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## **Rhybudd o Hawlfraint**

Atgoffir staff a myfyrwyr y Brifysgol bod hawlfraint yn bodoli yn y darn hwn a'r gwaith y'i cymerwyd ohono. Gwnaed y copi digidol hwn o dan delerau trwydded CLA sy'n eich caniatáu i:

- gyrchu a lawrlwytho copi;
- argraffu copi;

Mae'r Copi Digidol hwn ac unrhyw gopi digidol neu argraffedig a roddir i chi neu a wneir gennych o dan delerau'r Drwydded hon i'w defnyddio mewn perthynas â'r Cwrs Astudio hwn. Cewch gadw copïau o'r fath hyd ddiwedd y cwrs, ond dim ond at eich defnydd eich hun.

Rhaid i bob copi (gan gynnwys rhai electronig) gynnwys y Rhybudd o Hawlfraint hwn a rhaid eu dinistrio a/neu eu dileu os a phan fydd y Brifysgol yn mynnu hynny.

Ac eithrio o dan delerau cyfreithiau hawlfraint, ni chaniateir copïo, storio na dosbarthu pellach (gan gynnwys negeseuon e-bost) heb ganiatâd deilydd yr hawlfraint.

Mae gan yr awdur (ac mae'r term hwn yn cynnwys artistiaid a chreawdwyr gweledol eraill) hawliau moesol yn y gwaith ac ni chaiff staff na myfyrwyr achosi, neu ganiatáu, afluniad, anffurfiad nac unrhyw addasiad arall i'r gwaith, nac unrhyw driniaeth niweidiol arall ohono, a fyddai'n rhagfarnu anrhydedd neu enw da'r awdur.

Cwrs Astudio: **864A JCO\_JPS Counselling and Psychology**

Enw'r Person Dynodedig sy'n awdurdodi'r sganio: **Anne Harvey**

Teitl: **Animal Learning and Cognition – An Introduction (2<sup>nd</sup> Edition)**

Enw'r Awdur: **John M Pearce**

Enw'r Cyhoeddwr: **Psychology Press**

Enw'r creawdwr gweledol (fel y bo'n briodol):

# 2

## Associative Learning

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Often in an animal's environment one event will reliably predict another. The ingestion of certain flavours will be followed by illness, whereas others will lead to beneficial consequences. Some environments will frequently be visited by predators, others will not. In addition, the action of the animal itself may result in consistent consequences: Following a certain route might take it to food or water, whereas different paths might lead to danger. Any animal that knows about these relationships will benefit because it will be able to anticipate future events and behave appropriately in preparation for them. But how can this knowledge be acquired? In an unchanging world animals could be born with it so that, for instance, the consumption of food of a certain flavour would automatically and consistently result in it being consumed or rejected. The world, however, is not unchanging. At the very least the location of food will change from generation to generation, and so too might the relationship between the taste or sight of food and its gastric consequences. Accordingly, animals must themselves discover which events reliably signal important consequences, and an important way of achieving this is by the process of associative learning.

Associative learning can be said to have taken place when there is a change in an animal's behaviour as a result of one event being paired with another. Two different methods that have proved

extremely useful for the study of associative learning were described in the historical survey at the end of the previous chapter. One method is exemplified by Pavlovian conditioning, where the two events that are paired together are a neutral conditioned stimulus (CS) and a biologically significant unconditioned stimulus (US). The other method is instrumental conditioning in which a response made by the animal constitutes one event, and the outcome of that response constitutes the second event. In this chapter, as well as the next one, we shall concentrate on what Pavlovian conditioning has revealed about the mechanisms of associative learning. We shall then turn to an examination of instrumental conditioning in Chapter 4.

At first sight there may seem to be little of interest in studying the process that enables a dog to salivate in the presence of a light paired with food, or a rabbit to blink whenever it hears a tone that signals a mild cheek shock. But once it is acknowledged that these conditioned responses (CRs) are a product of a process that is essential for learning about the sequential structure of the environment, then they become of fundamental importance. Their occurrence allows us to study in detail a fundamentally important learning process.

The first part of this chapter describes some basic conditioning techniques that have proved particularly useful for the study of associative

learning. In most conditioning tasks the CS serves as a signal for the occurrence of the US, and this procedure is known as excitatory conditioning. But it is also possible for a CS to indicate the omission of a US, and here the term inhibitory conditioning is employed. Both excitatory and inhibitory conditioning are believed to be effective because they result in a relatively permanent change within the animal. In the second part of this chapter we shall look at what is known about the nature of this change. The third, and final, part of the chapter will consider the factors that determine how an animal will react to a CS that has been paired with a US.

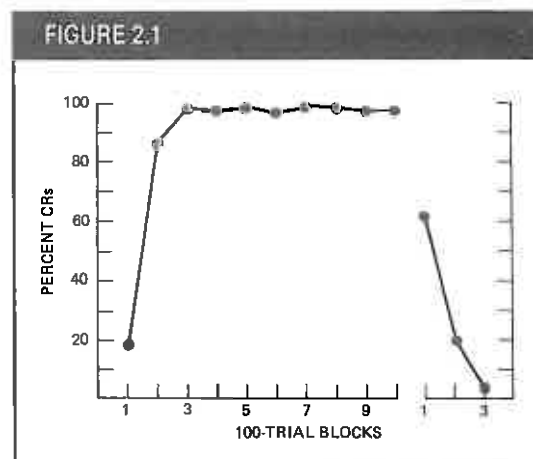
## CONDITIONING TECHNIQUES

### Excitatory conditioning

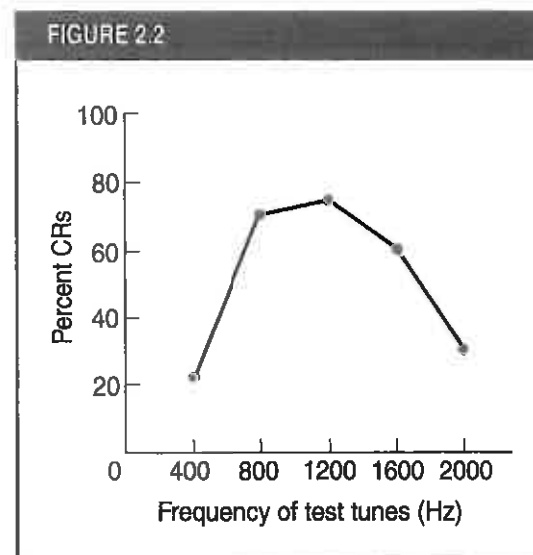
**Eye-blink conditioning.** For eye-blink conditioning the subject, normally a rabbit, is restrained in a stock or harness, and a number of light-weight sensors are placed near its eye. Rabbits possess an outer and an inner eyelid, and this equipment can permit the recording of a small movement of either. Conditioning consists of the presentation of a relatively brief CS—say a 300-millisecond tone—followed by the delivery of a mild shock to the cheek. In most cases the intensity of the shock is just sufficient to produce a blink. After a number of CS–US pairings, the CS, which by itself should not make the rabbit blink, is often found to elicit this response. The results from a typical study are presented in the left-hand side of Figure 2.1, which shows the percentage of trials on which a blink was detected during the CS across successive blocks of 100 trials. The right-hand side depicts the effects of *extinction* in which the CS is presented but is no longer followed by shock. A term that is frequently used in discussions of learning curves is the *asymptote*, which refers to the top part of the curve that is flat and reflects a stable level of responding.

Moore (1972) describes an experiment in which rabbits first received conditioning in which a 1200Hz tone signalled the delivery of shock. Test trials were then given in which the same tone was

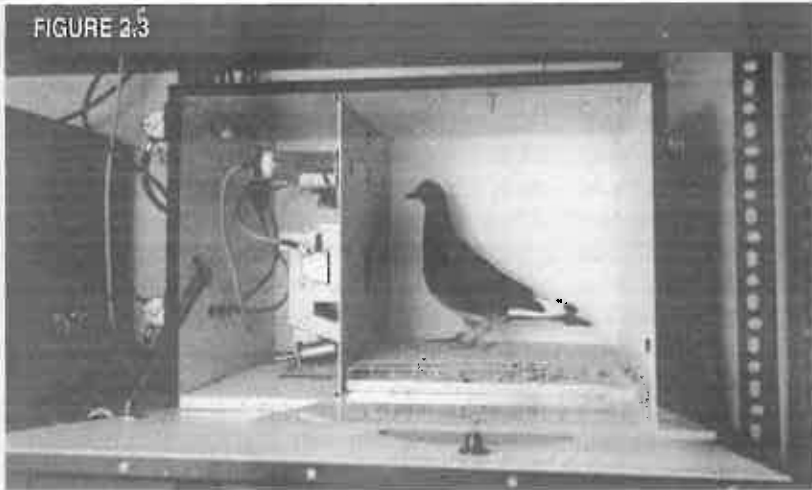
presented intermixed with tones of different frequencies. The results from these test trials can be seen in Figure 2.2. The percentage of trials on which a CR was recorded was maximal for the tone of 1200Hz, but when other tones were presented the likelihood of this response declined. Moreover, the extent of this decline was greater for stimuli that



The acquisition and extinction of an eye-blink CR to a tone CS by rabbits (adapted from Gibbs, Latham, & Gormezano, 1978).



The strength of an eye-blink CR to tones of different frequencies after conditioning with a tone of 1200Hertz (adapted from Moore, 1972).



A typical conditioning chamber for pigeons containing three response keys.

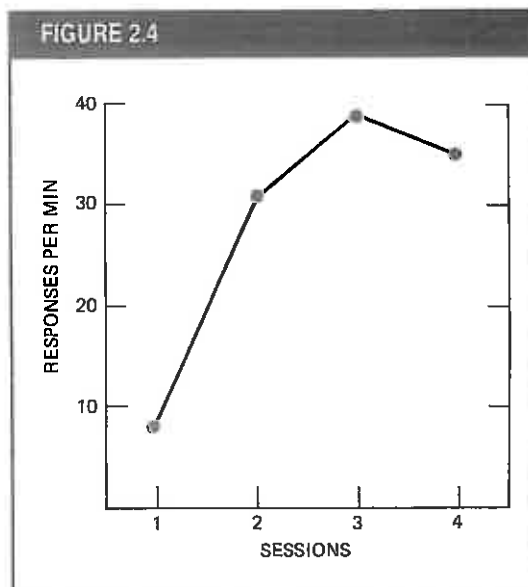
were further removed from the training stimulus. The fact that responding occurs at all with conditions that differ from those present during training demonstrates *stimulus generalisation*, and when the extent of this generalisation is incomplete this is said to reflect *generalisation decrement*.

**Autoshaping.** With autoshaping, a hungry pigeon is placed in a conditioning chamber such as that depicted in Figure 2.3. At intervals of about 1 minute a response key is illuminated for about 5 seconds, and the offset of this stimulus is followed by the delivery of food to a hopper. At first subjects may be unresponsive to the key, but after a few trials they will peck it rapidly whenever it is illuminated. Note this is not an example of instrumental conditioning as the pigeon does not have to peck the key to obtain food. Instead, it is an example of Pavlovian conditioning as the mere pairing of the illuminated key with food is sufficient to engender a CR of key-pecking. A typical learning curve produced by this training is presented in Figure 2.4.

**Conditioned suppression.** In a procedure known either as conditioned suppression or conditioned emotional response (CER), subjects, very often rats, are first trained in an operant chamber in which they must press a lever in order to obtain food. Conditioning, which takes place in this chamber while the subject is pressing the lever, then consists of pairing a stimulus that lasts for

about 1 minute with a relatively mild shock delivered through the grid floor. There may be four such trials in each session, which itself may last for an hour or more.

When it is first presented, the signal for shock will have little influence on the rate of lever pressing. But as conditioning trials continue, so a gradual decline in the rate of responding will be



The rate of key-pecking by a group of pigeons for which the illumination of a response key by white light for 10 seconds signalled the delivery of food. There were 10 conditioning trials in each session (unpublished study by Pearce).

recorded until eventually the lever may not be pressed at all during the CS. As soon as the shock has been delivered, however, responding rapidly recovers to its normal rate and remains at this level until the next trial. It is important to be aware that the cessation of lever pressing has no influence on the outcome of the trial, so that shock is presented irrespective of the animal's behaviour. The decline in responding during the CS is regarded as evidence of successful Pavlovian conditioning.

The measure of conditioning is the extent to which the CS reduces the rate of lever pressing. The slower the response rate during the CS, the more effective conditioning is assumed to be. Because rats vary considerably in the rate at which they press a lever for food, it has not proved useful to look directly at the rate of responding during the CS as a measure of conditioning. Instead, a *suppression ratio* is computed according to the formula  $a/(a + b)$ . The value of  $a$  is determined by the rate of lever pressing during the CS, and  $b$  is the rate during a short interval immediately prior to CS onset. A ratio of 0.50 indicates that these rates are equal and that conditioning is ineffective, whereas a ratio of 0.00 shows that no responses at all were performed during the CS and that conditioning has been maximally effective. Figure 2.5 (left-hand side) presents the results from a

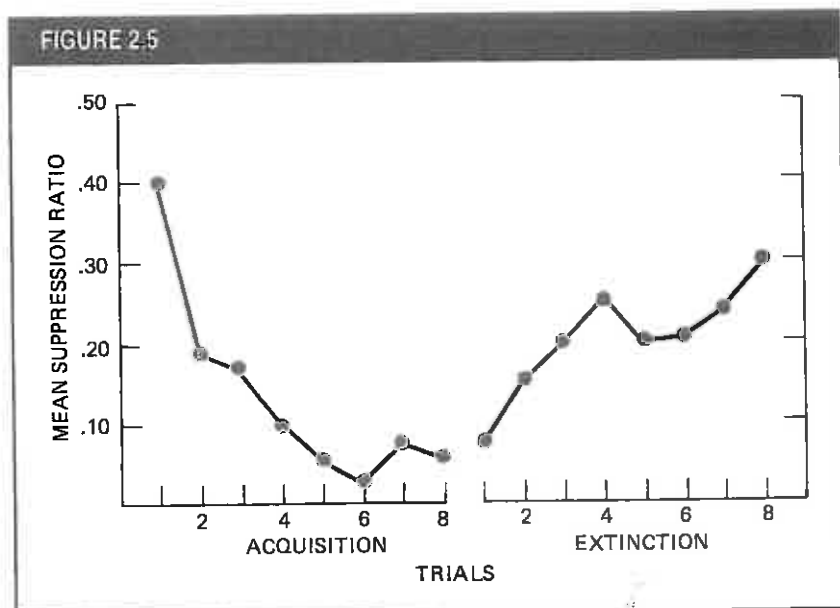
typical study in which the value of the average suppression ratio for a group of rats declines across successive trials. The right-hand side of this figure shows the effects of extinction, when the CS was no longer followed by the foot shock.

**Taste-aversion conditioning.** The final example of a technique for Pavlovian conditioning was mentioned briefly in Chapter 1. If an animal is made ill after consuming a particular food, by being injected with a mild poison such as lithium chloride, it will develop a marked aversion to the flavour of that food. This technique has a number of characteristics that set it apart from many other methods of conditioning. It is often extremely effective with only a single trial, and very long intervals between the CS and the onset of illness can be employed with little detriment to learning. None the less, in most respects the effects of this procedure resemble those of other methods of conditioning, and for this reason it has proved an extremely useful tool for the study of the general principles of associative learning.

#### The need for control procedures

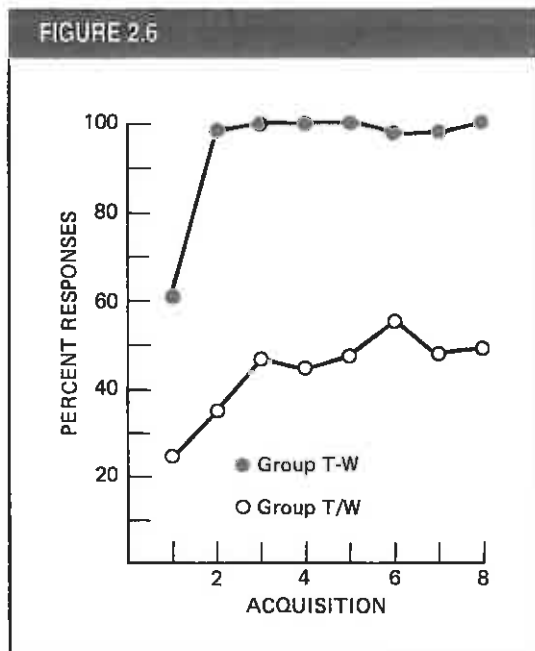
The examples reported earlier give some indication of the methods that can be used to engender a CR. In the introduction to this chapter, however, it was

Acquisition and extinction of conditioned suppression by rats to a 60-second CS that was paired with foot shock (adapted from Hall & Pearce, 1979).



argued that our interest in Pavlovian conditioning lies not so much in the opportunity it offers for changing an animal's behaviour, rather this type of conditioning is important because it allows us to study the way in which animals learn about regularly occurring sequences of stimuli. Although the reported findings suggest this has taken place, there are a number of alternative accounts that must be discounted before we can conclude that a CR is a manifestation of associative learning. This point is made particularly forcefully in an experiment by Sheafor (1975). Two groups of thirsty rabbits received training in which they were presented with a brief tone and a squirt of water into the mouth. For Group T-W the tone preceded the water, whereas for Group T/W the tone and water were separated by an interval of 12 minutes.

The results from this study are presented in Figure 2.6, which shows, for each group, the percentage of trials with the tone that were accompanied by a movement of the jaw. For Group



Percentage of trials on which a jaw movement was recorded in the presence of a tone, as a function of 6-day blocks, with 1 tone presentation each day. The tone was paired with water for Group T-W and unpaired with water for Group T/W (adapted from Sheafor, 1975).

T-W the frequency of this response increased to a substantial and consistent level across the first 48 sessions. As the tone preceded the delivery of water, this jaw movement could be regarded as a CR showing that subjects had detected the relationship between the two stimuli. From this point of view the results from Group T/W are surprising as the tone and water were unpaired and yet substantial jaw movement was also recorded during the tone.

The findings for Group T/W are worrying as they indicate that a response that can be considered to be a CR occurs to the tone, even when it is not paired with water. In these circumstances it would be unwise to regard the existence of jaw movement as evidence that rabbits had learned that the tone was a signal for water, and it becomes necessary to consider when a response can be safely used to indicate such learning.

One solution to this problem is to treat a control group in much the same way as Group T-W, by giving it the same exposure to the tone and water, but these events should not be consistently paired. If pairing the tone and water enables animals to learn that the tone is a signal for water, then such training should produce a stronger CR than for the control group. According to Rescorla (1967), a useful control treatment is to present the CS and US randomly in respect to one another; he referred to this as the truly random control. An alternative method, which was employed for Group T/W, is to ensure that the CS and US are never paired. The considerable level of responding by this group to the tone indicates that it would be unwise to attribute all the jaw movements elicited by this stimulus in Group T-W to associative learning. Nevertheless, the substantially greater level of responding by Group T-W than by Group T/W indicates that the pairing of the tone and water was responsible for at least some of the responding, and this is the necessary evidence to infer that associative learning has taken place.

There is insufficient space to speculate in depth on the reasons for the jaw movements during the tone in Group T/W, but it may be of some interest to consider Sheafor's (1975) explanation. He proposed that the experience of water in the test chambers resulted in rabbits persistently expecting

this US. Normally, this expectancy does not result in a response, but one can be readily triggered if a relatively salient stimulus such as a tone is presented.

Whatever the merits of this account, the point to stress is that a response that resembles a CR does not only occur when a CS and US are paired. Occasionally, such a response may be observed when the CS is presented, either alone or unpaired in respect to the US. In view of this possibility the best way of being certain that a response is a consequence of associative learning is to compare the level of responding produced by a conditioning schedule with that engendered by the appropriate control. Unfortunately the use of control groups is time-consuming, and they are not always employed. Yet, without them, the conclusions that can be drawn from an experiment will be limited.

### Inhibitory conditioning

Excitatory conditioning was said to be of interest because it allows us to study the way in which animals are able to learn that one stimulus signals another. But in an animal's environment, stimuli may conceivably signal that important events will not occur. Such stimuli are of potential importance because they might indicate places that are free from danger, or regions where food and water are not found. If Pavlovian conditioning allows animals to learn that one stimulus signals another, then we might also expect the appropriate training will allow them to learn the opposite—that one stimulus indicates another will not occur. Inhibitory conditioning refers to any method of training in which a stimulus is used specifically to signal the omission of a US and, as the next experiment shows, animals are quite capable of learning about the significance of such a stimulus.

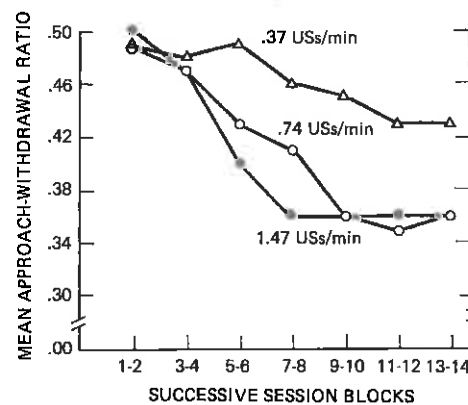
Hearst and Franklin (1977) placed pigeons into a chamber containing a food hopper and two response keys. The keys were illuminated one at a time for 20 seconds in a random sequence, with an interval averaging 80 seconds between successive illuminations. During this interval food was occasionally delivered to the hopper, but food was never available when a key was lit. The position of the subject in the chamber was continuously

monitored throughout this training. At first, the pigeons were indifferent to the illuminated keys, but as training progressed they displayed a marked tendency to move away from a key whenever it was illuminated. This finding suggests that pigeons are capable of learning that stimuli signal the omission of food and that they may withdraw from such stimuli. One technique, therefore, for inhibitory conditioning is to ensure that the US is delivered in the absence but not the presence of the CS.

There were a number of groups in this study that differed in the frequency with which food was delivered during the inter-trial interval. When this frequency was relatively high, the movement away from the lit key was stronger than when food delivery was infrequent. This effect can be seen in Figure 2.7, which shows changes in a measure called an approach-withdrawal ratio across sessions for the groups. A ratio of 0.50 indicates that birds were unaffected by a lit key, whereas a ratio of 0.00 indicates a very strong movement away from this stimulus.

Needless to say the study of inhibitory conditioning did not start with the experiment by Hearst and Franklin (1977). Long before their

FIGURE 2.7



Mean approach-withdrawal ratio recorded in the presence of a 10-second key-light for groups of pigeons that received food at the rate of 0.33, 0.74, or 1.48 presentations per minute in the absence but not the presence of this stimulus (adapted from Hearst & Franklin, 1977).

study, Pavlov (1927) had devised an alternative method to study the effects of this type of training. An example of Pavlov's pioneering technique is provided by Zimmer-Hart and Rescorla (1974). In the first stage of the experiment a tone signalled shock for conditioned suppression training. Trials in which the tone was paired with shock were then intermixed among trials in which it was accompanied by a light and not followed by shock. Initially, the magnitude of conditioned suppression during the compound was much the same as that during the tone (see Figure 2.8), but as training progressed, the presence of the light on compound trials counteracted the suppressive effects of the tone. This pattern of responding suggests animals learned that the light signalled the omission of shock and that this opposed the properties of the tone.

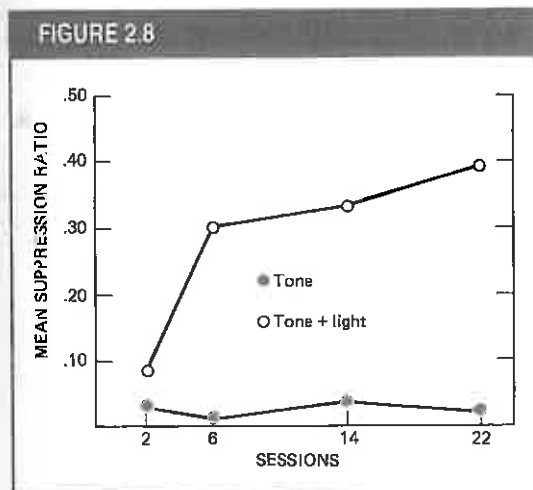
### The detection of conditioned inhibition

A problem that occurs in many studies of conditioned inhibition is that it is not immediately apparent that animals have learned anything about the conditioned inhibitor—that is, the stimulus that signals the omission of the US. This is because conditioned inhibitors rarely elicit a CR on their

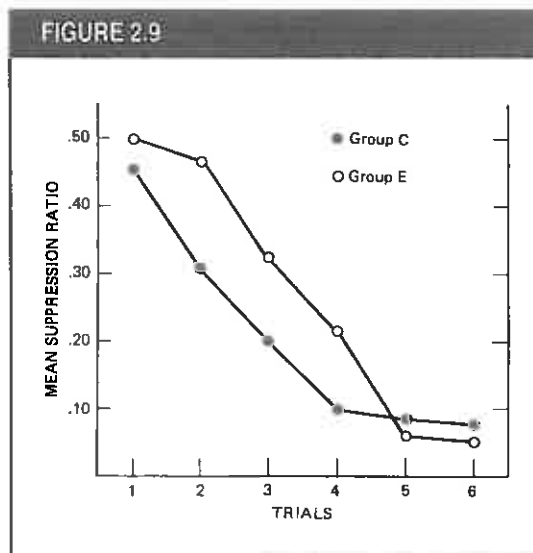
own. The study by Hearst and Franklin (1977) is unusual in this respect because their subjects moved away from the key light, but frequently a conditioned inhibitor by itself has no effect at all on behaviour. To return to the study by Zimmer-Hart and Rescorla (1974), had they presented the light alone rather than in compound with the tone, it would have had very little influence on the rate of lever pressing. How then can we be certain that animals have learned anything about this stimulus? One answer to this question, at least for the Zimmer-Hart and Rescorla (1974) study, would be to point to its effects on the compound trials. But on these trials it is possible that the subjects learned nothing about the light itself; they may merely have learned that the configuration of the light and tone together was followed by nothing. In order to refute this explanation, and to show that a conditioned inhibitor can have properties of its own, two techniques have been developed to reveal the existence of conditioned inhibition: the summation and the retardation test (Rescorla, 1969; Williams, Overmier, & LoLordo, 1992).

*The retardation test.* This test involves pairing the conditioned inhibitor directly with the US. If the initial inhibitory conditioning has been successful, then it should disrupt this excitatory conditioning. A formal explanation of this effect is elaborated in Chapter 3, but for the moment it should not be too surprising.

A demonstration of a successful retardation test is provided by Pearce, Nicholas, and Dickinson (1982). After receiving training similar to that employed by Zimmer-Hart and Rescorla (1974), Group E was given conditioned suppression training in which the inhibitory CS was paired with shock. Group C also received these pairings but without any prior training. The course of excitatory conditioning with the stimulus is depicted in Figure 2.9. Evidently the retardation test was successful because conditioning progressed more slowly for Group E than Group C. One important point to note is that on the first test trial the CS had no influence at all on responding in Group E. On this basis there would be little reason for believing that it had acquired any special properties as a result of the



Mean suppression ratios for rats given excitatory conditioning with a tone intermixed among trials with a light-tone compound followed by nothing (adapted from Zimmer-Hart & Rescorla, 1974).



Acquisition of conditioned suppression to a CS that was novel (Group C) or one that had previously signalled the omission of shock (Group E) (adapted from Pearce et al., 1982).

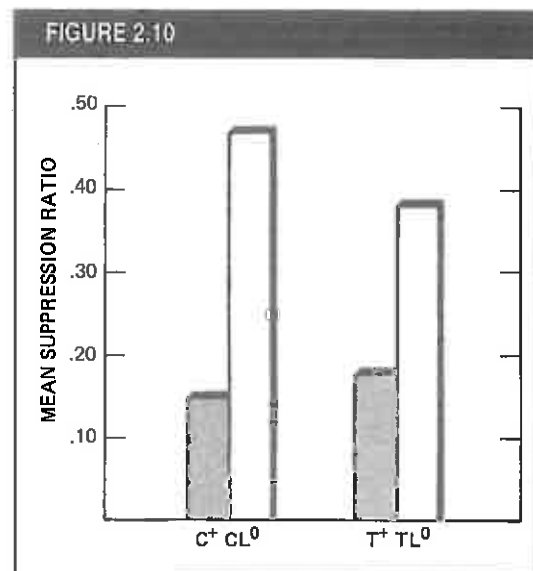
prior training. This emphasises the need for special tests to reveal the effects of inhibitory conditioning.

*The summation test.* The experiment by Zimmer-Hart and Rescorla (1974) revealed that the light counteracted the CR elicited by the tone. This effect was attributed to the stimulus serving as a signal for the omission of the US. If this is correct, then this property of a conditioned inhibitor should be evident whenever it is accompanied by a CS that has been paired with the US in question. A demonstration of this transfer can be found in another conditioned suppression study by Pearce et al. (1982).

Rats were first trained with three types of trial: a tone paired with shock, a clicker paired with the same shock, and a clicker-light compound followed by nothing. Eventually a strong CR was observed in the presence of the tone and the clicker, but not during the clicker-light compound. In order to test whether the influence of the light on the clicker could transfer to the tone, a single test session was administered. Trials in which the tone

was presented alone were intermixed among trials with a light-tone compound. The results in the right-hand pair of histograms of Figure 2.10 show that the strength of the CR, as indexed by the suppression ratio, was substantially greater to the tone than to the compound. For purposes of comparison, the left-hand pair of histograms show the difference in responding to the clicker and the clicker-light compound for the final training session. Evidently the influence of the light transferred very well from the clicker to the tone, and this constitutes a successful summation test for conditioned inhibition.

For a variety of reasons Rescorla (1969) has argued that the ideal method for determining whether a stimulus is a conditioned inhibitor is to conduct both the retardation and the summation tests. If the stimulus passes both of these tests, then it can be concluded with some confidence that it is indeed a conditioned inhibitor.



Mean suppression ratios on the final session of training for a group of rats that had received clicker-shock trials (C<sup>+</sup>) intermixed among trials in which a clicker-light compound was followed by nothing (CL<sup>0</sup>, left-hand pair of histograms), and on a test session when they were given a tone that had previously signalled shock (T<sup>+</sup>), and a compound composed of the tone and the light (TL<sup>0</sup>, right-hand pair of histograms) (adapted from Pearce et al., 1982).

## THE NATURE OF ASSOCIATIVE LEARNING

Both excitatory and inhibitory conditioning can result in a relatively permanent change in the way an animal reacts to an initially neutral stimulus. In order to be effective, therefore, these procedures must produce an equally permanent change within the animal. The purpose of this section is to elucidate the nature of this change. Few would deny that successful conditioning depends on modifications that take place within the nervous system. In the first part of this section we consider briefly what is known about the physiological processes that underpin associative learning. In fact, rather little is known about these processes and a number of researchers have found it more useful to concentrate on identifying the knowledge that is acquired during the course of Pavlovian conditioning. The findings that have resulted from pursuing this line of enquiry are reviewed in the remainder of this section.

### A neural model of excitatory learning

It may come as something of a surprise to discover that some of the more important advances in our understanding of the physiological basis of learning have derived from research with the rather unattractive animal shown in Figure 2.11. The figure shows two views of the large marine snail, *Aplysia californica* (the head is at the right-hand end). *Aplysia* live on seaweed, they weigh as much

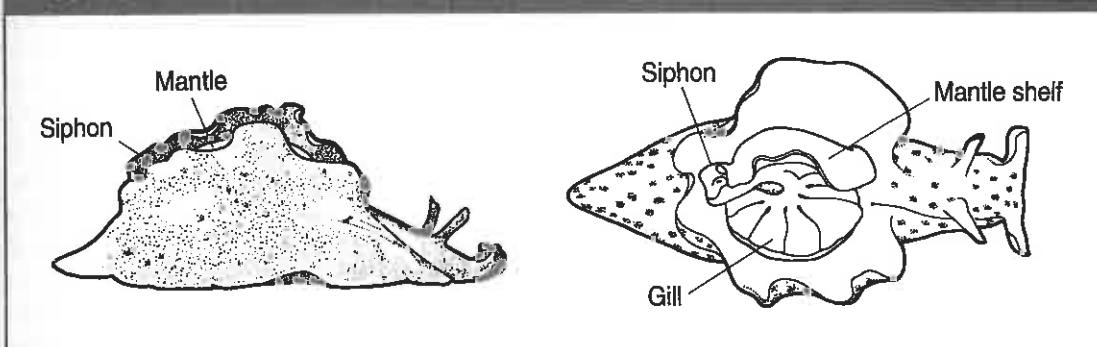
as 7 kilograms, and they can grow to about 1 metre in length.

In case the reader should wonder why anyone would want to study conditioning in this creature, the answer lies in part in the structure of its nervous system. This contains a rather small number (20,000) of relatively large (1 millimetre in diameter) neurons, which makes it easy to identify individual neurons, as well as neural pathways. These properties have made it possible to understand the changes that take place in the nervous system of *Aplysia* during Pavlovian conditioning.

If a stimulus is applied to the siphon, or the mantle shelf, of an *Aplysia* it will withdraw its respiratory organ, the gill (Carew, Pinsker, & Kandel, 1972). Of present interest is the finding that the strength of the withdrawal reflex is enhanced if stimulation of either the siphon or the mantle shelf is followed by an electric shock to the tail. For example, Carew, Hawkins, and Kandel (1983) presented a discrimination in which mild stimulation of the siphon of some animals, or the gills of others, was followed immediately by a tail shock for 1 second. After 2.5 minutes, the other region was then stimulated but on this trial shock was not presented. For the sake of convenience, stimulation of the region that signalled shock will be referred to as CS+, whereas stimulation of the region that did not signal shock will be referred to as CS-.

The histograms in Figure 2.12 show the duration of gill withdrawal on a test trial with each

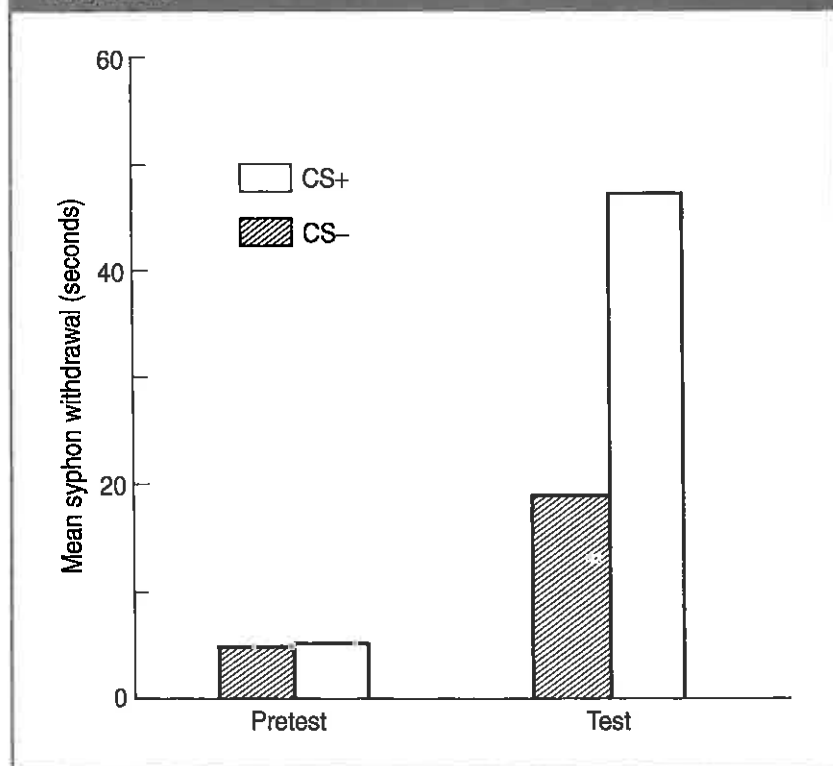
FIGURE 2.11



A view of *Aplysia californica* from the side (left-hand sketch) and from above (right-hand sketch).

Mean duration of siphon withdrawal by *Aplysia* to a stimulus that was either paired with shock (CS+) or presented by itself (CS-) on test trials that were conducted before and after conditioning (adapted from Macphail, 1993).

FIGURE 2.12



CS prior to conditioning and on a test trial after conditioning. Shock was not presented on these test trials. At first, both CS+ and CS- elicited gill withdrawal for about 5 seconds, but at the end of conditioning this response was considerably stronger in the presence of CS+. The slight increase in responding that occurred to CS- indicates that even the unpaired experience of this stimulus and the tail shock was sufficient to enhance the strength of the response elicited by CS-. However, the fact that the strength of responding to CS+ was very much greater than to CS- demonstrates the importance of the paired relationship between CS+ and the tail shock. In other words, the stronger responding to CS+ than to CS- provides a convincing demonstration of successful Pavlovian conditioning with *Aplysia*. In one respect, this demonstration of Pavlovian conditioning is unusual because it shows a strengthening of a response that was already elicited by the CS. This type of conditioning is referred to as *alpha* conditioning, which can be contrasted with the

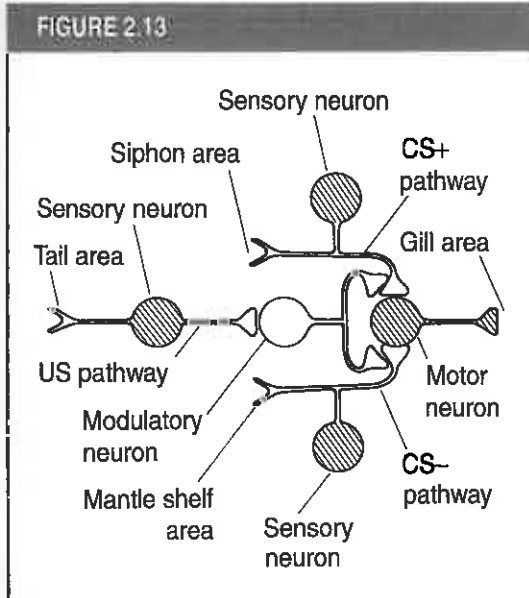
findings from many other studies where at least a component of the CR bears no resemblance to the responses initially elicited by the CS.

A sketch of one of the neural pathways that are involved in the conditioning that has just been described is shown in Figure 2.13 (Kandel & Hawkins, 1992). The two sensory neurons can be excited by stimulating the siphon (upper neuron) or the mantle shelf (lower neuron). These neurons make synaptic contact with a motor neuron that is responsible for gill withdrawal. Thus in normal circumstances, stimulating the siphon area will excite a sensory neuron that will then excite the motor neuron and cause the gill to withdraw. The figure also shows a third sensory neuron that can be excited by a shock to the tail. This neuron is in synaptic contact with a modulatory interneuron that in turn makes contact with synapses of the other sensory neurons. Needless to say, this sketch is a gross oversimplification of the actual circuitry as each neuron is in contact with many other neurons.

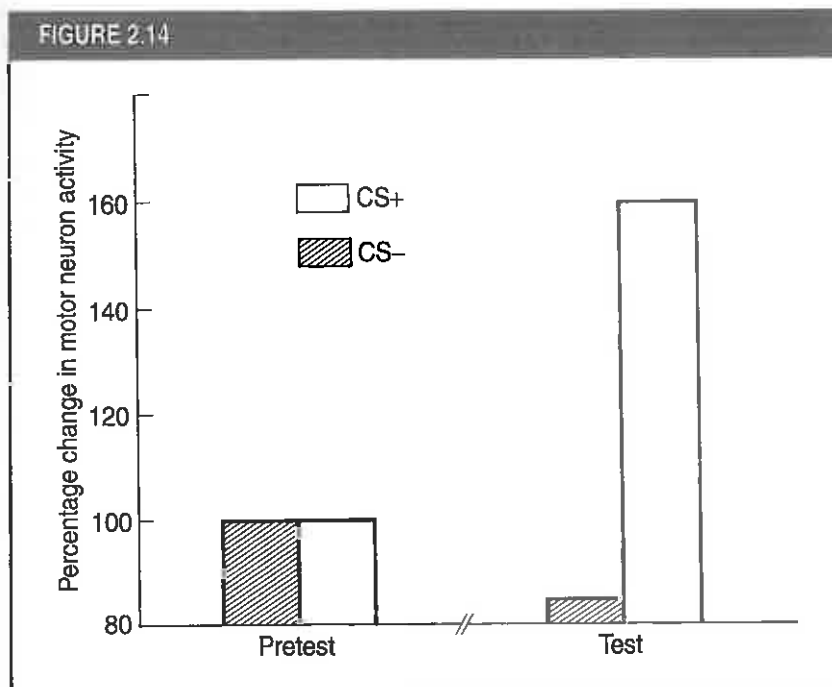
In order to identify the changes that take place in this circuit during conditioning, Hawkins et al. (1983) capitalised on the large size of the neurons, and placed stimulating electrodes in a sensory

neuron for the siphon area and for the mantle shelf. Stimulation of a sensory neuron for the siphon (CS+) was followed immediately by a tail shock, whereas stimulation of a sensory neuron for the mantle shelf (CS-) was never followed by shock. In addition, a recording electrode was placed in a motor neuron that was in contact with the two selected sensory neurons. The level of activity in the motor neuron was recorded after CS+ and CS- on a pretest trial, that was conducted prior to conditioning, and on a test trial that was conducted after five conditioning trials with each stimulus. The results from the tests, expressed as a percentage of the activity recorded on the pretest trials are shown in Figure 2.14. The figure makes it clear that conditioning enabled CS+ to increase considerably the level of electrical activity in the motor neuron, whereas CS- had little effect on the activity in this neuron.

In essence, this experiment by Hawkins et al. (1983) demonstrates that when the stimulation of one sensory neuron is followed a short time later by a tail shock, then its ability to excite the motor neuron is increased. Kandel and Hawkins (1992) have argued that this enhanced influence of the sensory neuron is due to biochemical changes that



A simplified diagram of the neural pathways that are involved in conditioning with *Aplysia*.



Mean percentage of change in motor neuron activity in *Aplysia* to stimulation of one sensory neuron that was paired with tail shock (CS+) and to stimulation of another sensory neuron that was never followed by shock (CS-), on test trials that were conducted before and after conditioning (adapted from Macphail, 1993).

take place at the synapse between the sensory and motor neuron. The catalyst for these changes is provided by the interneuron. Whenever shock is administered to the tail, the interneuron releases serotonin at its synapses with sensory neurons. If a sensory neuron should fire at much the same time as this release of serotonin, then a relatively permanent change takes place within the sensory neuron that enables it to release a greater amount of neurotransmitter than would normally occur. Subsequent stimulation of the sensory neuron will then release this abnormally large amount of neurotransmitter and result in a strong response in the motor neuron.

Thus the basis of associative learning appears to be an enhancement of the ease with which one neuron can excite another. There is no evidence to suggest that this learning depends on the growth of new neural connections, or synapses. Instead, learning simply depends on a change in the effectiveness of existing connections. We shall see over the course of the next few chapters that this finding is remarkably in keeping with current theoretical views about learning.

Stimulus generalisation can also be explained with the sort of circuit that Kandel has identified. Instead of exciting a single sensory neuron, a CS is likely to excite a collection of sensory neurons each of which could acquire the capacity to excite a motor neuron. The strength of the response to a CS would then be determined by the number of motor neurons it excites. The presentation of a slightly different CS will excite some, but not all, of the sensory neurons excited by the original CS. The new CS will thus elicit a CR, and provide evidence of stimulus generalisation; but the strength of the CR will be weaker than to the original CS. If it is assumed that the degree of similarity between two stimuli determines the number of sensory neurons that they both excite, then this account correctly predicts that the amount of stimulus generalisation will be determined by the similarity of the test and training stimuli.

### A memory model for associative learning

Because the nervous system of vertebrates is very much more complex than of invertebrates, we do not yet know if the physiological changes that have

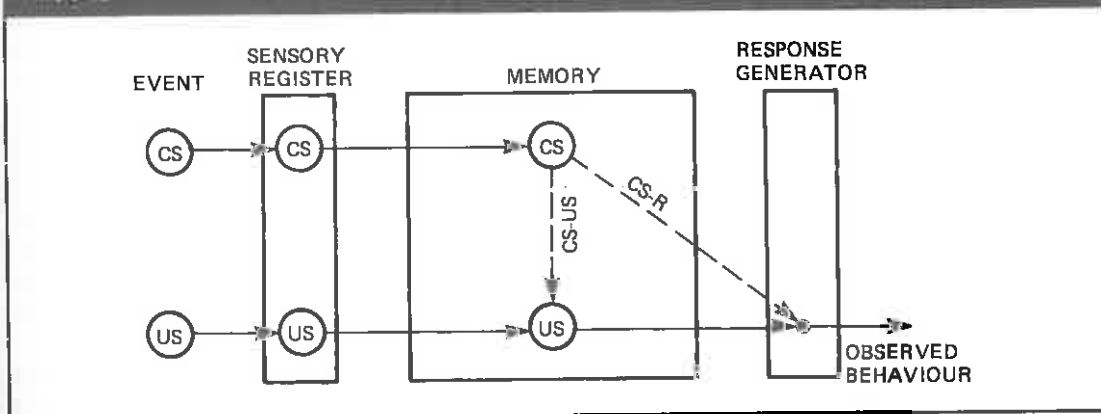
just been described also underlie associative learning in this group of animals. As a consequence, theorists with an interest in the changes responsible for learning in vertebrates tend not to talk in terms of physiological processes. Instead, they prefer to work within the framework provided by an information-processing model of conditioning. An example of such a model is shown in Figure 2.15.

Stimuli such as a CS or a US can be detected by a sensory register that excites a memory or representation of these events in a memory system. The US will in addition excite a centre in a system concerned with response generation and thus elicit an unconditioned response. As a result of the repeated pairing of a CS and a US, there are two possible changes that can take place within this model. On the one hand, a CS–R connection might develop, so that whenever the CS is presented it will directly excite the US-response centre and lead to a response that mimics the one elicited by the US. In other words, this conceptualisation is based on the assumption that Pavlovian conditioning results in the growth of S–R connections, or associations. These proposals are very much in keeping with the way in which the S–R theorists mentioned in Chapter 1 conceptualised the conditioning process. They are also consistent with the findings by Kandel with *Aplysia*. The sensory and motor neurons in these animals can be said to provide a rudimentary counterpart to the stimulus and response centres shown in Figure 2.15.

Alternatively, Pavlovian conditioning could result in the growth of a connection between the CS and US representations. Subsequent presentations of the CS will then excite the representation of the US, and this in turn will excite a response. Although the findings with *Aplysia* do not support this possibility, experiments with vertebrates lend it considerable support.

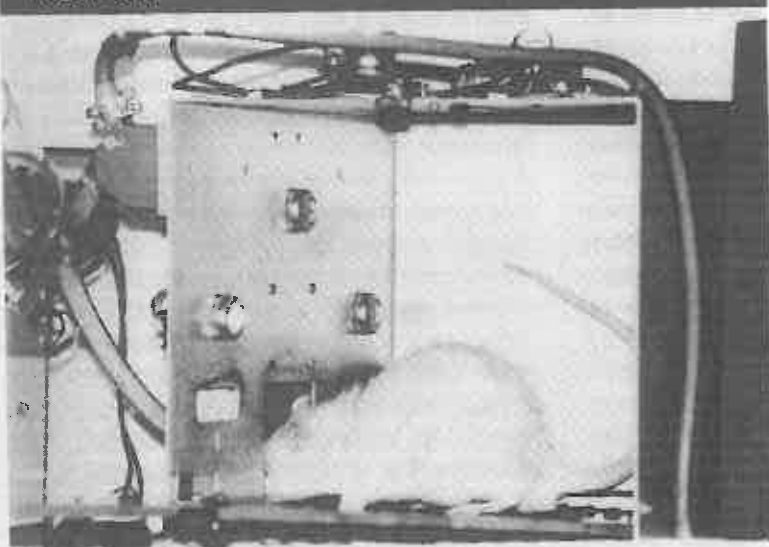
The idea that the CS retrieves a memory of the US, which is then responsible for generating the CR, can be tested in a relatively straightforward manner. If the memory of the US can somehow be altered once conditioning has been completed, then this should result in a change in the animal's behaviour when the CS is next presented. That is, the CS should elicit a response that is appropriate to the revised memory of the US. A good example

FIGURE 2.15



Two possible accounts of what is learned during Pavlovian conditioning; the solid arrows are permanent connections, the dashed arrows are a consequence of conditioning. A CS and US can be detected by the sensory register, which leads to representations of these events being activated in memory. Whenever the US representation is activated it will produce a response by activating a centre in the system concerned with response generation. According to one account, conditioning will result in the growth of a CS-US association so that the CR will be an indirect consequence of the CS activating the US representation. The alternative S-R account assumes that conditioning strengthens a CS-R association and thus allows the CS to excite the CR directly.

FIGURE 2.16



A typical CR of magazine activity by a rat during a CS that signals the delivery of food (from Kaye, 1983).

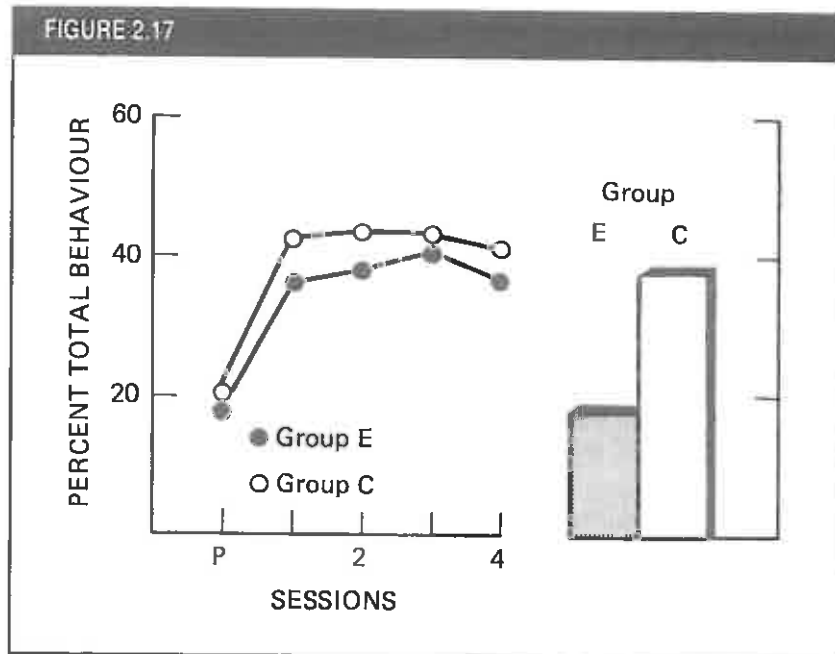
of an experiment that is based on this rationale is provided by Holland and Straub (1979).

Two groups of hungry rats were occasionally presented with a 10-second noise that was followed by the delivery of food in a conditioning chamber. After a number of sessions of this training the noise resulted in subjects moving towards the magazine

where food was delivered (see Figure 2.16 and the left-hand side of Figure 2.17). On each of the next four days, in which noise was not presented, rats in Group E (experimental) were allowed unrestricted access to food pellets for 5 minutes in their home cages before being injected with lithium chloride to condition an aversion to the pellets. This

FIGURE 2.17

The amount of magazine activity by two groups of rats during a noise CS on a pre-exposure session (P), when it was presented alone, and on four conditioning sessions when it signalled food (left-hand side). The histograms show the amount of magazine activity during the noise for a test session after the food pellets had been paired with illness for Group E, but not Group C (adapted from Holland & Straub, 1979).



conditioning was successful because on the fourth session subjects consumed very few of the pellets. The treatment for Group C (control) was similar except that the lithium chloride injections and free access to food were presented on separate days so that the liking for the pellets was unaffected. Finally, both groups were returned to the conditioning chambers where the noise was again presented but this time without food. As revealed in the right-hand side of Figure 2.17, the tendency of Group E to approach the magazine on the test session was considerably less than for Group C.

These results are entirely consistent with the proposal that Pavlovian conditioning results in the growth of CS-US associations. On the test session, the noise for Group E will activate a representation of food that has been rendered unattractive by the taste-aversion training. The activation of this representation will then be unlikely to excite magazine activity, because there is little point in moving to a magazine for food that is undesirable. For Group C, on the other hand, the representation of food should be just as effective as on the final session of appetitive conditioning, and these rats should be very willing to go to the magazine during the noise.

We should also consider the implications of these results for an S-R analysis of conditioning. According to this theory, the initial training will result in an association being formed between the tone and the response of approaching food, so that whenever the CS was presented it will automatically make the animal move towards the magazine. An important feature of S-R theory is that the responses elicited by a CS can be altered only by pairing the CS with an event that elicits a different response. Because the CS was not presented in the second stage of the experiment, there was no opportunity for its influence to be altered in one group, but not the other, and both groups should thus have responded similarly in the test stage. The clear difference between the results of the two groups in the final stage of the experiment is thus very difficult for S-R theory to explain. There was, however, some responding on the test trials by Group E, which is difficult to explain if Pavlovian conditioning results only in the formation of CS-US associations. Strictly speaking, if the taste-aversion training was completely effective, then the rats should make no effort at all to approach the magazine in the test stage. Perhaps, therefore, the responses on the test

trials in Group E were a consequence of S-R associations that were formed during the initial training. If this is correct, then we must conclude that the training by Holland and Straub (1979) resulted in both S-R and CS-US learning. Further evidence is presented shortly that shows that Pavlovian conditioning will, at least on occasion, permit the growth of S-R associations. But first, we shall examine two further studies that demonstrate that this training can also foster CS-US associations.

Table 2.1 summarises the design of an ingenious experiment by Holland (1990). Hungry rats in a conditioning chamber occasionally heard either a tone or white noise for 10 seconds. The tone signalled the delivery of sucrose solution flavoured with wintergreen, and the noise signalled a similar solution flavoured with peppermint. As a result of this training, Holland (1990) hoped that the rats would anticipate wintergreen-flavoured sucrose whenever they heard the tone, and peppermint-flavoured sucrose whenever they heard the noise. The rats were then allowed to drink sucrose flavoured with wintergreen for 5 minutes, in the absence of any auditory stimulus, before being injected with the poison lithium chloride. The purpose of this treatment was to condition an aversion to the flavour of wintergreen. Finally, the animals were allowed to consume plain sucrose solution in the presence of each auditory stimulus. By carefully observing the animals, Holland discovered that they reacted very differently in the presence of the two stimuli. During the noise the rats showed a typical ingestive reaction, comprising rhythmic mouth movements, tongue protrusions, and paw licking. On the other hand, in the presence of the tone they showed a marked aversive reaction, which consisted of gaping, chin rubbing, head shaking, and flailing of the

forelimbs. Holland argued that this second response was due the tone retrieving a memory of the wintergreen-flavoured sucrose. The rats then reacted as if this flavour, which had been made aversive by the second stage of training, were actually present. Holland (1990) cites a number of additional findings that lend considerable support to this conclusion.

These last results imply that activating a memory of a stimulus is in many respects equivalent to presenting the stimulus itself. If this is correct, then it should be possible to conduct conditioning with an activated memory of a stimulus in much the same way as it is possible to conduct conditioning with that stimulus. A remarkable experiment by Holland (1981) provides striking support for this prediction. Two groups of rats were first placed into a conditioning chamber where every few minutes a tone was presented for 10 seconds and then followed immediately by a distinctively flavoured food pellet. In the next stage of the experiment both groups again received the tone but this time it was not followed by food. For the experimental group the tone was followed by an injection of lithium chloride, whereas for the control group these two events were presented in an unpaired fashion. Holland argued that during the second stage the tone should activate a memory of flavoured food with which it had been paired and, for the experimental group, once activated this memory would then become associated with the poison. A test of this proposal was conducted in a final session in which both groups had free access to the food. In keeping with Holland's predictions, the experimental rats revealed an acquired aversion to the food by eating rather little of it, relative to the controls.

TABLE 2.1

Summary of the Design of an Experiment by Holland (1990).

| <i>Stage 1</i>               | <i>Stage 2</i>               | <i>Test</i>           |
|------------------------------|------------------------------|-----------------------|
| Tone → Sucrose + Wintergreen | Sucrose + Wintergreen → LiCL | Tone + Plain Sucrose  |
| Noise → Sucrose + Peppermint |                              | Noise + Plain Sucrose |

## STIMULUS-STIMULUS LEARNING

The results in the previous section show that, at least for vertebrates, Pavlovian conditioning may result in the growth of a connection between internal representations of the CS and US. There is no good reason, however, for believing that associative learning will be confined to those occasions when a US is presented. The following examples show that associations can develop between two stimuli, even when neither of them has any unconditioned properties.

### Serial conditioning

In serial conditioning a sequence of stimuli precedes the US—for example, a tone might be followed by a light, which would be followed by food. Despite being rather distant from the US, the initial element of the sequence will often elicit a CR, although it may be weaker than the response observed in the presence of the element that is closer to the US. An interesting feature of serial conditioning is revealed in a study by Holland and Ross (1981), who trained rats with the sequence light–tone–food. The normal conditioned response to a light that signals food is rearing or magazine approach; for a tone it is either head jerking or magazine approach. After a number of sessions of serial conditioning it was found that during the light there was little magazine activity but there was a considerable amount of head jerking. This led Holland and Ross (1981) to suggest that during serial conditioning the presence of the first element causes animals to anticipate the second one and to respond as if it were actually present.

### Sensory preconditioning

A rather different demonstration for the development of stimulus–stimulus associations is provided by sensory preconditioning. In an experiment by Rizley and Rescorla (1972), rats first received the sequence of a light followed by a tone for a number of trials. The tone was then paired with shock and, finally, the light was found to elicit a substantial fear CR when it was presented for testing. The generally accepted explanation for this finding is that during the first stage subjects

acquired a light–tone association, and in the second stage a tone–shock association. When the light was then presented alone it would activate a memory of the tone, which, in turn, would activate a memory of the shock and lead to an aversive CR.

### Second-order conditioning

The final method that shows evidence of associations being formed between two stimuli is known as second-order, or higher-order conditioning. We shall see, however, that depending on certain details this training can result in different outcomes.

Two types of conditioning trial are administered for second-order conditioning. Initially, first-order conditioning is conducted in which a neutral stimulus, CS1, is paired with a US until a stable CR is recorded. At this point additional trials are introduced in which a new stimulus, CS2, precedes CS1, but the US is omitted. With sufficient training a CR can be observed during CS2 even though this stimulus itself is never paired with the US.

Pavlov (1927) was the first to report this effect, although a relatively recent example will be described (Rashotte, Griffin, & Sisk, 1977). Pigeons first received autoshaping in which the illumination of a key by white light for 6 seconds signalled food; additional trials were then introduced in which the key was illuminated by blue and then white light, for 6 seconds of each colour. Food was not presented on these second-order trials. Figure 2.18 shows, for the second-order conditioning stage, the percentage of trials in any session on which at least one peck was directed towards these stimuli. The success of second-order conditioning is revealed by the increase in responding to CS2.

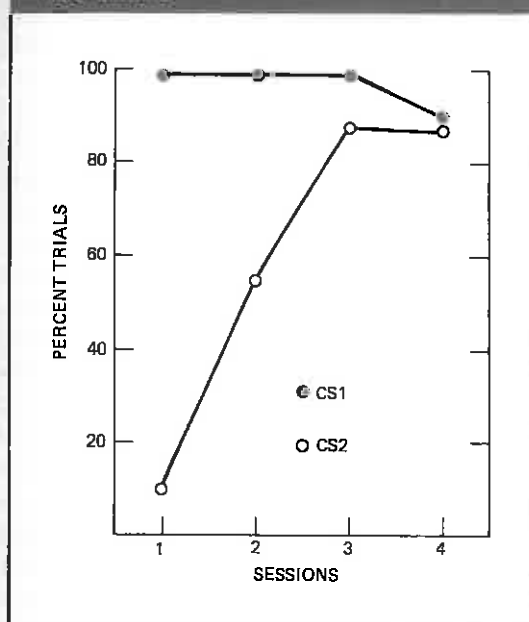
If second-order conditioning results in the formation of the same sort of associations as first-order conditioning, then pairing a second-order CS (CS2), with one that has already been paired with a US (CS1) should foster a CS2–CS1 association. As a consequence, the occurrence of CS2 should activate a representation of CS1, which should then activate a representation of the US and elicit a CR. There is certainly some evidence to support this proposal, but there is also some that contradicts it.

Evidence that favours this analysis can be found in a further stage of the study by Rashotte et al. (1977). An outline of the various stages of the experiment can be found in the upper half of Table 2.2. After second-order conditioning, Rashotte et al. (1977) gave Group E a series of extinction trials in which the white key-light (CS1) was presented

alone. This training was intended to abolish its association with food, and it was soon found that pecking at the white key declined to a very low level. When the blue key-light (CS2) was again shown for the final test trials, it should still activate a representation of the white key, by virtue of the prior second-order conditioning. However, activation of this latter representation should no longer excite a memory of food, and pecking at blue should not take place. For Group C, which did not receive the extinction training with white, the presence of both an effective blue-white and a white-food association should allow blue to activate a representation of the food and engender a high rate of responding. In keeping with this analysis it was found on the test session that Group C responded significantly more rapidly than Group E in the presence of CS2.

Evidence to the contrary, that second-order conditioning does not enable CS2 to retrieve information about CS1, is provided by Rizley and Rescorla (1972). The design of their experiment is very similar to that of Rashotte et al. (1977) and is presented in the lower half of Table 2.2. The methods differed principally in that Rizley and Rescorla (1972) used conditioned suppression. Two groups of rats received first-order conditioning with a tone signalling shock, and second-order conditioning in which a light was followed by the tone and no shock. Group E was then given extinction training with the tone. Although this treatment abolished the CR to the tone, the subsequent presentation of the

FIGURE 2.18



Number of trials in each second-order conditioning session for which at least one peck was recorded to the previously trained white CS1 and to the second-order blue CS2 (adapted from Rashotte et al., 1977).

TABLE 2.2

Summary of the Stimuli Used in the Stages of the Second-order Conditioning Studies by Rashotte et al.<sup>a</sup> and by Rizley and Rescorla<sup>b</sup>.

|         | <i>First-order conditioning</i> | <i>Second-order conditioning</i> | <i>Extinction</i> | <i>Test</i> |
|---------|---------------------------------|----------------------------------|-------------------|-------------|
| Group E | White → Food                    | Blue → White                     | White             | Blue        |
| Group C | White → Food                    | Blue → White                     | —                 | Blue        |
| Group E | Tone → Shock                    | Light → Tone                     | Tone              | Light       |
| Group C | Tone → Shock                    | Light → Tone                     | —                 | Light       |

<sup>a</sup> Rashotte et al. (1977): upper two rows.  
<sup>b</sup> Rizley and Rescorla (1972): lower two rows.

second-order light CS elicited a very strong CR, which did not differ in magnitude from that performed by Group C. This finding makes it difficult to believe that a light-tone association was formed during second-order conditioning, for if it had been, extinction with the tone should have reduced the CR recorded during the light. Moreover, this outcome is not unique: Holland and Rescorla (1975) have obtained a similar effect with rats using appetitive conditioning.

One explanation for the findings by Rizley and Rescorla (1972) is that second-order conditioning resulted in an S-R association being formed between CS2 and the response elicited by CS1. Thus as a result of the first-order conditioning the tone may have aroused a CR of fear, for want of a better word, which was associated directly with the light. If this account is correct, then manipulations of the tone-shock association should not influence the light-fear association and hence leave unaffected the prior second-order conditioning.

What then determines the nature of the associations that are formed during second-order conditioning? According to Rescorla (1980), one answer to this question is the similarity of CS1 and CS2. When the stimuli are similar, such as the illumination of a key by different colours, then a CS2-CS1 association will be formed. When the stimuli are very different, for example if they are from different modalities, then CS2 will become associated with the response elicited by CS1. Of course, this account is incomplete. It does not explain why stimulus similarity should be so important in determining the outcome of second-order conditioning. And as it stands, it leads to the incorrect expectation that first-order conditioning will only permit S-R associations because the CS and US are so different.

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## THE NATURE OF US REPRESENTATIONS

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### Conditioned excitation

Thus far we have said that the CS is able to activate a memory or representation of the US, but what does this mean as far as animals are concerned? I do not wish to imply for one moment that when the

CS is presented to a rat it has a mental experience of remembering the US in much the same way as we may remember what we ate for our last meal. There are simply no methods that would allow us to determine whether or not animals have this type of mental experience. Holland (1990) favours the proposal that after conditioning, the CS is able to activate some of the perceptual mechanisms that are normally activated by the US. A similar idea has been proposed to account for certain aspects of human memory (e.g. Farah, 1985; Finke, 1980). One implication of this proposal is that whenever a CS is presented it will evoke a sort of hallucination of the US with which it is paired (Konorski, 1967). Whether or not this is true remains to be determined, for the present it is safe to conclude that at least in some circumstances a CS can activate, or retrieve, information about the US. All this means is that once information about the US is activated it can influence the animal's behaviour, and enable further learning about the US even though it is absent.

Given such a conclusion, it then becomes meaningful to enquire about the nature of the information that is activated. According to Konorski (1967), unconditioned stimuli possess two different characteristics—specific and affective. Specific characteristics are those that make the US unique: the place where it is delivered, its duration, intensity, and so on. Affective characteristics, by contrast, are those that the US has in common with other stimuli and reflect its motivational quality. Thus food, water, and an opportunity to mate have the common *appetitive* characteristic that animals will actively search for them. Conversely, electric shock, illness, and loud noise possess the common *aversive* characteristic that animals will do their best to minimise their contact with them. For humans, this distinction can be summarised by saying that appetitive events arouse a state of satisfaction, whereas aversive events arouse an unpleasant state of discomfort or pain.

Konorski (1967) suspected that a CS may be capable of retrieving information about the specific or about the affective attributes of the US, or indeed about both simultaneously. We can return to the study by Holland (1990) for evidence that a CS can

retrieve information about the specific attributes of the US. In that study, he found that pairing wintergreen-flavoured solution with illness affected the responses during a tone that had been paired with the same flavoured solution, but not during a noise that had been paired with a peppermint-flavoured solution. Unless the noise and tone could retrieve specific information about the flavours of the solutions with which they had been paired, they should both have elicited the same responses on the test trials.

For evidence that a CS is capable of retrieving information about the affective characteristics of a US, we must consider the effects of an experimental manipulation known as blocking. In the first stage of an experiment by Kamin (1969) Group E, but not Group C, was given pairings of a noise with shock. For the second stage both groups received a compound composed of the noise and a light that was repeatedly paired with shock. Finally, test trials involving the light by itself were given. On the test trials with the light there was virtually no evidence of a CR in Group E, whereas one of considerable strength was recorded for Group C. For Group E, therefore, the original training with the noise was somehow responsible for preventing, or blocking, learning about the light during compound conditioning.

The reason why blocking occurs will be considered in some detail in the next chapter. For the present, it is important to note that blocking can be disrupted if the US is changed for the second stage of training. Thus Dickinson (1977) has found that blocking does not occur if the US is food in Stage 1 and shock in Stage 2. This type of finding has led to the informal suggestion that blocking will be most effective when the US that is delivered in Stage 2 corresponds to the memory of the US that was presented in Stage 1. But should this correspondence be between the affective or the specific properties of the US? This question is impossible to answer on the basis of the study by Dickinson, because both properties were changed. However, an experiment by Ganesan and Pearce (1988) found blocking was not at all disrupted when the US was changed from water in Stage 1 to food in Stage 2. Such a finding suggests that blocking will be effective, provided that the

general, affective properties of the US remain unchanged throughout the training stages of experiment. In other words, for blocking to have taken place in the study by Ganesan and Pearce (1988), the CS presented in Stage 1 must have become associated with a memory of the nonspecific, appetitive attributes of the water US. For a similar finding see Williams (1994).

A second reason for believing that a CS can activate an affective representation of the US comes from studies showing that conditioning can sometimes be facilitated if the CS has previously been paired with a different US of related affective value. Pearce, Montgomery, and Dickinson (1981), for instance, conducted rabbit eye-blink conditioning in which, for Group E, a brief light signalled shock to the cheek; Group C did not receive this training. Then, in the test phase of the experiment, both groups were conditioned with the light signalling shock to the opposite cheek. Acquisition of an eye-blink CR in these circumstances was considerably more rapid for Group E than Group C, which suggests that the original conditioning with the light resulted in it retrieving information that was not entirely specific to the cheek where the US was applied. The implication of this study, and this is certainly the view advocated by Konorski (1967), is that once an association has been formed between a CS and the affective properties of a US, this facilitates the learning necessary for the occurrence of specific CRs, such as eye-blink, when the US is applied elsewhere.

There are, therefore, good reasons for believing that a CS can retrieve information about either the specific or the affective properties of a US. Unfortunately, rather little is known about the circumstances that promote learning about these different properties, and that determine when information about these properties will be effective. For example, prior to our experiment (Ganesan & Pearce, 1988) we were uncertain as to whether or not blocking would be effective when the US was switched from water to food.

### Conditioned inhibition

It is natural to assume in the case of excitatory conditioning that representations of the CS and US become associated, as these events are paired. But

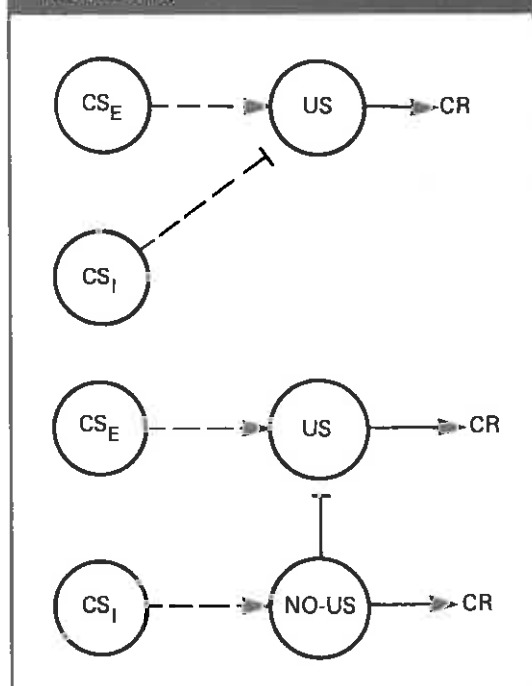
where inhibitory learning is concerned, the event associated with the inhibitory CS is less obvious. After all, this stimulus is not usually followed by any tangible event.

One possibility is that as a result of signalling the omission of a US, the presence of an inhibitory CS makes it more difficult to activate a representation of the US. This point of view has been expressed by Konorski (1948) and Rescorla (1979). Both assume that an excitatory CS is capable of activating a representation of the US with which it is paired. If this excitatory stimulus,  $CS_E$ , should be presented in compound with another stimulus and the US is withheld, an inhibitory link is assumed to be formed between the representation of the latter stimulus,  $CS_I$ , and the US representation excited by  $CS_E$ . This relationship is depicted in the upper half of Figure 2.19. The subsequent presentation of  $CS_I$  will then serve to dampen the US representation that is activated by any excitatory CS with which it is concurrently paired. A consequence of this dampening will be to reduce the strength of the excitatory CR. If  $CS_I$  should be paired with the US in a retardation test, then, although an association will grow between a representation of CS and the US, the existence of the inhibitory link will initially prevent the CS from activating the US representation, and a CR will not be recorded.

A crucial implication of this account is that a conditioned inhibitor should not have any response-eliciting properties of its own. An inhibitory link will serve only to modulate the strength of CRs whenever the US representation is activated. But we have seen that a conditioned inhibitor by itself may influence behaviour. In the Hearst and Franklin (1977) experiment a conditioned inhibitor was shown to elicit withdrawal. Whereas in other studies it has been found that rats will consume relatively large volumes of a favoured solution that has previously signalled the omission of a lithium chloride injection (Batson & Best, 1981; Best, Dunn, Batson, Meachum, & Nash, 1985). Findings such as these suggest the need for an alternative account of what is learned during inhibitory conditioning.

In his more recent theorising, Konorski (1967; see also Pearce & Hall, 1980) proposed that

FIGURE 2.19.



Two possible models of the learning that occurs during inhibitory conditioning. The arrows and stopped lines, respectively, depict excitatory and inhibitory links; the solid lines depict permanent links; the dashed lines depict conditioned links; and the circles denote representations in memory.

inhibitory conditioning permits the growth of a conventional association between the CS and what Konorski (1967) called a no-US representation. The activation of this representation was deemed to have two effects. It can dampen any concurrently excited US representations and thus weaken excitatory CRs, and it may also elicit responses in its own right (see lower half of Figure 2.19). If this account is to be accepted, then it is essential to specify what constitutes a no-US representation.

Superficially, the notion of such a representation might seem strange, but a moment's reflection should reveal what is meant by this term. Being told that something is going to happen and then discovering that it will not can often produce strong emotional reactions. The withdrawal of a promised reward, like a large sum of money, might result in frustration or disappointment, whereas an opposite

reaction of relief or joy might accompany the news that something unpleasant, like a visit to the dentist, is no longer going to happen. Konorski (1967) proposed the no-US representation contained information about these diffuse reactions, and they are the counterpart to the affective representations formed of the US during excitatory conditioning. It is also conceivable that the no-US representation encodes precise information about the omitted US, and this would be equivalent to the specific component of a US representation. In fact there is evidence to support both proposals.

The outcome of a rabbit eye-blink conditioning study indicates the affective nature of a no-US representation (Pearce et al., 1981). Inhibitory conditioning was initially performed in which a light signalled shock to one cheek and a light-clicker compound was followed by nothing. Subsequently, to examine the inhibitory properties of the clicker, a retardation test was conducted in which it signalled shock to either the same or the opposite cheek to that used during training. The test revealed that excitatory conditioning was disrupted to the same extent irrespective of which cheek was shocked. The implication of this finding is that during inhibitory training the clicker was associated with a no-shock representation that was sufficiently general to disrupt conditioning with a US applied to any location. Perhaps, in this instance the information provided by the no-shock representation was simply that shock would not follow the clicker. If it had been more specific, then the activation of this representation would have disrupted conditioning more when the shock was applied to the original, rather than to the opposite, cheek.

An indication that, in certain circumstances, inhibitory conditioning can result in the CS being associated with a specific representation comes from a report by Cotton, Goodall, and Mackintosh (1982). Groups of rats received training in which a tone was paired with a moderately strong shock, and a tone-light compound signalled a weak shock. Thus the light signalled a reduction rather than omission of shock. Different groups were then given a summation test in which the light was paired with a clicker that had previously signalled either the strong shock (Group S), or the weak

shock (Group W). If the initial training resulted in the light retrieving an affective representation signalling, say, relief from an unpleasant event, then its properties should be evident in both groups. In fact it was only in Group S that the light passed the summation test, which implies that it retrieved relatively specific information about the strong shock that was omitted and this restricted the circumstances in which it could function as a conditioned inhibitor.

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### THE PERFORMANCE OF THE CONDITIONED RESPONSE

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Thus far we have been concerned principally with identifying the kind of information that animals acquire during the course of Pavlovian conditioning. We now need to understand how this information is able to influence an animal's behaviour. The discussion has already hinted at the way in which a simple CS-US association can control behaviour. The presentation of a CS is believed to excite a representation of the US, which in turn will excite a response centre that will then elicit a CR. On this basis, therefore, the CS might be expected to elicit a response that is very similar to the one elicited by the US. That is, the CS might be thought to serve as a substitute for the US.

There is certainly some evidence to support this stimulus-substitution account for the nature of the Pavlovian CR. Hungry pigeons direct eating responses towards a response key that signals the imminent delivery of food, whereas a thirsty pigeon will make drinking responses to the same key if it signals the delivery of water (Moore, 1973). But, as we shall see, the way in which the US determines the nature of the CR is more complex than has just been implied. We shall also see that the CS can have an influence on the responses that are performed in its presence.

### Influence of the US on the CR

*Consummatory CRs.* Konorski (1967) believed that whenever a CS retrieved information about the specific properties of the US, then a consummatory

CR would be performed. Normally, such a response was expected to mimic at least a component of the response to the US. Thus in the study by Moore (1973) that has just been mentioned, the different responses of pigeons to an illuminated key that signalled either food or water provide two clear examples of consummatory CRs. Other examples can be found in the salivation by dogs to a CS that is paired with either food or the delivery of a weak solution of acid into the mouth (Pavlov, 1927). And one further example can be found in experiments where a stimulus that is followed by a mild electric shock to the cheek will cause the eye to blink in a manner similar to that seen when the shock itself is presented (Gormezano, 1965).

*Preparatory CRs.* Konorski (1967) further proposed that when a CS retrieved information about the affective properties of a US, it would elicit a preparatory CR. In contrast to consummatory CRs, a preparatory CR was assumed not to be intimately tied to the responses elicited by the US. An appetitive preparatory CR might consist of a general increase in activity, whereas for aversive conditioning it might consist of immobility. This is not to say that these CRs are without direction. Konorski (1967) argued that for appetitive conditioning the preparatory CR will consist of approaching the CS, and that the equivalent response for aversive conditioning is more likely to be withdrawal. Clear support for both claims can be found in a series of experiments by Karpicke, Christoph, Peterson, and Hearst (1977).

Rats were trained to press a lever for food in a chamber containing two light bulbs, one near the lever and one further away. While subjects were pressing the lever, the bulbs were occasionally illuminated, and this signalled the imminent delivery of either food (Experiment 1) or electric shock (Experiment 5). There was a decline in instrumental responding when the CS was presented in either study, but the magnitude of this effect was dependent on the position of the illuminated bulb. When the bulb nearer to the lever signalled food, there was less disruption of lever pressing than when the more distant bulb signalled this US. Presumably a preparatory CR of approach-

ing an appetitive CS is likely to be most disruptive when the CS is far from the lever. In contrast, it was the illumination of the near light bulb that produced the greater reduction in lever pressing during aversive conditioning. In this instance, a tendency to withdraw from a light signalling shock will interfere most with instrumental responding when it is close to the lever.

*Compensatory CRs.* Subsequent developments have indicated that Konorski's (1967) account of preparatory conditioning is too simple. Solomon and Corbit (1974) have suggested that the delivery of a US will immediately arouse what they refer to as an *a*-process. This can be regarded as an emotional state directly related to the motivational quality of the US. An electric shock may excite an *a*-process that involves the physiological changes associated with fear. Thus far the account is not too dissimilar to Konorski's (1967) views, with the *a*-process corresponding to the physiological changes necessary for a preparatory CR. Where the accounts differ is in Solomon and Corbit's (1974) proposal that a US also excites, but rather slowly, a *b*-process that opposes the *a*-process and diminishes reactivity to the US. This leads to the possibility that when a CS and US are paired, the CS may excite either of the *a*- or the *b*-processes aroused by the US. Before exploring the implications of this proposal, we must first consider the evidence for the existence of these opposing processes and examine the way they interact.

Church, LoLordo, Overmier, Solomon, and Turner (1966) recorded the change in heart rate in dogs produced by a series of electric shocks. In keeping with the opponent-process analysis, the shocks were found to have two effects. Whenever the shock was applied, there was an immediate *a*-process reaction of an increase in heart rate, but as soon as the shock ceased the effects of the opponent *b*-process became evident as a temporary reduction in heart rate. With repeated exposure to shock there was a change in this pattern. Shock onset was accompanied by only a modest increase in heart rate, and its offset led to a pronounced decline in the rate of this response. Moreover, it is not only heart rate that is influenced by the repeated

exposure to the shock: Dogs also seem to be much less distressed by this event after several training sessions (Solomon & Corbit, 1974).

The explanation offered by Solomon and Corbit (1974) for these findings can be understood most readily by referring to Figure 2.20, which shows the presumed strength of the *a*- and *b*-processes to a stimulus event such as shock after a few (panel A) or many (panel B) trials. The middle row shows the effects of these trials on the underlying opponent processes. As far as the *a*-process is concerned, the amount of training has no effect. This response is always aroused rapidly by shock onset and declines equally rapidly following its offset. The amount of exposure does influence the strength of the *b*-process. At first, this response is rather weak and gains in strength only slowly after the shock is turned on, but when subjects are more familiar with the shock, then the *b*-process grows rapidly and its magnitude is considerably greater. Throughout training, once the shock has been turned off, the decline of the *b*-process is slower than that of the *a*-process.

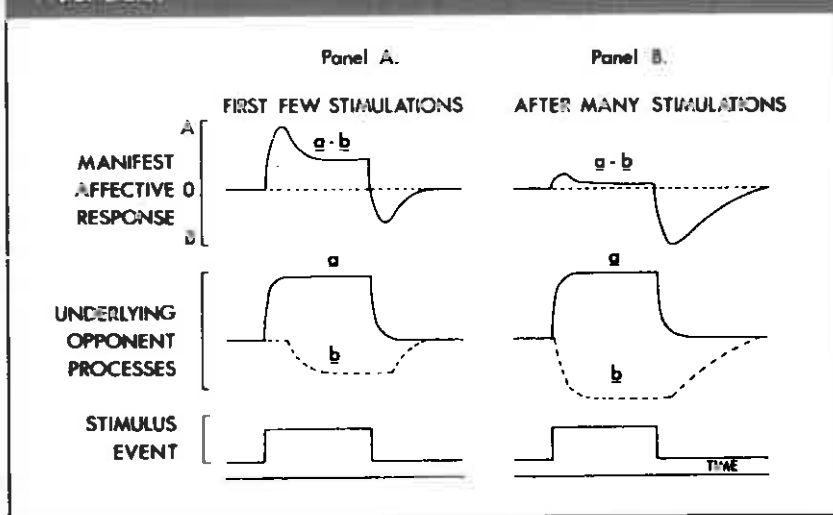
The upper row of Figure 2.20 shows the net response that would be observed as a result of the inevitable interaction of the *a*- and *b*-processes. In principle the figure shows the impact of subtracting the *b*-process from the *a*-process and the way this would manifest itself in such measures as heart rate. The curves reflect exactly the changes in

reactivity to shock that were reported by Church et al. (1966).

It is reasonable to assume that if, during conditioning, the CS becomes associated with a representation of the *a*-process, then it will elicit a preparatory CR in much the same way as Konorski (1967) envisaged. But what sort of CR could be expected if the CS should become associated with a representation of the *b*-process aroused by a US? One answer is suggested by the work of Siegel (1977) on drug tolerance.

**Drug tolerance as a CR.** When rats are first injected with morphine, it has a strong pain-killing (analgesic) effect. But with the repeated administration of the drug a tolerance to it develops, so that doses of increasing magnitude are required to obtain the same degree of analgesia. The development of such morphine tolerance can be understood in terms of Pavlovian conditioning (Schull, 1979; Siegel, 1977). The stimulation accompanying the injection of morphine can be regarded as a CS, and the effect of the drug as the US. In keeping with Solomon and Corbit's (1974) analysis, the CS could then become associated with the *a*-process aroused by the drug, which would consist of the typical reactions to the drug including analgesia. Alternatively, the CS could become associated with the *b*-process that opposes these effects. Schull (1979) has suggested that morphine

FIGURE 2.20



*Panel A:* The strength of the *a*- and the *b*-processes (middle row) aroused by a stimulus event (bottom row) when it is first presented, and the net reaction to this event that results from subtracting the *b*- from the *a*-process (upper row). *Panel B:* The same effects as those shown in Panel A, but for a stimulus event that has been presented for many trials (from Solomon & Corbit, 1974).

tolerance develops because the CS becomes associated with the *b*-process. After several injections, therefore, the sensations produced by the needle (CS) will activate a *b*-process CR that will counteract the subsequent analgesic effects of the injected morphine.

Support for this account can be found in an experiment by Siegel (1977). On each of six successive sessions, two groups of rats were injected with morphine shortly before a test for the analgesic effects of the drug. The test consisted of recording the weight that could be applied to a subject's paw before it was withdrawn. After the first injection rats were prepared to tolerate a considerable pressure to their paw. But with the repeated administration of morphine a weakening of the analgesic properties was revealed by a decline in the pressure that the rats were prepared to tolerate after each injection of the drug. This pattern of results is depicted in the left-hand side of Figure 2.21.

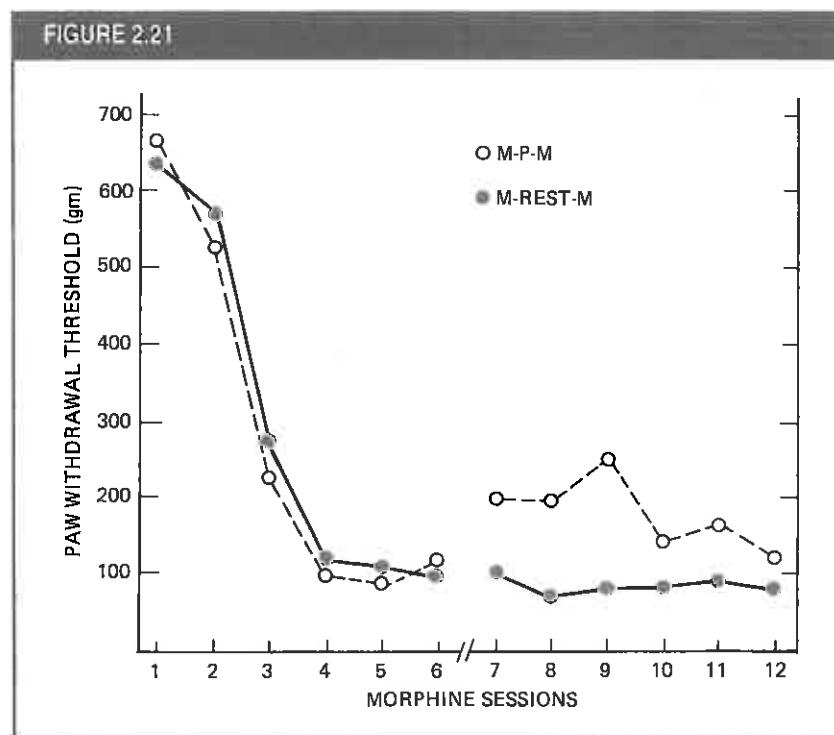
For the next 12 sessions the groups were treated differently. Group M-P-M was treated in much the same way as for the preceding sessions, except the

injections contained saline instead of morphine. This training can be regarded as extinction, because the stimuli produced by the injection were no longer followed by morphine, and their association with the *b*-process should therefore be weakened. No injections at all were administered to Group M-Rest-M for this stage of the experiment. Finally, both groups were given six further injections of morphine. For Group M-Rest-M these injections can be expected to elicit a substantial *b*-process CR and counter again the analgesic effect of morphine. In contrast, for Group M-P-M a *b*-process CR should not be aroused by the injection, because of the extinction trials, and the renewed administration of morphine should be accompanied by analgesia. The results of pressure tests after these injections, which are shown in the right-hand part of Figure 2.21, confirmed this analysis.

Findings such as these reported by Siegel (1977) clearly show that properties of the US can influence the CR, but they tell us very little about the circumstances that dictate the sort of CR that will be performed. This lack of knowledge is

FIGURE 2.21

The mean weight that two groups of rats were prepared to tolerate on their paws shortly after an injection of morphine (M). The left-hand side shows the results for the first six daily trials, the right-hand side shows the results for a further six injections. During the interval between these stages Group M-P-M but not Group M-Rest-M had received saline placebo (P) injections (from Siegel, 1977).



emphasised by experiments that are very similar to Siegel's (1977) in design, yet have found that at least a component of the CR resembles the *a*- rather than *b*-process elicited by the drug (Eikelboom & Stewart, 1979; Sherman, 1979). For the present, the factors that determine whether a CR will mimic or oppose the response elicited by the US remain obscure. A similar state of uncertainty holds for the distinction between preparatory and consummatory CRs. Konorski (1967) proposed that the former are more likely when the CS is of relatively long duration, whereas shorter CSs were believed to be responsible for consummatory CRs. Once again, however, there is insufficient evidence to allow an adequate evaluation of these proposals.

Even if the way in which the US influences the CR were fully understood, our knowledge of the factors that determine this response would still be incomplete. This is because the nature of the CS can also influence conditioned responding.

### **Influence of the CS on the CR**

A dramatic example of the way in which the CS influences the CR can be found in a conditioned taste-aversion study by Garcia, Rusiniak, and Brett (1977). Coyotes and wolves were made ill by feeding them chopped mutton that was wrapped in raw sheep hide and laced with lithium chloride. The effects of this conditioning episode were then examined by allowing the animals to approach live sheep. Rather than attacking them as they normally do, one coyote sniffed the sheep and then turned away retching; the reaction of the wolves was even more impressive, at first they:

charged the sheep and made oral contact several times with their characteristic flank attack but immediately released their prey. During the next half hour, the sheep became dominant as the wolves gave way whenever the sheep threatened with short charges. Gradually the wolves withdrew and responded to the sheep like submissive pups. (Garcia et al., 1977, pp.281-282)

The response of retching by the coyote is to be expected if the US determined the CR, but the additional reactions of the wolves are clearly influenced by the fact that the CS paired with

illness tasted and smelt of sheep, and that the live sheep, finding themselves not eaten by wolves, were prepared to attack their erstwhile predators.

In a different vein, Timberlake and Grant (1975) signalled the delivery of food to rats by inserting into the conditioning chamber for 10 seconds a platform on which another rat was strapped. As this event was always followed by food, an account of conditioning that assumes that the CS should elicit the same responses as the US leads to the expectation that the experimental subjects would attempt to eat the CS. Happily, there was no evidence of such cannibalism. Instead, whenever the CS was presented, the subject engaged in social behaviour with the restrained rat. This activity included pawing, grooming, and anogenital sniffing. To emphasise the importance that the nature of the CS played in this experiment, it was found that social responses were not directed towards a block of wood when it served as the CS. A further finding from the experiment was that social behaviour was not directed towards the rat on the platform, if its entry into the chamber was unrelated to the delivery of food. Thus the social response can be confidently said to be a consequence of conditioning, and it is determined by properties of the CS as well as the US.

### **Interpretation**

By now it should be evident that our understanding of the factors that determine the nature of a CR for a given conditioning task is far from complete. On some occasions the CR mimics the response to the US, on other occasions it appears to counter the response to the US, and in other tasks the CR is determined more by the properties of the CS. Clearly the simple memory model of conditioning that was sketched on p.39 is unable to explain this complex pattern of findings. In general, learning theorists have veered away from trying to specify the circumstances in which a particular CR will be performed, but this is not to say the problem has been ignored completely.

Several authors have proposed that the determinants of conditioned behaviour are organised into functional systems that are concerned with such activities as feeding, mating, defence, and parenting (Davey, 1989; Timberlake,

1994). These systems are activated by the appropriate stimuli, and serve to coordinate patterns of behaviour that are both innate and learned. Each system is assumed to control a wide range of actions, the selection of which is determined by the stimuli that are present. Thus in the case of appetitive conditioning, many of the actions controlled by the feeding system are assumed to be available to serve as potential CRs.

To explain the finding by Timberlake and Grant (1975) that social behaviour can serve as a CR, this behaviour must be assumed to constitute one of the activities that lie within the feeding system. The question is then raised as to whether it is reasonable to suppose that social behaviour belongs to the feeding system. Timberlake (1994) has justified this assumption by pointing out that young rats have a natural tendency to follow adult rats and to eat the food that they select. That is, social behaviour with adults is an integral part of feeding in young rats. We might predict, therefore, that any animal that is a solitary feeder throughout its life will be unlikely to demonstrate social CRs when it is presented with a conspecific that signals the delivery of food. Timberlake (1983) has confirmed this prediction with hamsters who tend to eat by themselves. He actually found a decrease in social behaviour in hamsters when they were exposed to another hamster immediately before food was delivered.

Whatever the merits of the details of this behaviour systems approach to Pavlovian conditioning, there is no doubt that it has the benefit of attempting to come to terms with the complexity of the factors that determine the nature of the CR. For this reason alone, this approach deserves serious attention.

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#### **CONCLUDING COMMENT: THE REFLEXIVE NATURE OF THE CONDITIONED RESPONSE**

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A common claim concerning conditioned responding is that the CS elicits the CR quite automatically, just as an innate reflex will be triggered by the appropriate releasing stimulus. As

a result, whereas properties of the CS and US can influence the form of the CR, this response is often quite unaffected by its consequences. In some circumstances this does not matter, because the CR will approximate behaviour that is in the animal's best interests. Signals for food are generally found in close proximity to food itself, and a preparatory CR of approaching an appetitive CS may well lead a hungry animal to its goal. Alternatively, an animal that flees from a signal for an aversive event will very often be fleeing from that event as well. This is not to say that CRs will always benefit the animal; given the appropriate circumstances, as the following examples will show, the automatic occurrence of a CR can occasionally lead to maladaptive behaviour.

In one study by Hearst and Jenkins (1974), pigeon autoshaping was conducted in a long conditioning chamber. The delivery of food was signalled by the illumination of a response key located more than 0.6 metres from the hopper. After a number of autoshaping trials the pigeons would approach and peck the key as soon as it was illuminated. Pecking then continued until the key light was turned off, whereupon the pigeon frantically rushed down the box to collect the grain that was briefly available at the hopper. Not surprisingly, subjects got very little food to eat as a result of this training. In this example, then, the CS elicited the typical CRs of approach and pecking, and their occurrence prevented the more sensible response of going to the magazine. The automatic, or reflexive, nature of the CRs is revealed by the persistence with which they were performed, even though they interfered with the collection of grain.

A similar outcome has been demonstrated by Williams and Williams (1969) using what is known as an omission schedule for autoshaping. Pigeons were given conventional autoshaping in which the illumination of a response key signalled food. But if the birds pecked the key during a trial, the light was turned off and food was not presented. Given this arrangement, it would be in the pigeons' best interests never to peck the key. But it seems that the behaviour of these birds is not always governed by their best interests: Even with extended training they all persisted in pecking the key to some extent,

thereby receiving only a fraction of the food that was potentially available. The implication of this finding is that even the intermittent pairings of the CS and food were sufficient to sustain a key-light–food association. Illumination of the key would then activate a representation of food and automatically produce a consummatory peck CR and cancel the delivery of food.

The final example of the disruptive influence of CRs comes from a study by Breland and Breland (1961), who experienced considerable difficulty in training a raccoon to pick up a coin and insert it in a money box for food. The problem did not lie with making the subjects pick up the coin, but with making them let go of it again. Boakes, Poli, Lockwood, and Goodall (1978) have suggested that this demonstration of “misbehaviour” occurs because the coin became an appetitive CS as a result of being paired with food. Consequently, the subject will be compelled to approach the coin whenever it is visible (preparatory CR) and perhaps

attempt to eat it (consummatory CR). On this basis it is quite understandable why the raccoons were unwilling to release the coin.

Pavlovian conditioning has the potential for allowing animals to learn a great deal about sequences of events that occur regularly in their environment. But if the only way this knowledge can influence behaviour is through a restricted range of reflex-like responses, then, as the studies just discussed demonstrate, its full benefits could not be realised. It now seems that in addition to eliciting stereotyped CRs, Pavlovian conditioning can exert a more flexible influence on what an animal does by modulating the vigour of instrumental responses. But we must wait until we have examined the instrumental learning process in Chapter 4 before this possibility is investigated further. In the meantime we turn in the next chapter to an examination of the conditions that determine whether or not Pavlovian conditioning will take place.