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## CHAPTER 12

# *The Role of Learning in the Operation of Motivational Systems*

ANTHONY DICKINSON AND BERNARD BALLEINE

### INTRODUCTION

Over half a century ago, Neal Miller (1951) set the agenda for the present chapter in his contribution titled "Learnable Drives and Reward" to the first edition of Stevens' *Handbook of Experimental Psychology*. Miller introduced his chapter with the claim that "People are not born with a tendency to strive for money, for discovery of scientific truth; or for symbols of social status. Such motives are learned during socialization. . . . Even primary drives themselves may be modified by learning, so that hunger becomes a desire for a particular type of food appetizingly prepared" (p. 435). The essence of Miller's claim is that behavior is not driven by some energetic-like state but rather is motivated by the desire for specific commodities, resources, and states of affairs and, moreover, that desires are learned rather than being an automatic consequence of even basic biological motivational states. Miller's claim was surprising; not only was it out of kilter with the contemporary theories of motivation, but it also lacked empirical foundation at the time. Our aim in this chapter is to marshal ev-

idence gathered over the last 50 years to substantiate that behavior is motivated by desires and that desires, even for the most basic and primary commodities (food, water, warmth, and sex), are learned. In this respect, therefore, the present chapter can be viewed as an extended addendum to Miller's original claim about the role of learning in motivation.

Before embarking on this enterprise, however, we must be clear about why the analysis of behavior requires a concept of motivation. The term was developed and applied to human behavior in the nineteenth century by the German philosopher Schopenhauer in an attempt to equate the forces controlling human action with physical forces, such as gravitation. However, motivational explanations have been with us for much longer. Descartes (1649/1911), for example, claimed that motivational states, which he referred to as "the passions," are the basis of action, both initiating a desire for specific objects and providing a force that impels behavior to the fulfillment of desire. For Descartes, the passions "dispose the soul to desire those things which nature tells us are of use, and to persist in this desire, and also bring about that same agitation of spirits which customarily causes them to dispose the body to movement which serves for the carrying into effect of

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these things" (1649/1911, article 52, p. 358). The two functions that Descartes identified for "passions"—the determination of the current goal of our actions and the activation or energization of these actions—capture an important distinction that is honored by contemporary analyses of motivation.

Perhaps the simplest demonstration of motivational processes in action comes from studies of shifts in motivational state. For example, Mollenauer (1971) fed her rats for 1 hr per day while training them to run from the start box of an alleyway to the goal box for a food reward. The animals in Group DEP received two trials 22 h after each daily meal so that they were hungry at the time of training. By contrast, those in Group NON were effectively nondeprived at the time of training because they received their pair of daily trials only 1 hr after each meal. Figure 12.1A shows performance during a series of test trials after 74 prior training trials. Not surprisingly, Group DEP ran consistently faster than did Group NON. Although an obvious explanation is that hungry rats are more motivated to seek food than are sated ones, an alternative account is that rats learn to run faster for food when hungry than when sated. Put simply, the issue is whether food is a more effective reinforcer under hunger with the result that animals learn to run faster in the deprived state. The motivational alternative is that Mollenauer's rats learned the same behavior under the two levels of deprivation but were simply more motivated to perform when hungry.

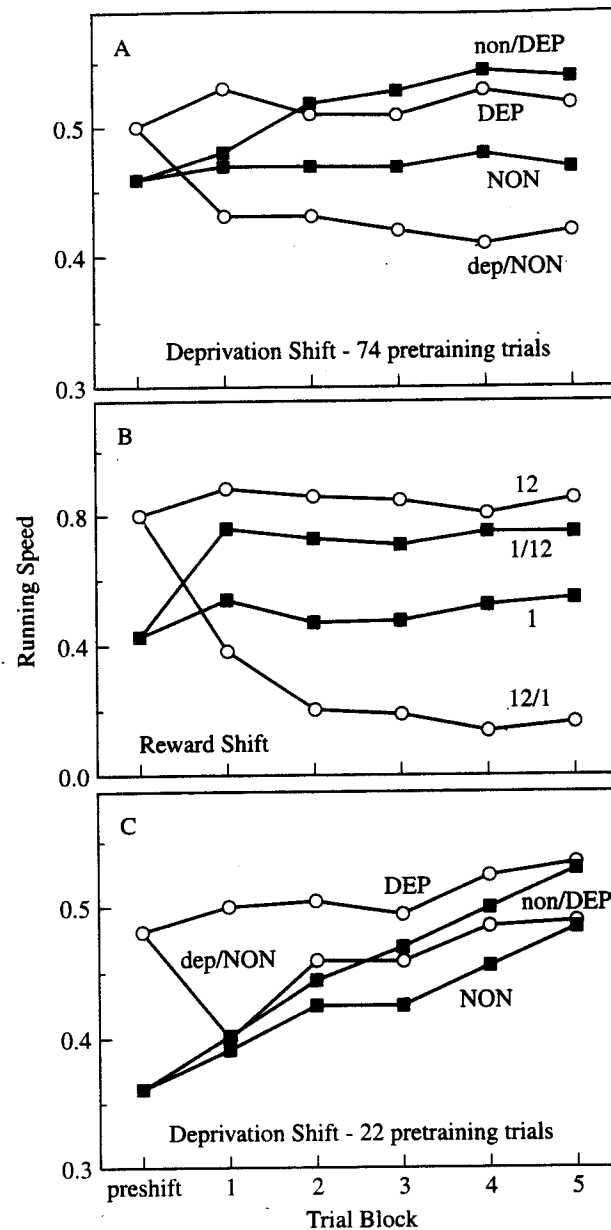
It was thought that these alternatives could be distinguished by shifting the deprivation state. Consider the case of the rats trained in the food-deprived state but then suddenly shifted to the nondeprived state. If the rats have simply learned to run faster when hungry, we should expect them to require a number of trials with the less effective reward in the nondeprived state before they learned to

run more slowly. By contrast, if varying the deprivation state acts by changing the motivation to perform food-seeking behavior, a reduction in the level of deprivation should have an immediate impact on performance. The performance of a third group of rats in the Mollenauer (1971) study, Group dep/NON, favors the motivation account. These rats, like Group DEP, were trained for 74 trials in the deprived state but were then suddenly tested in the nondeprived state. As Figure 12.1A shows, Group dep/NON ran slower than did Group DEP on the very first pair of trials after the shift in deprivation state. Mollenauer also observed a comparable performance shift by Group non/DEP in which the rats were initially trained in the nondeprived state but then were tested hungry. Although the performance shift was delayed by one pair of trials, by the second pair of postshift trials these rats were running faster than those trained and tested in the nondeprived state, Group NON, and as fast as the rats in Group DEP, which had been hungry throughout.<sup>1</sup>

Although the rapid impact of deprivation shifts suggests that states such as hunger can exert a direct effect on behavior, the nature of the underlying motivational process is less clear. Theories of motivation are, of necessity, tightly constrained by theories of learning. An action can be motivated by a desire for its outcome only if the agent has learned about the consequences of acting. In the absence of

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<sup>1</sup>The role of generalization decrement complicates the interpretation of shifts in motivational state. Not only did the shift from the deprived to the nondeprived state in Group dep/NON reduce the animals' motivational state, but it also changed the conditions from those present when the animals learned to run during training. Consequently, the immediate reduction in performance may, at least in part, have been due to generalization decrement, which would have summed with any motivational effect. In the up-shift case, by contrast, the motivating effect of increased hunger and generalization decrement would have worked against each other, thus producing the delayed shift in performance observed in Group non/DEP.



**Figure 12.1** Mean running speed on the final preshift trial block and on the postshift trial blocks. NOTE: The data in Panels A and C were estimated graphically from Figures 1 and 2 of Mollenauer (1971) for rats that received 74 and 22 preshift training trials, respectively, and are reproduced by permission of Academic Press. Each trial block consisted of a pair of daily trials. During the preshift training, Groups DEP and dep/NON were tested 22 hr after a feeding period, and Groups NON and non/DEP were tested 1 hr after a feeding period. Correspondingly, during the postshift training, Groups DEP and non/DEP were tested 22 hr after a feeding period, and Group NON and dep/NON were tested 1 hr after a feeding period. The data in Panel B were estimated graphically from the N panel of Figure 1 of Franchina and Brown (1971) and are reproduced by permission of the American Psychological Association. Each trial block consisted of six daily trials. During the preshift training, Groups 12 and 12/1 received 12 food pellets per trial, and Groups 1 and 1/12 received 1 food pellet per trial. Correspondingly, during the postshift training, Group 12 and 1/12 received 12 food pellets per trial, and Groups 1 and 12/1 received 1 food pellet per trial. SOURCE: Panels A and C from Mollenauer (1971). Reprinted with permission. Panel B from Franchina and Brown (1971). Copyright © 1971 by the American Psychological Association. Reprinted with permission.

action-outcome knowledge, the desire is behaviorally impotent, unable to select and motivate the appropriate action. However, such action-outcome knowledge was denied by the stimulus-response (S-R) theories that dominated the analysis of learning at the time of Miller's chapter. According to S-R habit theory, the outcome of an action simply serves to reinforce a connection between the stimulus context and the response (Thorndike, 1911), an associative structure that does not encode any information about the outcome; as a consequence, habit theory cannot support the selection of a response on the basis of the relevance of its outcome to the agent's motivational state. In other words, S-R theory does not permit, for example, nutritional need to motivate selectively a particular response because the agent has learned that this behavior has yielded food in the past.

Within S-R habit theory, therefore, there can be no motivational role for specific desires or drives, whether they be for "food appetizingly prepared" or for one's heart's desire; for this reason, S-R theorists (e.g., Hull, 1943) had to marry their theory of learning to a general drive theory of motivation. According to general drive theory, all primary motivational states funnel into one general motivational process that simply serves to energize any predominant habits. Consequently, a drive theorist would argue that this energization was most simply reflected in the immediate impact of the downshift in food deprivation on the running speed of Group dep/NON. General drive theory thus captures Descartes' "agitation of spirits" but not the soul's desires.

Despite the apparent success of drive theory, by the time Miller (1951) wrote his Stevens' chapter, it was well established that drive states could not be the sole motivational process. By investigating variations and shifts in magnitude of a food reward, Crespi (1942) discovered that rewards, like deprivation states, exert a motivational-like effect on

performance. Figure 12.1B illustrates the effect of shifts in reward magnitude in a study by Franchina and Brown (1971) that used a design analogous to that employed by Mollenauer (1971) to study deprivation shifts. In this experiment, Franchina and Brown also trained four groups of rats to run down a straight runway when food-deprived. Rather than varying the number of hours of food deprivation, however, they manipulated the size of the reward presented in the goal box. For two groups, Groups 1 and 12, the reward was 1 and 12 food pellets, respectively, throughout training and testing. Just as Mollenauer had found when rats were run at different levels of deprivation, reward magnitude also affected performance: Rats trained and tested with 12 pellets ran markedly faster than did those rewarded with 1 pellet.

The critical groups in this study are those that were trained with either 12 or 1 pellet and then shifted to the other reward magnitude for testing, Groups 12/1 and 1/12, respectively. Therefore, just as Mollenauer's deprivation-shift study assessed control by deprivation state, this experiment evaluated the influence of the reward on running speed by shifting its magnitude. A comparison of Figures 12.1A and 12.1B reveals that these shifts produced similar effects. An upshift in either food deprivation in Group non/DEP or food magnitude in Group 1/12 rapidly increased the running speeds to the levels of Groups DEP and 12, respectively. Correspondingly, Groups dep/NON and 12/1 showed similar profiles of reduced performance. Indeed, both downshifts produced a negative contrast effect (see Flaherty, 1996, for a review), in that Groups dep/NON and 12/1 ran slower than did the animals trained and tested either nondeprived in Group NON or with a low reward magnitude in Group 1. It is clear, therefore, that variations in reward magnitude produce motivational-like shifts in performance, an observation that led S-R theorists to assume that response habits were energized

not only by the current drive state but also by the incentive property of the reinforcer, a property that clearly had to be learned through experience with the reinforcer (Hull, 1952; Spence, 1956).

Once we allow that the reinforcer or outcome can exert a motivational influence, why do we need to assume that the motivational state induced, for example, by food deprivation has an independent, drive-like effect on performance? Just as a larger or more appetizing meal is a greater incentive, so perhaps a meal eaten in a state of hunger is also a greater incentive than is one consumed while sated. In other words, we can dispense with the whole concept of drive by assuming that primary biological motivational states act by modulating the incentive properties of the commodities and resources relevant to those states.

The development of motivational theory since the publication of Miller's (1951) chapter has been concerned primarily with the issue of how animals learn about the incentive properties of rewards and punishers, and how these properties exert their motivational influence on behavior. This being said, the study of motivation within experimental psychology has been largely neglected during the second half of twentieth century in favor of research on both general (Chaps. 1 and 2, this volume) and domain-specific learning processes (Chaps. 8 and 9, this volume). Unlike the neobehaviorist S-R theorists, contemporary students of learning have not, by and large, addressed the issue of how learning processes interact with motivational systems to generate behavior. It is true that we now know a great deal more about the mechanisms by which specific motivational systems, such as hunger (Chap. 15, this volume), thirst (Chap. 16, this volume), and fear (Chap. 13, this volume), control their consummatory behavior, feeding, drinking, freezing, and fleeing. Moreover, our understanding of the neurobiological systems engaged by rewards and reinforcers has also been transformed in the last few decades

(Chap. 14, this volume). What has been neglected, however, is the processes by which primary motivational states, such as hunger and thirst, interact with learning to regulate simple instrumental behavior. In other words, we have little understanding of what was happening during the first few postshift trials that led Mollenauer's and Franchina and Brown's rats to run faster when they were more hungry or when they received a larger reward and slower when they were less hungry or when they received a smaller reward. It is this issue that we address in the present chapter.

## PAVLOVIAN INCENTIVE LEARNING

In a study of the motivation of drug taking, Ludwig, Wikler, Stark, and Lexington (1974) gave detoxified alcoholics the opportunity to press a button for pure alcohol; after every 15 presses a small quantity of alcohol was dispensed into a cup just below the button. In addition, the subjects were asked to rate their "craving" for alcohol periodically throughout the test period. The main variable in this study was the nature of the cues that were present prior to and during the test. The experimental group received powerful cues that presumably had been associated with alcohol consumption in the past. At the start of the session, they were given a small taste of their favorite liquor and, in addition, a quart bottle of this drink was placed in full view during the test. By contrast, the control group received only pure alcohol as the priming taste.

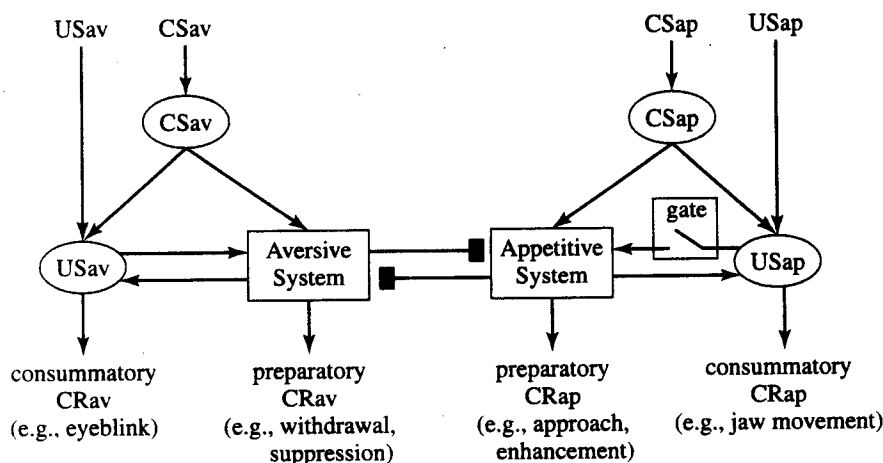
The presence of these alcohol-associated cues had a marked effect on performance; not only did the experimental subjects give much higher alcohol craving scores, but they also worked harder at the button-press response. Moreover, these two measures were highly related on an individual basis with a correlation of greater than 0.9 between the strength of the craving score and the level of instrumental performance for the alcohol reward. Thus,

it would appear that stimuli associated with an incentive acquire the capacity to induce a craving for that commodity and to motivate behavior that gains access to it. We refer to this acquisition process as Pavlovian incentive learning because it depends on the Pavlovian contingency between the conditioned stimulus (CS), in this case the alcohol-associated cues, and the unconditioned stimulus (US) or primary incentive, the alcohol itself.

### Motivational Conditioning

Although numerous authors have suggested that Pavlovian CSs acquire motivational properties (e.g., Berridge, 2000a; Bindra, 1974, 1978; Mowrer, 1960; Rescorla & Solomon, 1967; Toates, 1986), the most sophisticated account of Pavlovian conditioning that includes a motivational component is that developed by Konorski (1967). Konorski argued that Pavlovian conditioning comes in two forms: *consummatory* and *preparatory* conditioning (Chap. 1, this volume). Dickinson and Dearing (1979) developed a simplified version of Konorski's model, which is illustrated in Figure 12.2. Although this model

differs in many respects from the original theory (Konorski, 1967), we shall refer to it as Konorskian. Consummatory conditioning occurs when the form of the conditioned response reflects the specific sensory-perceptual properties of US. An example of this form of conditioning is Pavlov's classic procedure in which a signal, or CS, predicting a food US comes to elicit salivation in dogs. However, contemporary research on consummatory conditioning has predominantly employed procedures developed by Gormezano and his colleagues using the rabbit. For example, the appetitive jaw-movement conditioning reinforced by an intraoral fluid US or the defensive eye blink conditioned by an aversive orbital airpuff or shock US are examples of consummatory conditioning (Gormezano, 1972). Konorski assumed that consummatory conditioning reflects the formation of an association between the representation of the CS and a representation of the US that encodes its sensory and perceptual properties (see Figure 12.2). Activation of this US representation via the association elicits the consummatory conditioned responses.



**Figure 12.2** The Konorskian model of the stimulus representations and motivational systems mediating Pavlovian incentive learning (after Dickinson & Dearing, 1979).

NOTE: CSav: aversive conditioned stimulus; USav: aversive unconditioned stimulus; CRav: aversive conditioned response; CSap: appetitive conditioned stimulus; USap: appetitive unconditioned stimulus; CRap: appetitive conditioned response.

Konorski's (1967) second form of Pavlovian conditioning, which he designated as preparatory, reflects the acquisition of responses that are not specific to the particular US employed but, rather, are characteristic of the motivational class to which that US belongs. Examples of preparatory conditioning are CS-induced autonomic responses, such as changes in heart rate, and general behavioral responses, such as approach and withdrawal. Konorski assumed that these preparatory conditioned responses result from the activation of a motivational system by the CS and, moreover, that there are two routes by which this activation can occur. The first is via the US representation itself (see Figure 12.2). Indeed, within this model, it is the ability of the US representation to activate a motivational system that determines whether the US is motivationally potent.

Konorski (1967) also claimed that a CS could activate a motivational system through a direct association, thereby producing purely preparatory conditioning (see Figure 12.2). The basis of this claim is the observation that preparatory and consummatory conditioning can be dissociated under certain conditions. For example, when Vandercar and Schneiderman (1967) signaled mild eye-shock USs by a tone, this CS elicited both a conditioned eye blink and a heart rate change. Training with a longer CS-US interval, however, abolished the consummatory eye-blink conditioning without affecting the preparatory heart rate conditioning. This dissociation accords with Konorski's claim that long, tonic CSs, such as contextual stimuli, favor the preparatory form of conditioning, whereas both forms occur with short, phasic signals.

The reason for believing that preparatory conditioning engages motivational processes comes from evidence that preparatory CSs can modulate consummatory responding. Bombace, Brandon, and Wagner (1991) es-

tablished a relatively long auditory CS as a signal for a shock to the rear leg of a rabbit and a second, short visual stimulus as a CS for an eye-blink response. Bombace et al. were in a position to test the motivational property of the long auditory CS by presenting the visual CS embedded within the auditory stimulus. The critical finding was that the visual CS elicited a conditioned eye-blink response of greater amplitude when presented during the auditory stimulus.

The augmentation of the eye-blink response could not have reflected a simple response summation because the auditory CS, being both tonic and associated with a different, leg-shock US, did not elicit the eye-blink response. Rather, it appears that a preparatory CS motivates the performance of a consummatory response, and it is for this reason that Figure 12.2 shows not only a connection from the US representation to the motivational system but also a feedback connection from the motivational system. As a consequence of this feedback, exciting the motivational system by a preparatory CS augments activity in the US representation thereby enhancing the magnitude of any consummatory conditioned responses even when they are elicited by another CS.

Figure 12.2 illustrates just two motivational systems, an appetitive one and an aversive one. This structure therefore implies that different USs from the same affective class activate a common motivational system. We have already considered evidence for motivational transfer across aversive USs in the Bombace et al. (1991) study. A preparatory CS reinforced with a leg-shock US augmented a consummatory eye-blink response conditioned with an eye-shock reinforcer. It might be argued, however, that these two USs both elicit somatic pain and discomfort and therefore, not surprisingly, are mediated by a common system. Possibly more surprising is evidence from studies of transreinforcer blocking



suggesting that the commonality between aversive reinforcers extends beyond those involving somatic pain.

Blocking refers to the observation that pretraining one CS often reduces conditioning to a second, added CS when a compound of these two stimuli is paired with the reinforcer (Kamin, 1969; see Chap. 2, this volume). The pretrained CS is said to block conditioning to the added CS. Whereas the standard blocking procedure employs the same reinforcer during pretraining and compound training, Bakal, Johnson, and Rescorla (1974) reported that pretraining with a foot-shock US blocked conditioning with a loud auditory US. Blocking is usually ascribed to the fact that only surprising or unexpected reinforcers support conditioning (Kamin, 1969; Rescorla & Wagner, 1972) and, as the pretrained CS predicts the reinforcer during compound training, little conditioning accrues to the added CS. Foot shock and a loud noise differ greatly in terms of their sensory-perceptual properties so that the transreinforcer blocking cannot have arisen from the prediction of these properties of the reinforcer. What they do have in common, however, is that they are aversive, and therefore transreinforcer blocking is usually taken as evidence that the two reinforcers activate a common motivational or reinforcement system.

Transreinforcer blocking also provides the best evidence for commonalities in appetitive motivation. The case for multiple motivational systems is particularly strong in the appetitive domain; Konorski (1967) certainly thought so. Not only are the various forms of appetitive consummatory conditioning—feeding, drinking, or courting—mediated by different US representations, which determine the form of these responses, but also each of these classes of consummatory behavior is modulated by its own motivational state. Even so, studies of transreinforcer blocking

suggest that these different forms of consummatory conditioning may well engage a common motivational system.

Ganesen and Pearce (1988) pretrained rats with either a water or food reinforcer before giving compound training with the other US. Conditioned approach to the food or water source, the magazine, during the added CS was blocked by pretraining with the alternative reinforcer. In other words, pretraining with the water reinforcer blocked conditioning with the food reinforcer and vice versa. Moreover, this transreinforcer blocking did not depend on the rats' being both thirsty and hungry throughout training. Following pretraining with the water reinforcer under the combined deprivation state, the pretrained CS blocked conditioning to the added CS with the food reinforcer even though the rats were only food-deprived during the compound conditioning. Nor did the effect depend on the two reinforcers' maintaining the same conditioned response: Blocking occurred even when the food and water were dispensed to different magazines.

This transreinforcer blocking effect is a dramatic demonstration of a commonality between the conditioning processes engaged by food and water reinforcers. In fact, Ganesen and Pearce interpreted their results in terms of the type of Konorskian model outlined in Figure 12.2 by assuming that CSs associated with food and water activate a common appetitive motivational system. In discussing such motivational interactions, however, it is important to distinguish between the commonality and interactions between *motivational systems* engaged by CSs and interactions between primary *motivation states*, such as the states of hunger and thirst induced by food and water deprivation. Whereas transreinforcer blocking suggests that food and water CSs activate a common appetitive system, there is good evidence that thirst actively inhibits

feeding and food conditioned behavior. We return to this distinction between motivational systems and motivational states when discussing the issue of motivational control. Before doing so, however, we must consider why Dickinson and Dearing (1979) distinguished between the appetitive and aversive systems in their Konorskian model.

### **Appetitive-Aversive Interactions**

Although the transreinforcer modulation and blocking establish motivational commonalities, it is equally clear that we must draw a distinction at least between appetitive and aversive systems. There is a wealth of evidence that CSs of one affective class, if anything, have an inhibitory influence on responses controlled by CSs of the opposite affective class (Dickinson & Pearce, 1977). This inhibitory interrelationship is most clearly illustrated by counterconditioning. In the first stage of a study by Lovibond and Dickinson (1982), an appetitive jaw-movement response was conditioned to a CS by pairing it with an intraoral sugar water US in rabbits. Once the jaw-movement response had been conditioned, the schedule was changed so that an aversive eye-shock US replaced the water US on half the trials. Consequently, the CS signaled the sugar water on half of the trials and the eye shock on the remaining trials during the counterconditioning stage.

The critical observation concerned the fate of the conditioned jaw movement response during counterconditioning. If concurrent aversive conditioning just serves to augment the general motivational potency of the CS, the appetitive jaw-movement response should, if anything, have been augmented. At variance with this prediction, however, the jaw-movement response was suppressed as the defensive eye-blink response was conditioned. It is unlikely that the inhibition of the

appetitive responding reflected a peripheral response interaction because Scavio (1974) had previously established that rabbits can blink and swallow at the same time without any interference. Consequently, a plausible interpretation of the counterconditioning of the appetitive response by the aversive US is that there are, at least, separate aversive and appetitive motivational systems; the former exerts an inhibitory influence, on the latter, an influence that is illustrated by the appropriate inhibitory connection in Figure 12.2.

Figure 12.2 also contains a reciprocal inhibitory connection from the appetitive to the aversive system, although the evidence for this connection is somewhat weaker. Lovibond and Dickinson (1982) were unable to countercondition an established defensive eye-blink response by pairing the CS with sugar water. However, this failure may have arisen from an inequality of the relative strength of the aversive and appetitive reinforcers because Scavio (1974) has reported such counterconditioning when the strength of the aversive conditioning was weakened by extinction. During extinction of the eye-blink response, the frequency of the defensive response declined more rapidly when the CS was paired with interoral water.<sup>2</sup> Therefore, on the basis of this and other evidence (Dickinson & Dearing, 1979; Dickinson & Pearce, 1977), we favor the view that the appetitive and aversive motivational systems exert a mutually inhibitory influence.

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<sup>2</sup>Scavio (1987) himself has argued against the claim that appetitive CSs exert an inhibitory influence on defensive conditioning because prior appetitive conditioning has been observed to facilitate subsequent aversive conditioning (e.g., Dickinson, 1976; Scavio & Gormezano, 1980). However, this positive transfer may well reflect attentional/associability processes (see Chap. 2, this volume) rather than motivational interactions. The counterconditioning procedure, unlike a retardation test for inhibition, minimizes a role for attentional/associability processes.

As well as providing an explanation of counterconditioning, the opponent-process system offers an account of the properties of conditioned inhibitors. A conditioned inhibitor is a stimulus that acquires the capacity to inhibit the conditioned response elicited by an excitatory CS as a result of being paired with the omission of a predicted reinforcer. It has long been known that an inhibitory CS of one affective class appears to have some of the properties of an excitatory CS of the opposite affective class. Thus, a CS paired with the omission of an expected food reward, a so-called frustrative stimulus, is aversive in that rats will learn to escape from it (Daly, 1974). Correspondingly, a CS predicting the omission of an expected, aversive shock has rewarding properties in that the animal will preferentially perform responses that generate this CS (LoLordo, 1969). Moreover, by the transreinforcer blocking assay, conditioned exciters and inhibitors of opposite affective classes engage a common motivational system. A frustrative CS, pretrained to predict the absence of an appetitive food US, can block aversive conditioning with a shock US in rats (Dickinson & Dearing, 1979; Goodman & Fowler, 1983).

The Konorskian opponent-process model can explain these commonalities by assuming that the release of a motivational system from inhibition by the opponent system leads to a rebound excitation. Thus, for example, a CS for food excites the appetitive system, which in turn inhibits the aversive system. The presentation of an appetitive inhibitor then attenuates activation of the appetitive system, releasing the aversive system from inhibition and thereby producing rebound aversive excitation. This model therefore explains the commonalities of what have been called "hope" and "relief" and "fear" and "frustration" (Mowrer, 1960) by assuming that each pair of affective states is mediated by the same motivational system.

## Motivational Control

Although the motivational impact of different appetitive CSs may well be mediated by a common system in the Konorskian model, we have already noted that different appetitive motivational states can exert inhibitory-like interactions. There is an extensive, classic literature on the effects of a so-called irrelevant drive within the context of general drive theory (see Bolles, 1975, for a review), and it is well known that dehydration actively inhibits feeding (e.g., Rolls & McFarland, 1973) and food seeking (e.g., Van Hemel & Myers, 1970). Indeed, the presence of the cues associated with feeding may actually be aversive when rats are thirsty (e.g., Pliskoff & Tolliver, 1960). The inhibitory interaction between hunger and thirst in the control of Pavlovian behavior is illustrated also in a series of studies by Ramachandran and Pearce (1987). The asymptotic level of magazine approach elicited by a CS paired with either food or water was reduced by the presence of the irrelevant motivational state—thirst in the case of the food reinforcer and hunger in the case of the water reinforcer. The suppression produced by the irrelevant deprivation state was motivational in origin because removal of the irrelevant state during an extinction test restored performance to the level observed in rats trained under the relevant state alone.

It might be thought that this motivational interaction is at variance with our conclusion that hunger- and thirst-relevant USs activate a common motivational system on the basis of the Ganesen and Pearce (1988) transreinforcer blocking effect. As we have noted, however, it is important to distinguish the interaction between motivational systems from the interaction between the mechanisms by which primary motivational states, such as hunger and thirst, modulate the capacity of relevant stimuli to activate these systems.

Ramachandran and Pearce (1987) themselves argued that the interaction between hunger and thirst does not occur at the level of the appetitive motivational systems within the Konorskian model but rather that it reflects the mechanism by which primary motivational states modulate the activation of specific US representations.

That there has to be some form of state modulation of a CS's capacity to activate the relevant US representation is required by the simple fact that the strength of appetitive conditioning depends directly on the deprivation state of the animal. To take but a couple of examples, the strength of consummatory responses—licking in the case of rats (DeBold, Miller, & Jensen, 1965) and jaw movement in the case of rabbits (Mitchell and Gormezano, 1970) both conditioned by an intraoral water US—was monotonically related to the degree of fluid deprivation. In order to accommodate control by primary motivational states within their Konorskian model, Dickinson and Dearing (1979) assumed that these states gate the capacity of an excited US representation to activate the common appetitive motivational system and thereby the motivational feedback on the US representation (see Figure 12.2).

Clearly, each gate has to be US-specific within this model, so that hydration modulates fluid representations and nutritional needs modulate food representations. The implication of the Ramachandran and Pearce (1987) results for the model, therefore, is not only that hunger enhances the activation of the appetitive motivational system by a nutritional US representation through the gating mechanism but also that thirst counteracts this enhancement and thereby reduces the motivational feedback upon the food US representation.

Indeed, studies of specific hungers (Chap. 15, this volume) suggest that US gating must be even more specific than a simple hunger-

thirst distinction. For example, Davidson, Altizer, Benoit, Walls, and Powley (1997) exposed food-deprived rats to pairings of one CS with a carbohydrate US, sucrose pellets, and another with a fat US, peanut oil, before returning the animals to the nondeprived state for testing. During this test the CSs were presented in extinction so that performance would have been based solely on CS-US associations acquired during training. Prior to this test, one group was placed in a glucoprivic state, whereas a lipoprivic state was induced in another group by pharmacological manipulation. Importantly, the rats in the lipoprivic state showed more magazine approach during the peanut oil CS than during the sucrose CS, whereas the reverse pattern was observed in the glucoprivic state. This reinforcer specificity implies that there must be separate US gating for these two states and the relevant reinforcers.

Davidson (1993, 1997) would probably argue against this account of motivational control on the grounds that the behavioral control exerted by hunger induced by food deprivation has to be learned. It has long been known that deprivation states can be used as discriminative cues (Webb, 1955); for example, Davidson and his colleagues (Davidson, 1987; Davidson & Benoit, 1996; Davidson, Flynn & Jarrard, 1992) demonstrated that the level of food deprivation in rats rapidly acquires control over freezing when this state predicts the occurrence of foot shocks in a particular context. Moreover, Davidson (1993, 1997) drew an analogy between this form of motivational control and the conditional control exerted by so-called occasion setters in Pavlovian conditioning (see Chap. 1, this volume; Schmajuk & Holland, 1998). An occasion setter is a stimulus that signals when another Pavlovian CS is reinforced (or not reinforced); as a result of experience with this conditional contingency, the animal comes to respond (or not respond)

to the CS only when the occasion setter is present.

Although it may well be the case that the control exerted by food deprivation over responses from a different motivational class, such as freezing, may well involve a form of conditional learning, the question at issue is whether such learning also mediates the control exerted by hunger over responses elicited by a CS for food. Davidson (1997) argues that it does. He described an experiment in which food-deprived rats were once again trained to approach a magazine into which sucrose pellets were delivered before the strength of the approach response was tested in an extinction test. Half of the rats were tested food-deprived, and the other half were tested undeprived. Importantly, the state of food deprivation on the test had no effect on the approach response unless the animals had previously eaten the sucrose pellets in the undeprived state. Only rats that had previously eaten the pellets when undeprived and were then tested in this state showed a reduced level of responding. Davidson (1997) interpreted this finding as evidence that motivational control of Pavlovian food seeking by hunger must be learned through experience with the food reinforcer in both the deprived and undeprived states. As this form of differential experience is assumed to be necessary for the acquisition of conditional control by an occasion setter, Davidson argued that hunger acts as an occasion setter that predicts when the approach response will be reinforced in the training context.

There are, however, reasons for questioning the generality of this finding. Indeed, one might think that Davidson et al.'s (1997) demonstration of reinforcer-specific control by lipoprivic and glucoprivic states is a demonstration of the direct impact of motivational states. It is always possible, however, that the conditional control by these states was acquired during the Pavlovian training under

general food deprivation, which presumably involved both the gluco- and lipoprivic states. It should be noted, however, that their rats had never received prior experience with the sucrose pellets and the peanut oil in the absence of a nutritional need. Furthermore, whatever the source of motivational control was in the Davidson et al. study, it is well established that the induction of certain motivational states can have a direct impact on conditioned behavior even if the animals have never previously experienced this state.

A classic example is salt seeking under a sodium appetite. Following prior experience with a salty-flavored solution, the induction of a sodium appetite enhances the preference of rats for the salt-associated flavor. This preference is conditioned because the flavor solution is sodium free at test and, importantly, occurs even though the rats have no prior experience of a sodium deficiency (e.g., Berridge & Schulkin, 1989; Fudim, 1978). Therefore, the motivational state induced by a sodium need has a direct impact on a preference conditioned by a Pavlovian association with salt even though the animals have no prior experience of the sodium and flavor in the need state. Similarly, Kriekhaus (1970) had previously shown that rats in a sodium need for the first time will preferentially approach a source at which they have previously received salt while thirsty.

Even so, we still need an account of why the motivational control of food seeking in the Davidson et al. (1997) study required prior experience of the food in the undeprived state. In our laboratories we have repeatedly observed a direct impact of shifts in the level of food deprivation on the frequency of approach to a food source without prior experience of the food in the shifted state (e.g., Balleine, 1992). The reason for this discrepancy may well lie with the contingency controlling the approach behavior. Although students of conditioning often assume, as we have, that approach to

a food source is a Pavlovian response (e.g., Holland, 1979), the relative contribution of Pavlovian and instrumental contingencies to this behavior may well vary with the specific procedure employed. A cornerstone of our motivational theory (discussed later) is that the process of motivational control differs when mediated by instrumental response-reinforcer and Pavlovian stimulus-reinforcer contingencies. Thus, it may well be that the instrumental relationship played a more significant role in the approach response in the Davidson et al. (1997) procedure, and that for this reason they failed to observe a direct impact of the shift in motivational state (discussed later).

Another problematic finding for a simple gating theory of motivation control arises from a study by Killcross and Balleine (1996) on the motivational control of latent inhibition. Latent inhibition refers to the retardation of conditioning that occurs when a CS is simply preexposed (Lubow & Moore, 1959; Chap. 2, this volume). What Killcross and Balleine found was a motivational specificity in latent inhibition. Their rats received preexposure to one CS under hunger and another under thirst before both CSs were reinforced with either food pellets or saline when the animals were concurrently food- and water-deprived. Importantly, the rate of conditioning with a particular reinforcer was retarded when the CS had been preexposed under the motivational state relevant to that reinforcer—hunger in the case of the food pellets and thirst in the case of the saline. The animals appeared to have learned during preexposure that a CS is unrelated to the class of reinforcers relevant to their current motivational state. At present, we can do no more than acknowledge that this form of learning is not readily explained by the simple version of the Konorskian model.

In conclusion, we assume that Pavlovian conditioned responses are directly modulated

by primary motivational states, a modulation that is captured by their ability to gate the activation of the appetitive system by representations of the relevant reinforcers (Figure 12.2). Further evidence for this claim is to be found in studies of the motivational impact of Pavlovian CSs on instrumental behavior.

### **Pavlovian-Instrumental Transfer**

We introduced the role of Pavlovian conditioning in motivation by reference to the Ludwig et al. (1974) study demonstrating that alcoholics worked harder for alcohol in the presence of alcohol-associated stimuli. To explain this potentiation in terms of the motivational properties of CSs, we must assume that these stimuli potentiate not only Pavlovian responses but also instrumental behavior, such as the button-push response by which the alcoholics self-administered the ethanol. In fact, the idea that a stimulus associated with a positive reinforcer or reward exerts a motivational effect on behavior originates with an early study by Estes (1943). He reported that a tone paired with food elevated lever pressing by rats that had been previously reinforced with the food reward even though this response had never been trained in the presence of the tone. One problem that has always bedeviled the interpretation of such Pavlovian-instrumental transfer concerns the extent to which the Pavlovian influence is due to the interaction between the responses elicited by the signal for the reward and the transfer response, in this case lever pressing. As we have already noted, a CS signaling the delivery of food elicits approach to the source of the food; therefore, the issue is whether the elevation of lever pressing by the tone represents a true motivational effect of the CS or simply a facilitatory interaction of the responses conditioned to the tone with the instrumental response of lever pressing, for example, by maintaining proximity to the lever.

Although response interactions can contribute to Pavlovian-instrumental transfer (e.g., Karpicke, Christoph, Peterson, & Hearst, 1977), it is also clear that not all examples of transfer can be reduced to this mechanism. For example, Lovibond (1983) conditioned a jaw-movement response to a CS by pairing it with infusions of a sucrose solution directly into the mouths of thirsty rabbits. In order to assess whether this CS modulated instrumental responding, the rabbits were also trained to press a lever for the intraoral sugar solution in separate sessions and then, for the first time, presented with the CS while they were working for the sugar. In agreement with Estes' observation, the CS elevated the rate of lever pressing. In this case, however, we can be confident that this transfer effect did not reflect an interaction between the Pavlovian conditioned jaw-movement response and the instrumental lever pressing because eliciting jaw movements directly by the presentations of the intraoral sugar solution suppressed lever pressing.

### *Reinforcer-Specificity of Transfer*

Pavlovian-instrumental transfer suggests that activation of the appetitive system not only potentiates Pavlovian preparatory and consummatory responses but also enhances instrumental behavior. Given this claim, two questions arise within the framework of the Konorskian model (Figure 12.2). The first is whether the transfer is mediated by the activation of the appetitive system via the representation of the reinforcer or by direct activation by a purely preparatory CS. This distinction is important because it determines whether transfer is sensitive to primary motivational states. The second issue follows from the first; if the transfer effects are mediated by the US representation, are they sensitive to the similarity of the Pavlovian and instrumental reinforcers? In other words, if an animal is work-

ing instrumentally for a particular food, does the influence of a CS depend on whether it predicts the same food, a different food, or even a reinforcer from a different motivational category? We consider each of these issues in turn.

There is no doubt that transfer can be mediated by a representation of the Pavlovian reinforcer. Balleine (1994; see also Dickinson & Balleine, 1990) exposed thirsty rats to Pavlovian pairings of a CS with either a sucrose or a sodium chloride solution before switching the motivational state to hunger by depriving the animals of food and training them to lever press for food pellets. When the CSs were presented while the animals were lever pressing in extinction, the sucrose CS, but not the saline CS, elevated responding above the baseline level. However, this selective potentiation only occurred when the animals were hungry during the test. If they were water-deprived prior to the test, the sucrose and saline CSs produced comparable enhancements. This result shows that Pavlovian-instrumental transfer respects the relevance of the anticipated reinforcer to the motivational state of the animal on test. The sucrose solution, unlike the sodium chloride, is relevant to both hunger and thirst. Moreover, the reinforcer-specificity of the transfer could only have occurred if the motivational effect was mediated by the sucrose representation activated by the CS and modulated by the current motivation state of the animal.

Balleine (1994) also observed a similar selective transfer across the opposite motivational shift from hunger to thirst. In this case, the CS was associated with either the sucrose solution or food pellets under hunger before the rats were trained to lever press for water while thirsty. If tested thirsty, the sucrose CS elevated responding, whereas the pellet CS depressed responding below the baseline level, thereby demonstrating, once more,

the inhibitory effect of thirst on the motivational effects of purely food-associated CS (as discussed earlier; Ramachandran & Pearce, 1987). Again, this selective transfer was not due to a difference in the general effectiveness of the reinforcers because the sucrose and pellet CSs produced comparable enhancement when lever pressing was tested under hunger.

Finally, it should be noted that sensitivity to the motivational state on test occurred even though the animals had never previously experienced the sucrose reinforcer in the test state. This finding serves to reinforce our conclusion in the preceding section that the control of the motivational effects of CSs does not depend on prior experience with the reinforcer in the test state and is, therefore, adequately modeled by the motivational gating of the activation of a general appetitive system by a relevant reinforcer representation.

In their study of alcoholics, Ludwig et al. (1974) noted a high correlation between ratings of the alcohol craving induced by the alcohol-associated cues and their capacity to motivate button pushing. This correlation accords with the reinforcer specificity observed in the Balleine (1994) transfer effects. The role of the US representation in the motivational influence of CSs enables such stimuli to induce a craving for alcohol in the alcoholics and, presumably, the sucrose solution in thirsty or hungry rats. We cannot assume from this conclusion, however, that these stimuli motivate instrumental behavior because the instrumental action gives access to the craved resource. Indeed, this cannot be the case in the transfer observed by Balleine (1994). The sucrose CS motivated lever pressing even when this response had been trained with very different outcomes from the sucrose solution, either food pellets or water.

In fact, when the commonality of the Pavlovian and instrumental reinforcers is put in conflict with the relevance of the Pavlovian

reinforcer to the test motivational state, it is the latter that determines transfer. In a study very similar to that of Balleine (1994), Dickinson and Dawson (1987a) also established the sucrose and pellets CSs while the animals were hungry. The only difference was that the rats were also trained to lever press for pellets at the same time as the Pavlovian conditioning. However, even though lever pressing was associated with pellets, it was the sucrose rather than pellet CS that potentiated lever pressing when the animals were tested in extinction while thirsty. The corresponding pattern of results was also seen when Dickinson and Balleine (1990) tested transfer across a thirst-to-hunger shift with sucrose and saline CSs. The sucrose CS sustained greater lever pressing on test even though this response was trained with the saline reinforcer. In these cases, therefore, the motivational impact of the CSs was general even though their influence was mediated by a US-specific representation.

In some circumstances, however, the transfer does depend on the relationship between the Pavlovian and instrumental reinforcers. Colwill and Motzkin (1994; see also Colwill & Rescorla, 1988) associated one CS with food pellets and another with a sucrose solution before training the hungry rats to lever press and chain pull for these two reinforcers. When the CSs were presented in an extinction test, the rats performed the instrumental response trained with the same reinforcer as the US more than that trained with the different reinforcer. It is far from clear, however, that this transfer reflects a motivational effect in that response rate in the presence of the CS associated with the instrumental reinforcer was no higher than the baseline rate in the absence of the CS. In other words, the differential transfer arose from the fact that the CS depressed the instrumental response trained with the different reinforcer. Colwill and Motzkin (1994) themselves favored an



interpretation in terms of associative cuing of the responses by the CSs through their common reinforcers (Trapold & Overmier, 1972) rather than a motivational modulation of instrumental performance.

We therefore defend the claim that the motivational influence of an appetitive CS does not augment preferentially instrumental responses that share a common reinforcer but rather produces a general behavioral facilitation. This conclusion accords with a Konorskian model (Figure 12.2), which assumes that CSs for different appetitive reinforcers activate a common motivational system.

### *Conditioned Suppression*

Finally, we should note one further prediction of the Konorskian model that concerns, in this case, the effect of aversive Pavlovian CSs on rewarded instrumental responding. Estes (Estes & Skinner, 1941) was again the first to investigate the effect of an aversive CS on instrumental behavior by demonstrating that a tone paired with an electric shock suppressed food-rewarded lever pressing by hungry rats. However, our favorite conditioned suppression study is that reported by Di Giusto, Di Giusto, and King (1974). They gave students pairings of a tone and a mild electric shock before introducing the instrumental task, in which the students could display pictures of art works by pressing a button. Presentations of the CS during instrumental performance suppressed button pressing. Importantly, this suppression was not accompanied by any change in muscle tension, suggesting that suppressive effects of the CS was not due to the elicitation of interfering behavior. Within the framework of the Konorskian model, conditioned suppression is mediated by a loss of appetitive motivation brought about by the inhibitory influence of the aversive motivational system.

### **Summary**

In our introduction we described two motivational effects: the rapid adjustment of the running speed of rats for food rewards brought about by shifts in food deprivation (Mollenauer, 1971) and reward magnitude (Franchina & Brown, 1971). Moreover, we suggested that both these effects were mediated by variations in the incentive properties of the rewards. In this section, we have argued that these incentive properties act through Pavlovian learning and that the Konorskian model provides the machinery to explain this Pavlovian incentive learning. The initial approaches to the goal box and the receipt of food there would have established the stimuli of the runway as Pavlovian CSs capable of activating the appetitive system via a representation of the food reward. The activation of this system would then have either elicited the running as a Pavlovian preparatory approach response or potentiated running as an instrumental response through the transfer process. The fact that the level of appetitive consummatory conditioning is determined by the US magnitude (e.g., Sheafor & Gormezano, 1972) allows the Pavlovian process to explain why a shift in reward magnitude produces a motivational effect on running. The impact of deprivation shifts also follows directly from the fact that the activation of the appetitive system by the US representation is gated by the relevant primary motivational state. A prediction of this model of Pavlovian incentive learning is that consummatory appetitive responses should be elicited while the animal is running; indeed, thirsty rabbits showed a gradient of increasing conditioned jaw-movement responses as they approached the goal box of a runway for a water reward (Gormezano, 1980).

Another condition of Mollenauer's (1971) study suggested, however, that Pavlovian incentive learning does not provide an

exhaustive account of the impact of motivational states on performance. In addition to the groups that received a shift in deprivation after 74 preshift training trials, she also tested a further set of groups, which experienced the deprivation shift after much more limited training: only 22 trials. The postshift running speeds of these groups are illustrated in Figure 12.1C. The important feature of these data is that more trials were required for the full impact of the motivational shifts to emerge. Whereas after extensive training the speeds of the shifted groups, Groups dep/NON and non/DEP, converged upon those of the non-shifted groups, Group NON and DEP, respectively, within two pairs of trials (Figure 12.1A), convergence required five or six trial pairs after the more limited training (Figure 12.1C). This latter performance profile reflects the operation of a second form of incentive learning that is mediated by the instrumental contingency between the response and reinforcer rather than the Pavlovian relationship between CS and reinforcer.

## INSTRUMENTAL INCENTIVE LEARNING

In many situations a forager equipped only with Pavlovian incentive learning would face a dilemma. To shift paradigms, consider the case of a hypothetical castaway marooned on the proverbial desert island. Although this island is blessed with a fresh water supply, the only food source is an abundance of coconuts. Being from temperate latitudes, our castaway has no previous experience with coconuts; when motivated by hunger, however, he rapidly learns to puncture the shells for the milk and smash them open for the meat. One morning, however, our castaway wakes to find that the water source has failed, and he begins, for the first time, to experience increasing thirst.

Pavlovian incentive learning would, of course, focus behavior on coconuts even though the castaway has had no previous experience with them while thirsty. Past hunger-motivated foraging ensured that the coconut CS was associated with representations of both the milk and the meat. As a consequence, when tested in a state of thirst, coconuts would activate the appetitive system via the milk representation. We have no reason to believe, however, that this activation of the appetitive system would selectively motivate the appropriate instrumental response of piercing the shell rather than the inappropriate one of smashing it open. Recall that a CS paired with a sucrose solution under hunger potentiated food-reinforced instrumental responses when the rats were thirsty (Balleine, 1994; Dickinson & Dawson, 1987a).

Consequently, even though our castaway is thirsty instead of hungry, the sight and feel of the coconut should motivate not only actions that puncture the coconut but also those that smash it open with the consequent loss of the precious milk. Of course, once the two actions have been performed and produced their differential consequences, the castaway would rapidly learn to perform only the appropriate instrumental behavior. According to the Pavlovian account, however, the very first instrumental decision under thirst should not discriminate between the relevant and irrelevant actions. Consequently, Pavlovian incentive learning does not provide a solution to the dilemma of our thirsty castaway.

Surprisingly, and in accord with the Pavlovian account, thirsty rats do not always resolve this dilemma. Dickinson and Watt (Dickinson, 1997) trained hungry rats to lever press and chain pull concurrently with one action reinforced by a sucrose solution and the other by food pellets before testing their choice between these two actions when they were, for the first time, thirsty. This test was

conducted in extinction to ensure that the choice between the two responses was not affected by differential reinforcement during the test itself. As in the case of our castaway, on the basis of Pavlovian incentive learning alone, these rats should not have preferred one action over the other on test, as they were both performed within the same Pavlovian context. Indeed, this is just what Dickinson and Watt found (see also Dickinson & Dawson, 1988, 1989). When tested thirsty, rats performed the pellet-trained response just as frequently as the one reinforced with the sucrose solution.<sup>3</sup>

The failure of these rats to solve the castaway's dilemma contrasts with the success of those in a very similar study by Shipley and Colwill (1996). Like the Dickinson and Watt animals, their hungry rats were also trained to lever press and chain pull for a sucrose solution and food pellets; in this case, however, the sucrose-trained action was

preferred when the rats were tested thirsty in extinction. The important difference between the two studies the concentration of the sucrose solution. Dickinson and Watt (Dickinson, 1997) employed a concentrated 20% sucrose solution, whereas Shipley and Colwill (1996) used a more dilute 8% solution. Moreover, in an unpublished study from the Cambridge Laboratory, we have demonstrated that it is the concentration of the sucrose solution that determines the presence or absence of a preference for the sucrose-trained response. It is not that the concentrated solution is an ineffective reward when thirsty because rats will lever press and chain pull faster for this solution than for the food pellets (e.g., Dickinson & Dawson, 1988). Indeed, the concentrated 20% solution was employed in the experiments demonstrating that a sucrose CS trained under hunger potentiates instrumental responding under thirst (Balleine, 1994; Dickinson & Dawson, 1987a).

A possible reason why the concentration is important concerns the sucrose solution's similarity to water. As a result of their daily maintenance schedule, the rats were likely to have drunk water when thirsty before and therefore have had the opportunity to learn about its thirst-quenching properties. Whether or not the rats solve the castaway's dilemma then depends on whether this learning generalizes from water to the sucrose solution. Clearly, this generalization is more likely to have occurred for the weak sucrose solution employed by Shipley and Colwill than for the concentrated solution used by Dickinson and Watt. The implication of this analysis is that animals must learn about the relevance of the incentive properties of instrumental reinforcers to a particular motivational state before that state can control performance through an instrumental contingency.

In fact, Dickinson and Watt (Dickinson, 1997; see also Dickinson & Dawson, 1988,

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<sup>3</sup>It should be noted that there are a number of successful demonstrations of an instrumental-irrelevant incentive effect. Dickinson and Dawson (1987b) trained one group to lever press for the sucrose solution and another group to press for the food pellets while the rats were hungry. When performance was subsequently assessed in extinction under thirst, the sucrose-trained group responded more than did the pellet-trained group. The important feature of this between-subject design is that the training contexts of the two groups were selectively associated with either the sucrose solution or the food pellets, so that the irrelevant incentive effect can be explained purely in terms of the Pavlovian incentive learning to the contextual stimuli.

The same analysis can be given of the classic irrelevant incentive effect reported by Kriekhaus and Wolf (1968), in which thirsty rats were trained to lever press for either a sodium solution or a nonsodium solution. Following the induction of a sodium need, rats trained with the sodium solution showed elevated responding in extinction. This selective enhancement of a sodium-trained responding was abolished, however, when the Pavlovian status of the context in which the sodium and nonsodium responses were tested was equated by giving concurrent training with the two responses in the same context (Dickinson, 1986).

1989) provided direct evidence for such learning. Prior to instrumental training in standard operant chambers, rats must learn that the rewards are available in the magazine and that they must collect them promptly once delivered. Consequently, Dickinson and Watt gave their rats a number of pretraining sessions in which the food pellets and the sucrose solution were delivered aperiodically in the absence of the opportunity to lever press and chain pull. These manipulanda were simply removed from the chamber during the pretraining sessions. For the group of rats already described, this pretraining occurred while they were hungry, as they were during instrumental training. By contrast, a second group of rats received this pretraining under water deprivation so that they had experience of the sucrose solution and food pellets while thirsty prior to instrumental training under hunger.<sup>4</sup> If these rats learned that the sucrose solution was more valuable than the food pellets when they were thirsty, they should have performed sucrose-trained response preferentially during the extinction test under thirst. This is just what Dickinson and Watt observed; at the outset of the test, the rats performed this response at over twice the rate of the pellet-trained response, but only if they had previously experienced the reinforcers when thirsty.

In summary, whether animals solve the castaway's dilemma depends on whether they have had prior experience with the rewards, or at least similar commodities, under thirst. If they have such experience, then animals are capable of using their knowledge of the instrumental response-reinforcer contingencies (see Colwill & Rescorla, 1986; Dickinson,

1994; Chap. 1, this volume) to select the action that in the past has yielded the reinforcer relevant to their current need state. The importance of this experience is that it allows the animal to learn about the incentive properties of the sucrose solution and the food pellets when thirsty. We refer to this form of learning as *instrumental incentive learning* because, though not itself instrumental, it is expressed in behavior through knowledge of the instrumental contingency between action and reinforcer.

### Tolman's Cathexis Theory

The precursor to the concept of instrumental incentive learning is to be found in Tolman's (1949a, 1949b) cathexis theory of motivation (see Dickinson & Balleine, 1994). According to Tolman, instrumental performance is determined by the incentive value of the outcome of the instrumental action, or what he referred to as the goal-object. Moreover, Tolman argued that primary motivational states do not automatically confer value upon relevant outcomes; rather, both animals and humans must learn about relative incentive values in a particular motivational state through experience with the outcomes in that state. Therefore, unlike Pavlovian motivation, in which thirst automatically gates the activation of the appetitive system by a fluid US representation, an animal must learn about the incentive value of a fluid under water deprivation by actually drinking the solution when thirsty. Tolman's theory therefore anticipates the result found by Dickinson and colleagues (Dickinson & Dawson, 1988, 1989; Dickinson, 1997). Their rats failed to perform the action trained with the relevant sucrose solution when thirsty for the first time, which, according to Tolman, was because they had not formed a cathexis between thirst and the sucrose solution. When given the opportunity to do so by drinking the sucrose solution under water deprivation

<sup>4</sup>In fact, both groups of rats were placed on an alternating schedule of food and water deprivation during the pretraining: one group received the sucrose solution and food pellets on days when they were hungry, and the other group received them on days when they were thirsty.

during pretraining, the reinstatement of thirst on test conferred a positive incentive value on the solution and thereby motivated the appropriate instrumental behavior.

Tolman assumed that a cathexis is instantiated by the formation of a connection between the motivational state and the representation of the relevant outcome, which then allows the motivational state to activate the outcome representation and thereby confer incentive value upon the outcome. The Tolmanian concept of incentive learning therefore predicts an asymmetry in the impact of motivation shifts on performance, a prediction that was examined in Balleine's (1992) study of hunger shifts. Balleine trained rats to respond for either food pellets or a starch solution in a nondeprived state before testing their performance when food deprived in extinction. Cathexis theory predicts that the hungry rats should respond no more vigorously than would nondeprived animals unless they have previously experienced the foods when hungry. Without this experience, there would be no cathexis between the state of hunger and the representation of the food, so the induction of hunger could not enhance the incentive value of the food. In accord with this prediction, Balleine (1992) found that hungry and nondeprived rats pressed at the same low rate on test, but that this rate was elevated in hungry rats if they had received preexposure to the food when deprived.

In contrast to the role of incentive learning in motivational upshifts, cathexis theory predicts that a downshift should have an immediate impact on performance. Training the rats to respond while food-deprived should establish a connection between the state of hunger and the representation of the food reward that enables the induction of this state to endow the food with incentive value. Consequently, a downshift to the nondeprived state should produce an immediate loss of incentive

value by removing the activation of the reward representation by the hunger state. At variance with this prediction, however, Balleine (1992) found that a reduction in food deprivation had no impact on performance unless the animals had previously experienced the food in the nondeprived state. Following training under food deprivation with either the food pellets or the starch solution, nondeprived rats responded just as frequently as did deprived ones in an extinction test unless they had previously eaten the particular food reward in the sated state.

Therefore, simply experiencing a food in the hungry state is not sufficient to establish motivational control over its incentive value. This failure of cathexis theory prompted us to suggest that instrumental incentive learning consists of the interaction of two learning processes (Dickinson & Balleine, 1994). The first is the process by which an animal learns about the incentive value of an outcome through experience with it. We called this form of learning the determination process because it is this process that determines the incentive value of the outcome. Of course, one of the factors that determines the incentive value is the presence of a relevant motivational state so that it was the determination process that led Balleine's (1992) rats to respond more rapidly for food when hungry than when sated. However, a motivation state can determine an incentive value without acquiring control of that value. This point is illustrated by the fact that the incentive value generalized across shifts in motivational state in the Balleine (1992) study when the rats had no prior experience of the food rewards in the shifted state. The high incentive value established when rats were hungry during training generalized to the nondeprived state on test and maintained performance. Correspondingly, when the animals were trained nondeprived, the consequent low incentive value also controlled performance when the animals were tested

hungry. For the motivational state to acquire control over incentive value, the animals had to receive prior experience with the outcome in the shifted state, and the acquisition of this motivational control over incentive value is the second component of the instrumental form of incentive learning.

In summary, motivational states serve two important functions in instrumental incentive learning. The first is that of *determining* the incentive value of an instrumental outcome, and the second is that of *controlling* the incentive value so that the value that controls performance at any given time depends on the current motivational state of the animal.

### Motivational Control of Incentive Value

For Balleine's (1992) rats, motivational control required differential experience with the food in both the deprived and nondeprived states, and the necessity of differential experience suggested to us (Balleine, 2000; Dickinson & Balleine, 1994) that motivational states acquire control over instrumental incentive value through the normal discrimination learning processes underlying the acquisition of conditional control. As we have already noted, Davidson (1993, 1997) made this very claim in relation to the motivational control of Pavlovian conditioning, and we have already discussed the extensive evidence from his laboratory that deprivation states can acquire conditional control even over motivationally irrelevant responses. Although we take issue with his claim in respect to Pavlovian motivation, which we regard as being a direct form of control (as discussed earlier), we agree that the motivational control over the incentive value of instrumental outcomes depends on conditional learning.

The analogy between the acquisition of motivational control and standard conditional control is best illustrated by Bouton's (1993, 1994) account of the contextual control over

responding to a CS. Bouton argued that the context in which learning takes place acquires control over conditioned responding to a CS only when the CS has been both reinforced and extinguished so that its predictive status is ambiguous. Thus, just as the high incentive value of a food reward established by instrumental training under food deprivation generalizes to the nondeprived state, so conditioning in one context generalizes fully to a different context. By contrast, if conditioning in one context is followed by extinction in a second context, responding to the CS comes under contextual control. This control can be illustrated by a study in which Bouton and his colleagues (Bouton, Kenney, & Rosengard, 1990) used a drug-induced internal state, which is analogous to a motivational state, as the controlling context. Having been conditioned in a drug-free state, the CS was extinguished under a benzodiazepine agonist (BZ) before the rats were tested in the BZ and non-drug states. This two-state training induced control over responding by the BZ state in that the rats responded to the CS in the nondrug but not in the drugged state. This state-dependent control is, we argue, analogous to the control exerted by hunger over incentive value of food produced by experiencing the food in both the deprived and nondeprived states (Balleine, 1992).

If motivational states are in no way privileged in their acquisition of control over incentive value, artificially induced states should also readily acquire motivational control. The BZ state, in fact, provides an excellent model for testing this claim because it not only induces a highly discriminable internal state that can acquire conditional control over behavior but also enhances the rewarding property of foods in nondeprived rats (Balleine, Ball, & Dickinson, 1994). Therefore, in terms of the processes determining and controlling incentive value, the BZ state should function exactly like natural hunger

according to incentive learning theory. Allowing animals to eat a particular food under a BZ agonist should not only enhance the incentive value of that food but also result in this enhancement's being conditional or dependent on the internal state induced by the drug when the animal has received experience with food in both the drugged and drug-free states.

To test this prediction, Balleine et al. (1994) trained nondeprived rats to lever press for food pellets before allowing them to eat the pellets under the influence of a BZ agonist in separate feeding cages. When the rats were returned to the operant chambers for an extinction test, these rats pressed more than did animals that had eaten the pellets following vehicle injections. Critically, however, this incentive-learning effect only emerged if the animals were tested in the state induced by an injection of the agonist. In other words, the motivational control exerted by the drug exactly paralleled that produced by food deprivation, although there was no transfer of control between these states (Balleine et al., 1994).

Thus, an internal, drug-induced state that does not mimic natural hunger can acquire control over the incentive value of the food in the way that parallels the control exerted by hunger. This result certainly suggests that the acquisition of control over incentive value is mediated by a general learning process rather than one specific to natural motivational states.

### Determination of Incentive Value

Our analysis has done little so far to characterize the role of psychological states in motivational processes, whether it be in the determination of instrumental incentive value or in the activation of Pavlovian systems and their motivational feedback upon US representations (see Figure 12.2). This is not to say, however, that psychological states and re-

actions have no role in these processes. We have already noted that Ludwig et al. (1974) observed a correlation between the craving induced by alcohol-associated CSs and their motivational properties, and a number of authors have claimed a major role for affective experience by arguing that motivation is grounded on the hedonic reactions or, in other words, the pleasure elicited by rewards and appetitive USs (e.g., Cabanac, 1992; Toates, 1986).

### Hedonics and Incentive Value

There are various reasons for believing that hedonics play an important role in motivation. The hedonic reaction to a stimulus, like the incentive value of a reward, is modulated by motivational states, a process that Cabanac refers to as *alliesthesia*. For example, Cabanac (1971) asked human participants to make successive ratings of how much they liked a sweet-tasting glucose solution. Although these rating remained high for the group required to spit out the solution after each tasting, there was a progressive decline in the ratings when the solutions were swallowed. To what extent the differential hedonic evaluation depended on general nutritional state or specific satiety for the evaluated stimulus is unclear, although both processes probably play a role. There is ample evidence not only that a flavored food is rated as less pleasant shortly after a meal (e.g., Booth, Mather, & Fuller, 1982; Laeng, Berridge, & Butter, 1993) but also that consuming a particular food or fluid produces a flavor-specific reduction in hedonic ratings (see Hetherington, 1996; Hetherington & Rolls, 1996; Johnson & Vickers, 1993). Moreover, Gibson, and Desmond (1999) found that the hedonic evaluation of chocolate was in part determined by incentive learning. Chocolate was rated as more pleasant after it had been regularly eaten 2 hr rather than a few minutes following a meal when, presumably, the human participants were generally sated.

Assessment of taste reactivity in animals also suggests that hedonic evaluations are modulated by motivational state. Grill and Norgren (1978) reported that the very first intraoral infusion of a sucrose solution elicits a set of appetitive reactions by rats, such as rhythmic tongue protrusions and mouth movements, whereas a distasteful quinine solution elicits aversive reactions, such as gapes and head shakes. These basic patterns of affective reactions to tastes are exhibited by a wide range of species, including human infants and other primates (see Berridge, 2000b, for a review), and Berridge (1995, 2000a, 2000b) argued that they reflect an immediate and innate hedonic evaluation of the taste.

Taste reactivity can be dissociated from simple ingestion and rejection. Berridge (2000b) reviewed a number of brain lesions and pharmacological treatments that dissociate consumption and taste reactivity, but one particularly compelling example comes from a study of the suppression of sucrose drinking by different aversive consequences. Pelchat, Grill, Rozin, and Jacobs (1983) reduced the amount of a sucrose solution drunk by thirsty rats by pairing drinking of the solution with either foot shock or the induction of gastric malaise by an injection of lithium chloride (LiCl). Although both treatments were equally effective in suppressing intake, they had contrasting effects on the taste reactivity. Even though the rats would not drink the sucrose solution following the shock treatment, they still showed the full profile of appetitive taste reactivity with no aversive components. This pattern suggests that the rats still liked the sucrose solution but would not drink it because of its aversive consequences, much as we might avoid eating a favorite food if it regularly produces the pain of indigestion. By contrast, the LiCl treatment not only suppressed intake but also shifted the taste reactivity from the appetitive to the aversive pattern. This case is analogous to one in which

we develop an aversion or disgust reaction to a food as a result of its association with nausea.

Studies of taste reactivity confirm that the hedonic reactions to food and fluid are modulated by motivational state. The taste reactivity patterns elicited by sugar solutions are augmented by hunger (e.g., Berridge, 1991; Cabanac & LaFrance, 1990, 1991; Grill, Roitman, & Kaplan, 1996), and those elicited by saline are enhanced by a sodium appetite (e.g., Berridge, Flynn, Schulkin, & Grill, 1984; Berridge & Schulkin, 1989). On the basis of these observations, we (Balleine & Dickinson, 1998a; Dickinson & Balleine, 1994, 2000) have suggested that the hedonic reactions elicited by an instrumental outcome determine the assignment of incentive value. Therefore, according to this account, hedonics serves as the interface between the cognitive representation of incentive value that controls the performance of instrumental actions and the basic neurobiological mechanism engaged by nutritional deficits and other motivational states.

The main prediction of the hedonic theory of incentive value is that any manipulation that alters the taste reactivity patterns elicited by a food or fluid should produce a concomitant change in the incentive value of that food or fluid. We have already noted in our discussion of motivational control that BZ agonists enhance the incentive value of food rewards (Balleine et al., 1994); therefore, it is instructive that these drugs also augment the appetitive taste reactivity patterns (e.g., Berridge & Pecina, 1995; Söderpalm & Berridge, 2000). Conversely, given that LiCl-induced aversions not only attenuate appetitive taste reactions but also induce aversive ones (e.g., Pelchat et al., 1983), this treatment should devalue foods and fluids with this taste, a prediction confirmed in numerous instrumental studies of outcome devaluation (e.g., Adams & Dickinson, 1981; Colwill & Rescorla, 1985).



Moreover, the hedonic theory predicts that the crucial event for outcome devaluation is experience with the devalued outcome rather than the conditioning of the aversion. This point is illustrated by a study in which we (Balleine & Dickinson, 1991) trained thirsty rats to lever press for a sucrose solution in a single session. We then devalued this outcome by injecting the rats with LiCl immediately following this session, which should have conditioned an aversion from the sucrose. According to the hedonic theory of incentive value, however, this aversion conditioning should not have been sufficient by itself to devalue the sucrose solution. In the absence of any reexposure to the sucrose following the aversion conditioning, our rats would not have had opportunity to learn about the change in their hedonic reactions to this outcome, and therefore their instrumental performance should have been controlled by the positive incentive value assigned to the sucrose solution during instrumental training. Indeed, we failed to detect any devaluation effect following this treatment; the pairing of the sucrose solution and the LiCl had no detectable effect on instrumental performance in a subsequent extinction test.<sup>5</sup>

In order to induce an outcome devaluation effect, we had to reexpose the rats to the sucrose solution in separate drinking cages between the aversion conditioning and testing. When we did so, the reexposed rats pressed less in the subsequent extinction test than did both nonreexposed animals and control rats that did not receive the aversion conditioning in the first place. Although the pairing of the sucrose and LiCl conditioned a latent

aversion from the solution, this aversion remained opaque to the cognitive system controlling lever pressing until the animals were reexposed to the sucrose solution. The reexposure then enabled the rats to experience the change in their hedonic evaluation following the aversion conditioning, and on the basis of this experience, they assigned a lower incentive value to the outcome.

The claim that outcome devaluation is based on the hedonic reactions elicited by the sucrose solution at the time of reexposure is supported by pharmacological manipulations of these reactions. Limebeer and Parker (2000) reported that the antiemetic and antinausea serotonin antagonist, ondansetron, reduces the aversive taste reactivity pattern elicited by a sweet solution after aversion conditioning without any detectable impact on its consumption. If outcome devaluation following aversion conditioning is due to experience of the aversive taste reactions during reexposure, administration of the antiemetic prior to reexposure should reduce the devaluation effect. This result was reported by Balleine, Garner, and Dickinson (1995). An aversion was conditioned from both a sucrose and sodium solution by following a single training session with LiCl. During this session one action delivered the sucrose solution, and the other delivered the saline. The rats then received a single exposure to both solutions, one under ondansetron and the other under vehicle. On test, our rats performed the response trained with the outcome reexposed under ondansetron in preference to the one trained with the outcome reexposed under the vehicle. State-dependency did not contribute to this preference, as its magnitude was unaffected by whether the antiemetic was administered prior to the test.

In summary, the conditions producing outcome devaluation by taste-aversion conditioning parallel those required for devaluation by motivational shifts. To recap, Balleine's

<sup>5</sup> Under certain conditions, an outcome devaluation effect can be observed after a single outcome-LiCl pairing in the absence of any reexposure to the outcome (Parades-Olay & Lopez, 2000; Rescorla, 1992, 1994). Balleine and Dickinson (1992) analyzed some of the conditions under which LiCl-induced outcome devaluation depends upon reexposure.

(1992) rats continued to respond at a high level even though they were not food-deprived unless they had previously experienced the food reward in the sated state. We interpret this persistence as evidence that performance was controlled by the positive incentive value assigned to the outcome during training under hunger. Similarly, instrumental performance following aversion conditioning alone was controlled by the positive incentive value of the sucrose generated by training the rats thirsty in the Balleine and Dickinson (1991) study. An outcome devaluation effect required that the animals had the opportunity to learn about the change in their hedonic reactions to the sucrose solution before the aversion conditioning reduced instrumental performance. The main difference between the two cases is that the reduction of incentive value produced by aversion conditioning does not readily come under the control of the animal's motivational state (Lopez, Balleine, & Dickinson, 1992b).

Finally, we should note an apparent challenge to the hedonic theory of incentive value. Dopamine antagonists attenuate instrumental performance for appetitive rewards (for reviews, see Beninger & Miller, 1998; Berridge & Robinson, 1998; Smith, 1995) but not for appetitive taste reactivity (Peciña, Berridge, & Parker, 1997). In this case, however, it is far from clear that the drug affects instrumental performance through the determination of incentive value. Dickinson, Smith, and Mirenowicz (2000) replicated the procedures that we had previously used to demonstrate a role for instrumental incentive learning in motivational control by hunger (Balleine, Davies, & Dickinson, 1995; Balleine & Dickinson, 1994) but substituted the dopamine antagonist for the state of satiety. The rats were trained to perform different instrumental actions for food pellets and a sucrose solution before one of the outcomes was reexposed under the drug and the other under the vehicle. If experienc-

ing a reward under a dopamine antagonist determines a lower incentive value, this re-exposure should have produced a reduction in the subsequent performance of the associated action on test. However, Dickinson et al. (2000) could not detect any effect of the incentive learning treatment even when the animals were tested under the drug.

Rather than impacting upon instrumental incentive learning, dopamine antagonists may act through the Pavlovian form of incentive learning. Berridge and Robinson (1998; Robinson & Berridge, 1993) consistently argued that the dopamine system mediates the motivational properties of CSs. According to Berridge and Robinson, pairing a CS with an appetitive reinforcer endows the signal with incentive salience and the capacity to induce a state of wanting, which can be independent of the animal's liking for the reinforcer. Support for their claim comes from the observation that dopamine antagonists attenuated Pavlovian-instrumental transfer in rats at the doses that did not support instrumental incentive learning (Dickinson et al., 2000). Conversely, Wyvell and Berridge (2000) reported that a microinjection of a dopamine agonist into the nucleus accumbens of rats enhanced the potentiation of instrumental responding for sucrose pellets produced by an appetitive CS without affecting the appetitive and aversive taste reactivity profiles elicited by the intraoral infusion of a bitter-sweet sucrose-quinine solution. Therefore, it is likely that the effect of dopamine antagonists are mediated by the Pavlovian rather than the instrumental form of incentive learning and that the drug-induced reduction in simple instrumental performance reflects an attenuation of the motivational influence of contextual stimuli.

### *Representation of Incentive Value*

Recall that the outcome devaluation produced by reexposure to a reward associated

with gastric illness was ameliorated when an antiemetic was injected prior to reexposure but not when it was administered prior to the instrumental test (Balleine, Garner, & Dickinson, 1995). The finding that the antiemetic had no impact on the magnitude of the devaluation effect when administered prior to the instrumental extinction test has theoretical implications that go beyond the issue of state-dependency. If the control of instrumental action by incentive value depends on the reactivation of the hedonic response to the outcome at the time of performance, the presence of an antiemetic on test should have reduced the magnitude of the devaluation effect. The fact that it did not do so in the Balleine, Garner, and Dickinson (1995) study therefore suggests that once the assignment of incentive value has been made on the basis of hedonic evaluation, the representation of incentive value is relatively affect-free.

Moreover, in the case of foods at least, there is evidence that incentive value can be assigned to, or associated with, a purely sensory representation of the outcome. Balleine (2000) has recently reported an aversion-induced devaluation effect based entirely on the taste of the outcomes. The thirsty rats received a single training session in which one action was reinforced by an orange-flavored sucrose solution and the other by a grape-flavored solution. This session was then followed by a LiCl injection, which should have conditioned an aversion to both solutions. The animals then received reexposure to only one of the flavored solutions before a preference test between the two actions was conducted in extinction. In this test, the rats performed preferentially the action trained with the nonreexposed rather the reexposed outcome. Because the two outcomes differed only in their flavor, the selective devaluation effect implies that the incentive values of the outcomes were encoded in association with their gustatory representations.

Perhaps more surprising is the fact that state-specific incentive values are also encoded in association with outcome flavors. Once again, we (Balleine & Dickinson, 1998a) trained hungry rats to perform two actions for different outcomes, which in this case were a salty and a sour starch solution. In a second incentive-learning stage, the rats were given free access to one of the solutions for an hour. Presumably, the rats became satiated on the starch during this reexposure and, as a consequence, experienced its flavor in association with reduced hedonic response to the starch solution. Therefore, we expected the rats to assign a low incentive value to the flavor conditional on being satiated with starch. In accord with this prediction, the rats performed the action trained with the reexposed flavor at a reduced rate during an extinction test that followed satiation on the starch solution alone. It is important to note that this satiety was induced by prefeeding the rats for 1 hr with an unflavored starch solution and that the devaluation effect did not occur in the absence of the starch prefeeding.

The final strand of evidence for a sensory encoding of incentive value comes from studies of the role of insular cortex in incentive learning. The insular cortex contains the cortical representations of tastes in close association with visceral afferents; therefore, one might expect this region to be involved in incentive learning if the incentive value of a food outcome is bound to its flavor representation. To investigate the neurobiological encoding of incentive value, we (Balleine & Dickinson, 2000) lesioned the insular cortex before testing the rats in a standard incentive-learning paradigm. Once again, the hungry rats were trained to perform two actions for different outcomes, food pellets and a starch solution, before one of the outcomes was devalued by being reexposed in the nondeprived state. The control animals replicated the standard incentive-learning effect; when tested in

the undeprived state, they performed the action trained with the devalued outcome less than that trained with the nondevalued outcome. Importantly, however, this difference was abolished following insular lesions.

It is not that the lesioned animals were insensitive to the rewarding properties of the foods, for their acquisition and performance of the instrumental actions were normal. Moreover, they were sensitive to the manipulation of motivational state in that they responded faster when food-deprived and actually receiving the food rewards. They could also discriminate between the two rewards in that they exhibited a specific satiety effect. Prefeeding one of the foods before an instrumental test session selectively reduced responding for the prefed food. However, if this test was conducted in extinction so that performance depended on the representation of the incentive values of the foods rather than on their immediate impact during the test session, the lesion abolished devaluation by specific satiety. Unlike the control animals, the lesioned rats performed the actions trained with the two foods at comparable levels.

### **Summary**

In summary, our claim is that goal-directed instrumental action is motivated by the incentive value of the outcome that is encoded in association with a sensory/perceptual representation of the outcome. The assignment of a value to an outcome depends on the experience of the hedonic reactions elicited by that outcome—reactions that are modulated by the current motivational state. This process of assignment is the value-determination component of instrumental incentive learning. Finally, there is evidence that once an incentive value is assigned to an outcome representation, the capacity of that value to control action is relatively independent of the motivational and affective systems that determined the hedonic reactions to the outcome in the first place.

We must acknowledge, however, that this account is little more than descriptive, although Balleine (2000) has recently offered a mechanism for the determination of incentive value that employs a process of affective feedback.

### **Generality of Incentive Learning**

Although the manipulation of hedonic evaluation by a variety of procedures—deprivation-induced motivational state changes, aversion conditioning, pharmacological treatments—establishes a role for incentive learning in instrumental motivation, this research has been conducted largely with food rewards and simple operant responses. Consequently, an important issue concerns the generality of incentive learning across both motivational systems and instrumental responses.

### **Motivational Generality**

As we have already noted, some of the initial demonstrations of incentive learning involved shifts from hunger to thirst (Dickinson & Dawson, 1988, 1989). Moreover, changes in instrumental performance for fluid rewards brought about both by upshifts (Lopez & Paredes-Olay, 1999) and downshifts (Lopez, Balleine, & Dickinson, 1992a) in water deprivation depend on incentive learning. There is also evidence that incentive learning may play a role in sexual motivation. Everitt and Stacey (1987) trained male rats to press a lever to gain access to an estrous female before being castrated. This treatment, which reduces the level of circulating testosterone, impairs male sexual motivation. Nevertheless, the castrated animals, on being returned to the test chamber, initially pressed as rapidly as did intact rats. However, after only a single encounter with the female in their impotent state, the males reduced their rate of responding. The initial insensitivity of the female-seeking behavior to the reduction in testosterone suggests that instrumental performance was controlled by

the high incentive value assigned to the female during precastration copulation and that this value continued to control postcastration performance until the male had an opportunity to learn about the female's low incentive value in his current state.

Finally, what is probably the very first demonstration of incentive learning established its role in the motivational control of avoidance behavior. Hendersen and Graham (1979) trained rats to avoid the onset of a heat source in a warm environment before testing them in extinction in either the same warm conditions or in a cold environment. The assumption behind the study was that avoidance was motivated by the warm conditions, so that reducing the ambient temperature would reduce the motivation for the avoidance response. In fact, the test temperature had no effect on performance unless the rats had previously experienced the heat source when cold. Given this incentive-learning treatment, which presumably allowed them to learn about the positive incentive value of the heat source when cold, the level of avoidance responding was subsequently reduced when tested under a low ambient temperature.

There is one case, however, in which a shift in motivational state does appear to have a direct impact on the incentive value of an instrumental outcome. Dickinson and Balleine (1990) trained thirsty rats to lever press and chain pull for a sucrose solution and for saline before testing performance in extinction when the animals were hungry. The rationale behind this motivation shift is that the incentive value of the sucrose, but not the saline, should have been maintained across the shift from thirst to hunger. The results of the test confirmed this prediction. The hungry animals performed the response trained with the sucrose more than that trained with the saline when they were tested hungry (but not when tested thirsty). The important point, however, is that this irrelevant incentive effect occurred even though

the rats had no previous experience with the two solutions when hungry and therefore had no opportunity to learn about their relative value in this state. Moreover, the design of the experiment precluded nonspecific, Pavlovian modulation of performance (discussed earlier) resulting from motivational conditioning to the context by testing both responses in the same context.

The immediate impact of a thirst-to-hunger shift stands in marked contrast to the absence of a direct effect for the opposite shift—from hunger to thirst—which requires incentive learning (Dickinson, 1997; Dickinson & Dawson, 1988, 1989). We suspect that the difference arises from the asymmetrical interaction between hunger and thirst. Whereas hungry rats are not concurrently thirsty, water-deprived animals have a nutritional deficit incurred by an active inhibition of food consumption. As noted earlier in our discussion of Pavlovian incentive learning, thirsty rats appear to be concurrently hungry so that experience with the sucrose solution and saline during the instrumental training under water deprivation may have allowed our rats to learn about the relative incentive values of the two solutions not only with respect to thirst but also with respect to hunger. In other words, the acquisition of motivational control over the incentive values of sucrose and saline may have occurred during the instrumental training in the Dickinson and Balleine (1990) study.

Whatever the merits of this particular explanation, it is clear that incentive learning makes an important contribution to the control of instrumental performance by a variety of motivational states and systems. What is equally clear, however, is that the role of incentive learning varies with the nature and extent of instrumental training.

### *Instrumental Generality*

At the outset, we illustrated the influence of motivation with a demonstration by

Mollenauer (1971) that shifts in hunger had a rapid impact on running speed (Figure 12.1A), which, we suggested, reflected the effect of Pavlovian incentive learning to the runway cues. We have also noted, however, that the rapidity with which the rats adjusted to the shift in deprivation state varied with the amount of pretraining. The animals required more post-shift trials following limited (Figure 12.1C) rather than extensive training (Figure 12.1A). One explanation of the lag in adjusting to a deprivation shift following limited pretraining is that the animals required a number of experiences with the reward in the new deprivation state for instrumental incentive learning to change the incentive value of the food reward. This account implies, therefore, that the motivation of instrumental behavior changes with training from the instrumental to the Pavlovian form of incentive learning.

We have examined this possibility in an operant study in which hungry rats received either limited or extended training of lever pressing for a reward of food pellets (Dickinson, Balleine, Watt, Gonzalez, & Boakes, 1995). The animals then received an incentive-learning experience in which they were allowed to eat the pellets in separate feeding cages in either the deprived or undeprived state. Finally, we assessed performance during extinction when the rats were either hungry or sated on their maintenance diet. This study replicated the standard incentive-learning effect observed after limited training. The rats sated on test showed reduced performance only if they had previously eaten the food pellets in the undeprived state. By contrast—and in accordance with Mollenauer's results—after extended training the shift in motivation state had a direct impact on performance, which was not modulated by the incentive learning experience.

We (Dickinson et al., 1995) interpreted this change in motivational control in terms of the nature of the instrumental learning

process that controls performance at different points in training. For outcome revaluation to be effective, instrumental performance must be controlled by an action-outcome (A-O) representation. In other words, a change in the incentive value of an outcome can only affect performance in an extinction test in which the outcome itself is not present, if performance is controlled by knowledge of the relationship by the action and the outcome. Therefore, the processes of instrumental incentive learning must operate throughout an A-O representation. There is evidence from other outcome devaluation studies, however, that instrumental responding can become autonomous of the current incentive value of the outcome with overtraining under the appropriate conditions (e.g., Adams, 1982), and one account of the development of behavioral autonomy with training is that it reflects a transition in the control of performance from a cognitive process based on the A-O representation to an S-R habit process (e.g., Dickinson, 1985, 1989).

This account is compatible with the change in motivational control observed by Dickinson et al. (1995). After limited training, the A-O representation mediates motivational control through the incentive value of the outcome acquired by the process of instrumental incentive learning. This process cannot operate, however, when the instrumental response becomes predominantly an S-R habit with overtraining. Therefore, after overtraining, the primary motivational influence is that mediated by Pavlovian incentive learning, which, we have argued, renders performance directly sensitive to shifts in motivational state. The same analysis can explain the contrasting patterns of postshift running speeds observed by Mollenauer (1971) after varying pretraining.

Finally, motivational control varies not only with the amount of instrumental training but also with the location of the instrumental

action within an appetitive chain. In all the instrumental incentive learning studies we have considered so far, the target instrumental response, such as lever pressing or chain pulling, has acted as the first link in a behavioral chain that terminated in the opening of a flap door that gave access to the food magazine. In his initial incentive learning study, Balleine (1992) reported that flap opening, unlike lever pressing and chain pulling, did not require an incentive learning experience for motivational control and was directly affected by shifts in food deprivation. In other words, there was a motivational dissociation between the two responses. Rats that had been trained hungry but not received incentive learning pressed the lever frequently but did not enter the magazine when tested sated in extinction. The corresponding animals that were non-deprived during training pressed slowly but frequently entered the magazine when tested hungry.

In order to determine whether this variation in motivational control was a function of the response topography and manipulandum or the locus of the response in an appetitive chain, we (Balleine, Garner, Gonzalez, & Dickinson, 1995) locked the flap door of the chamber permanently open and trained our hungry rats to respond on a two-link chain schedule for food pellets. The response required in one link was lever pressing and in the other was chain pulling. When the rats were tested in extinction with both manipulanda present, the state of food deprivation had no impact on performance of the first-link response unless the animals had received previous experience with the food pellets in the undeprived state. Therefore, in replication of our previous findings, the motivational control of performance in the initial link of the instrumental chain depends on incentive learning. By contrast, performance of the terminal-link response was affected directly by the downshift in deprivation level.

It is clear, therefore, that processes of motivational control vary across the links of instrumental chains with terminal links being directly affected by motivational shifts and distal links being more dependent on incentive learning. The causes of this variation remain as yet unanalyzed, but the profile of motivational control suggests that terminal links, like overtrained responses, are more sensitive to Pavlovian influences.

## SUMMARY AND CONCLUSIONS

In summary, our analysis of motivation vindicates Miller's (1951) original claim that acquired behavior is motivated by desires rather than drives and, moreover, that desires are learned even in the case of such basic biological commodities as food and water. Desires, however, come in two forms. The first is mediated by what we have called Pavlovian incentive learning. We have analyzed this incentive process in terms of a Konorskian model in which the CS activates an appetitive motivational system via a representation of the US or reinforcer with the Pavlovian desire arising from a feedback activation of this representation. These Pavlovian desires are modulated by two further processes or mechanisms. The first is engaged by primary motivational states. The presence of a motivational state, such as hunger or thirst, enhances or gates the capacity of an activated representation of a relevant US to excite the appetitive system and thereby the motivational impact of a CS. The second is an aversive system that serves to inhibit the appetitive system. This aversive system is embedded within a structure similar to that engaged by appetitive stimuli, and it modulates the performance of defensive Pavlovian behavior in a manner analogous to the appetitive case.

Whether Pavlovian desires are in fact desires of good standing is less clear, however.

As we have noted, there is evidence that CSs can induce craving, and Berridge has certainly characterized the state induced by a CS as one of wanting. Moreover, the motivational impact of a CS on instrumental behavior is modulated by the presence of the motivational state relevant to the US. What appears not to be the case, however, is that a CS acts by enhancing the desire for the outcome of the instrumental action in that the CS impacts on instrumental performance trained with a reinforcer relevant to a different motivational state. Rather, appetitive CSs appear to cause the Cartesian "agitation of spirits" that "dispose the body to movement," much as Hullian general drive was assumed to do.

Desires that function by specifying their objects as goals of instrumental action operate through a different form of incentive learning. Within this system, the desire is characterized as the incentive value of the instrumental outcome, which has to be learned through experience of the hedonic reactions elicited by the outcome. Primary motivational states play two roles within this form of incentive learning. First, they contribute to the determination of incentive value by altering the hedonic reactions elicited by the outcome; second, they can acquire control over incentive value so that the value controlling action is higher in the presence of relevant motivational state than in its absence.

Finally, although the Pavlovian and instrumental incentive learning are dissociable and have been treated separately in our analysis, they do, of course, function in parallel and in a dynamic interaction throughout the behavioral stream with the nature of the interaction varying with the status of the current action. Instrumental incentive learning can only motivate cognitively mediated, goal-directed actions but not S-R habits, which are primarily under the motivational influence of the Pavlovian form of incentive learning.

Miller (1951) concluded his chapter with the lament that "the theoretical and experimental work has a long way to go before it bridges completely the gap between the fundamental biological drives and the wonderfully complex web of socially learned motives that determine adult human behavior" (p. 469). That gap, of course, remains wide, but the recognition of the central role of incentive learning in the control of behavior by even the "fundamental biological drives" does provide the foundation for bridging this gap that was lacking 50 years ago.

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