figure 6.4. To predict the absence of the US on nonreinforced trials accurately, the associative value of the CS^+ and the value of the CS^- have to sum to zero (the value represented by no US). Given the positive associative value of the CS^+ , the only way to achieve a net zero expectation of the US on nonreinforced trials is to make the associative value of the CS^- negative. Thus, the Rescorla–Wagner model explains conditioned inhibition by assuming that the CS^- acquires negative associative value (see the left panel of Figure 6.5).

Extinction of Conditioned Excitation and Inhibition

In an extinction procedure, the CS is presented repeatedly without the US. (We will have a lot more to say about extinction in Chapter 10.) Let us consider

FIGURE 6.5. Predicted Associative Values of Conditioned Excitatory Stimulus (CS⁺) and Conditioned Inhibitory Stimulus (CS⁻) During the Course of Conditioned Inhibition Training and Extinction



Note. During conditioned inhibition training (left panel), when the CS⁺ is presented alone, it is paired with the unconditioned stimulus (US); in contrast, when the CS⁺ is presented with the CS⁻, the US is omitted. The net associative value of CS⁺ and CS⁻ is the sum of the associative values of the individual stimuli. During extinction (right panel), the conditioned stimuli are presented alone, and the US never occurs.

predictions of the Rescorla–Wagner model for extinction. These predictions are illustrated in the right panel of Figure 6.5. When the CS⁺ is first presented without the US in extinction, there will be an **overexpectation** of the US, meaning the US is predicted but does not occur. With continued presentation of the CS⁺ by itself, the expectation elicited by the CS⁺ will gradually be brought in line with the absence of the US by gradual reductions in the associative value of the CS⁺. This process will continue until the net prediction of the US (V based on all the stimuli present) is reduced to zero.

The Rescorla–Wagner model predicts an analogous scenario for extinction of conditioned inhibition. At the start of extinction, the CS⁻ has negative associative value. This may be thought of as creating an underprediction of the US: The organism predicts less than the zero US that occurs on extinction trials. To bring expectations in line with the absence of the US, the Rescorla–Wagner model predicts that the negative associative value of the CS⁻ will be gradually reduced until the CS⁻ ends up with zero associative strength.

Problems With the Rescorla–Wagner Model

The Rescorla–Wagner model has stimulated a great deal of research and led to the discovery of many new and important phenomena in classical conditioning (S. Siegel & Allan, 1996). Not unexpectedly, however, the model has also encountered some difficulties since it was proposed in 1972 (R. R. Miller et al., 1995).

One of the difficulties with the model that became evident early on is that its analysis of the extinction of conditioned inhibition is incorrect. As we pointed out in the previous section (see Figure 6.5), the model predicts that repeated presentations of a conditioned inhibitor (CS^-) by itself will lead to loss of conditioned inhibition. This, however, does not occur (Witcher & Ayres, 1984; Zimmer-Hart & Rescorla, 1974). In fact, some investigators have found that repeated nonreinforcement of a CS^- can enhance its conditioned inhibitory properties (see, e.g., DeVito & Fowler, 1987; Hallam et al., 1992). Curiously, an effective procedure for reducing the conditioned inhibitory properties of a CS^- does not involve presenting the CS^- at all. Rather, it involves extinguishing the excitatory properties of the CS^+ with which the CS^- was presented during inhibitory training (Best et al., 1985; Lysle & Fowler, 1985).

Another difficulty is that the Rescorla–Wagner model views extinction as the opposite of acquisition, or the gradual weakening of the associative value of a CS towards zero. However, as we discuss in Chapter 10, a growing body of evidence indicates that extinction is not simply the reversal of acquisition. Extinction also appears to involve the learning of a new relationship between the CS and US (namely, that the US no longer follows the CS).

Attentional Models of Conditioning

Given that classical conditioning has been studied for about a century, a comprehensive theory must account for many diverse findings. No theory has been entirely successful in accomplishing that goal. Nevertheless, interesting new ideas about classical conditioning continue to be proposed and examined. Some of these proposals supplement the Rescorla–Wagner model. Others are incompatible with the model and move the theoretical debate in different directions.

North American psychologists have favored learning mechanisms like the Rescorla–Wagner model that focus on changes in the surprise value or effectiveness of the US. In contrast, British psychologists have approached phenomena such as the blocking effect by postulating changes in how well the CS commands attention. The general assumption is that for conditioning to occur, participants must pay close attention to the CS. Procedures that disrupt attention to the CS are expected to disrupt learning, whereas procedures that increase attention are expected to facilitate learning (Mitchell & Le Pelley, 2010).

How much attention a stimulus commands—and therefore how quickly an individual can learn about it—is called the *associability* of the stimulus. Recall that the Rescorla–Wagner model assumed that the salience of the CS was a constant—that is, fixed throughout training. Attentional theories, in contrast, assume that the associability of a CS changes with training. The theories differ in their assumptions about what determines the associability of a CS on a given trial. Pearce and Hall (1980), for example, assumed that how much attention a CS commands on a given trial is determined by how surprising the US was on the preceding trial (see also Hall et al., 1985; McLaren & Mackintosh, 2000). Individuals have a lot to learn if the US was surprising to them on the preceding trial. Therefore, under such conditions they will pay

closer attention to the CS on the next trial, and this will facilitate learning on that trial. In contrast, if a CS was followed by an expected US on the preceding trial, attention to that CS will decrease subsequently.

An important feature of attentional models is that the surprisingness of the US on a given trial is assumed to change attention commanded by the CS on future trials. For example, if Trial 10 ends in a surprising US, the increased salience of the CS will not be evident until Trial 11. Thus, US surprisingness is assumed to have a prospective or proactive influence on attention and conditioning. This is an important difference from US-reduction models such as the Rescorla–Wagner model, in which the surprisingness of the US on a given trial determines what is learned on that same trial.

The assumption that the US on a given trial can change what is learned about a CS on the next trial has received experimental support (e.g., Haselgrove et al., 2010; Mackintosh et al., 1977). However, this assumption has also made it difficult for attentional models to explain other findings. In particular, attentional models cannot explain the blocking that occurs on the first trial of Phase 2 of the blocking experiment (see, e.g., Azorlosa & Cicala, 1986; Balaz et al., 1982; Dickinson et al., 1983). According to attentional models, blocking occurs because in Phase 2 of the blocking experiment, the US is not surprising, and this reduces attention to the added CS. However, such a reduction in attention only occurs after the first Phase 2 trial. Therefore, attentional models cannot explain the blocking that occurs on the first trial of Phase 2 of the blocking experiment. Nonetheless, these models make other novel predictions that have been experimentally supported and continue to stimulate research (e.g., Haselgrove et al., 2010; Uengoer et al., 2020).

Temporal Factors and Conditioned Responding

Neither the Rescorla–Wagner model nor attentional models were designed to explain the effects of time in conditioning. However, time is obviously a critical factor. One important temporal variable is the CS–US interval. As we noted in Chapter 5, less conditioned responding is typically observed with procedures that involve longer CS–US intervals (see Figure 5.2). This relation appears to be primarily a characteristic of conditioned responses closely related to the US (e.g., focal search). If behaviors that are ordinarily farther removed from the US are measured (e.g., general search), responding is greater with procedures that involve longer CS–US intervals. Both findings illustrate that the duration of the CS is an important factor in conditioning.

Another important temporal variable is the interval between successive trials. Generally, conditioned responding is more evident with procedures in which trials are spaced farther apart. In addition, some investigators have argued that the intertrial interval and the CS duration act in combination to determine responding. This idea is the basis for *rate expectancy theory* (Gallistel & Gibbon, 2000). According to rate expectancy theory, the critical factor that determines the emergence of conditioned behavior is the **I/T ratio**, which is

calculated by dividing the duration of the intertrial interval (I) by the duration of the CS during a conditioning trial (T).

Rate expectancy theory predicts that conditioned responding will develop more rapidly with conditioning procedures that involve larger I/T ratios. Why should that be the case? A variety of answers have been offered (Gallistel & Gibbon, 2000; Jenkins et al., 1981), but they all capture the notion that the I/T ratio determines how well the CS reduces temporal uncertainty about the next occurrence of the US (Balsam & Gallistel, 2009). The CS reduces uncertainty about the US if it provides better information about the US than the background cues of the intertrial interval. With a high I/T ratio, the duration of the CS (T) is much shorter than the duration of the intertrial interval (I). This makes the CS much more informative about the next occurrence of the US than the background cues of the intertrial interval. Because of this, high I/T ratios facilitate the development of conditioned responding. The informational advantage of the CS over the background contextual cues of the intertrial interval is lost if the durations of I and T are similar. As a consequence, conditioned responding to the CS develops slowly with low I/T ratios.

Informational models of learning like rate expectancy theory have provided interesting ideas about learning and performance, but they have been a bit more controversial than the other theories we have considered. Empirical studies of the effects of the I/T ratio on learning have provided mixed results, with some findings in line with the theory and other findings inconsistent with it (e.g., Holland, 2000; Thrailkill et al., 2020). It will be interesting to see how such inconsistencies are resolved as investigators continue to explore how learned performance is driven by the information that a CS provides about a US.

The Comparator Hypothesis

Studies of the I/T ratio and informational models of learning have emphasized that conditioned responding depends not only on what happens during the CS but also on what happens in the experimental situation in general. The idea that both of these factors influence what we observe in conditioning experiments has been developed in greater detail by Ralph Miller and his collaborators in the **comparator hypothesis** (R. R. Miller & Matzel, 1988; Stout & Miller, 2007).

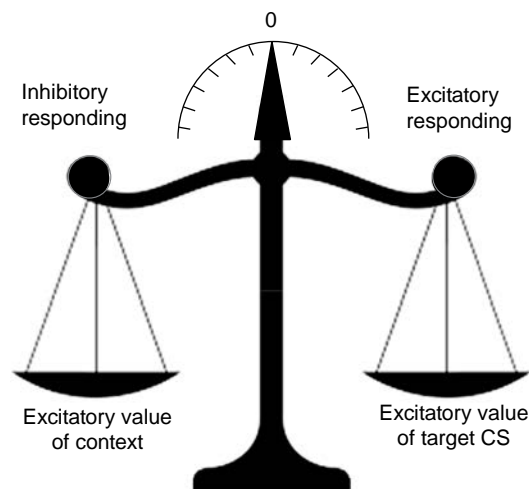
The comparator hypothesis is similar to informational models in assuming that conditioned responding depends on the relationship between the target CS and the US, as well as on the relationship between other cues in the situation (the background context, for example) and the US. The associative strength of other cues present during training with the target CS is especially important. Another constraint of the comparator hypothesis is that it only allows for the formation of excitatory associations with the US. Whether conditioned responding reflects excitation or inhibition is assumed to be determined by the relative strengths of excitation conditioned to the target CS compared with the

excitatory value of the contextual cues that were present with the target CS during training.

The comparator process is represented by the balance in Figure 6.6. In this figure, a comparison is made between the excitatory value of the target CS and the excitatory value of the other cues that are present during the training of that CS. If CS excitation exceeds the excitatory value of the contextual cues, the balance of the comparison will be tipped in favor of excitatory responding to the target CS. As the excitatory value of the other cues becomes stronger, the balance of the comparison will become less favorable for excitatory responding. In fact, if the excitatory value of the contextual cues becomes sufficiently strong, the balance may eventually tip in favor of inhibitory responding to the target CS.

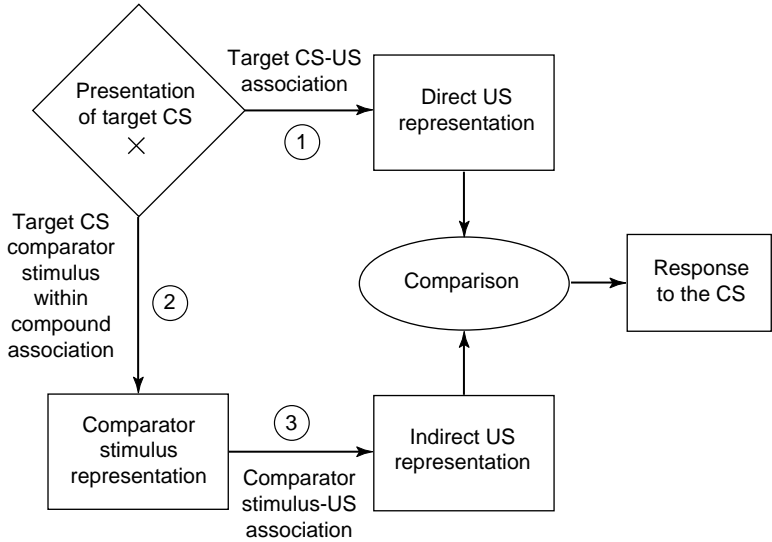
Unlike informational models, the comparator hypothesis emphasizes associations rather than time. A simplified version of the comparator hypothesis, presented in Figure 6.7, involves three associations. The first association (Link 1 in Figure 6.7) is between the target CS (X) and the US. The second association (Link 2) is between the target CS (X) and the comparator contextual cues. Finally, there is an association between the comparator stimuli and the US (Link 3). With all these links in place, when the CS occurs, it activates the US representation directly (through Link 1) and indirectly (through Links 2 and 3). A comparison between the direct and indirect activations of the US representation determines the degree of excitatory or inhibitory responding that is observed.

FIGURE 6.6. Illustration of the Comparator Hypothesis



Note. Responding to the target conditioned stimulus (CS) is represented by the reading of the balance. If the excitatory value of the target CS exceeds the excitatory value of the other cues present during training of the target CS, the balance tips in favor of excitatory responding. As the associative value of the contextual cues increases, the comparison becomes less favorable for excitatory responding and may tip in favor of inhibitory responding.

FIGURE 6.7. The Associative Structure of the Comparator Hypothesis



Note. The target conditioned stimulus (CS) is represented as X. Excitatory associations result in activation of the unconditioned stimulus (US) representation, either directly by the target (Link 1) or indirectly (through Links 2 and 3). Adapted from “Comparator Mechanisms and Conditioned Inhibition: Conditioned Stimulus Preexposure Disrupts Pavlovian Conditioned Inhibition but Not Explicitly Unpaired Inhibition,” by B. X. Friedman, A. P. Blaisdell, M. Escobar, and R. R. Miller, 1998, *Journal of Experimental Psychology: Animal Behavior Processes*, 24(4), p. 455 (<https://doi.org/10.1037/0097-7403.24.4.453>). Copyright 2018 by the American Psychological Association.

It is important to note that the comparator hypothesis says little about how associations become established other than to assume that temporal contiguity alone is important. Rather, it describes how CS–US and context–US associations determine responding to the target CS. Thus, unlike US-modification and attentional models, the comparator hypothesis is primarily a theory of *performance*, not a theory of learning. However, comparator processes can be incorporated into a more general theory of learning (e.g., Ghirlanda, 2018).

An important corollary to the comparator hypothesis is that the comparison between CS–US and context–US associations is made at the time of testing for conditioned responding. As a consequence of this assumption, the comparator hypothesis makes the unusual prediction that extinction of context–US associations following training of a target CS will enhance responding to that target CS. On the other hand, further strengthening of the context–US association is predicted to reduce responding to the target CS. The first of these predictions has been confirmed repeatedly (R. R. Miller & Witnauer, 2016), whereas the second prediction has met with more mixed results. US-modification and attentional theories of learning do not generally explain such results (but see Van Hamme & Wasserman, 1994).

The fact that postconditioning extinction of contextual cues enhances responding to a target CS indicates that responding to a target CS can be altered

by changing the properties of comparator cues. This type of result is called a *revaluation effect*. Research on the comparator hypothesis has identified a growing number of revaluation effects. One of the more provocative revaluation effects concerns the blocking effect.

In the critical phase of the blocking experiment, recall that a new stimulus (B) is conditioned in the presence of a previously conditioned CS (A). Because stimulus A is present when stimulus B is being conditioned, stimulus A serves as the comparator for stimulus B. According to the comparator hypothesis, stimulus B will not elicit much conditioned responding because its comparator (stimulus A) has high excitatory strength, tipping balance away from stimulus B. If the lack of responding to stimulus B reflects this type of comparison, a revaluation manipulation might unmask responding to stimulus B. In particular, the comparator hypothesis predicts that participants will increase responding to stimulus B if the comparator (stimulus A) is extinguished. Interestingly, this prediction has been confirmed in several experiments (Blaisdell et al., 1999; Richardson et al., 2018), although the generality of this effect has not been firmly established (e.g., Holland, 1999).

The comparator hypothesis has also been tested in studies of conditioned inhibition. The hypothesis attributes inhibitory responding to situations in which the association of the target CS with the US is weaker than the association of contextual cues with the US. The contextual cues in this case are the stimuli that provide the excitatory context for inhibitory conditioning. Interestingly, the hypothesis predicts that extinction of these conditioned excitatory stimuli following inhibitory conditioning will reduce inhibitory responding. Thus, the comparator hypothesis is unique in predicting that extinction of conditioned inhibition is best accomplished not by presenting the CS⁻ alone but by extinguishing the CS⁺ cues that provided the excitatory context for inhibitory conditioning. This unusual prediction has been confirmed in several studies (Best et al., 1985; Lysle & Fowler, 1985). (For additional revaluation effects, see R. R. Miller & Witnauer, 2016.)

SUMMARY

Each of the models we have described in this chapter emphasizes a different aspect of classical conditioning. Informational models focus on temporal variables in conditioning procedures, such as the I/T ratio. The comparator hypothesis has been extended to a wider range of phenomena, but it is a theory that emphasizes performance rather than learning mechanisms. Attentional models attempt to address the same wide range of phenomena as the Rescorla–Wagner model, but they also have some of the same difficulties as that model. All these models have been important in directing our attention to previously ignored aspects of classical conditioning, and each has identified important novel conditioning variables and manipulations that have yielded novel conditioning effects.

The theories that we described cover the highlights. Numerous additional theories have been proposed. Especially noteworthy have been those that address the fundamental question of how stimuli are encoded when they are presented in a stimulus compound. The Rescorla–Wagner model makes the simplifying assumption that stimuli presented in a compound are encoded as individual elements (where the whole is equal to the sum of its parts). Pearce (1987), on the other hand, developed an entirely different approach based on the idea that a stimulus compound is encoded not in terms of its individual elements but, rather, in terms of unique “configural” wholes. This elemental versus configural distinction continues to stimulate current research in Pavlovian conditioning today (see also Wagner, 2008).

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TECHNICAL TERMS

- S–R learning, page 84
- S–S learning, page 85
- US devaluation, page 85
- sensory, page 88
- hedonic, page 88
- Rescorla–Wagner model, page 89
- asymptote, page 90
- salience, page 90
- overexpectation, page 93
- I/T ratio, page 95
- comparator hypothesis, page 96

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