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## Aversively motivated behaviour

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IN this chapter we consider the role of the locale system in an animal's response to unpleasant, or threatening, situations, where a *threatening situation* is taken as one which predicts the possibility of pain. We first consider the various forms of threat and the ways in which animals identify and subsequently cope with these threats. Particular emphasis will be given to the distinction between threatening places and cues. Following this we discuss the effects of hippocampal lesions upon behaviour in threatening situations. It will be shown that animals with such lesions retain an appreciation of threat when it relates to cues and respond appropriately to such threats, but fail either to apprehend or adequately to respond to threatening places.

### 8.1. Behaviour under threat

The most powerful current theory of how an animal learns to cope with threat is traditional two-factor theory (Mowrer 1939, 1947, Konorski 1948, Rescorla and Solomon 1967, and others). This theory postulates two basic processes: (1) the Pavlovian or classical conditioning of *fear* to certain stimuli; (2) the instrumental learning of an adequate response. Traditional theory assumed that the appropriate response was maintained by the reinforcement involved in the reduction of fear. We return to a fuller discussion of this and other, more recent, theories later. Here, we wish to reformulate the two-process model in order to bring it into line with the cognitive approach of this book. We shall postulate that two processes are involved when an animal is confronted with a threatening situation: (1) the identification of the threat; (2) the choice of a particular hypothesis to cope with this threat.

#### 8.1.1. THE IDENTIFICATION OF THREAT

*8.1.1(a). Types of threat.* There are several ways in which different threats could be classified, and the scheme one chooses obviously reflects the bias of the investigator. Thus, one could separate threats on the basis of the role of learning in their establishment, the possibility of escape, the availability of prediction and/or control, and so on. Within the present framework we consider a separation based on places and cues as most

profitable. We hope to show in this chapter that such a distinction provides a powerful approach to the study of aversive learning and that it is essential to an understanding of the behaviour of hippocampal animals in threatening situations. We can further separate threats according to the animal's previous experience with them. Thus, *innate threats* have inherent properties, apparent upon an animal's first exposure to them (e.g. predators); *learned threats* are aversive through prior association with pain, or perhaps another threat (e.g. CS paired with shock, or a house of horrors); *potential threats* are objectively unknown quantities, novel places and cues, which are treated by the animal with caution, a mixture of fear and curiosity.\*

The fact that learned threats require prior association with pain, or some other threat, raises the possibility that there are fundamental differences in the way animals react to these as compared with innate threats. There are two reasons for assuming that this is not the case. First, there is evidence that the brain mediates reactions to both learned and innate threats in the same way.\*\* Second, basic behavioural reactions, barring the reflexive response to pain itself, are much the same for the two classes, as we see shortly. We would suggest that it is more important to separate threats on the basis of whether they relate to a place or a cue than on the basis of whether they are innate or learned. Similarly, we consider such factors as the escapability or predictability of threat as secondary to the place-cue distinction. Such factors can alter the kinds of behaviour animals display in threatening situations, but seem to be less important in determining the overall form of behaviour itself than are places and cues. Evidence relating to these assertions will be presented in the ensuing discussion, but we shall concentrate primarily upon the role of places and cues in animals' responses to threat.

*8.1.1(b). Discovering the threat.* We would suggest that animals rapidly learn *where* threat comes from. The receipt of pain, or the presence of a threatening item, in a particular place, causes that place to be identified as threatening. This type of learning would seem directly analogous to that discussed for appetitive situations in the previous chapter. That is, animals learn where rewards are to be found and subsequently associate these places with specific cues when possible. In threatening situations animals

\* Some insight into the mechanisms operating when an animal is confronted with a novel item (food) has been provided by Kalat and Rozin (1973). They showed that such foods are initially regarded as potentially dangerous and that only some time after they have been ingested without *adverse consequences* does the animal treat them as safe. A novel environment could be treated in the same way. While Blanchard, Kelley and Blanchard (1974) have concluded that novel environments elicit only fear, Cowan and Barnett (1975) suggest that they elicit primarily curiosity.

\*\* Goddard (1964), Blanchard, and Blanchard (1972a) and others have provided strong evidence that the amygdala mediates reactions to both innate and learned threats. Similar evidence implicates the amygdala in the 'tagging' of positive rewards. Thus, there are good reasons to suppose that the amygdala is concerned with the *valence* of environmental features.

initially respond on the basis of the dangerous place, directing their responses towards or away from that place.

In some situations it is not possible to identify a specific item as threatening, and behaviour continues to be directed towards, or away from, places. In other situations a threatening item can be identified, and behaviour becomes directed towards, or away from, it.\* In so far as threatening places and cues elicit different behaviours, the ability of the animal to discriminate the threatening cue will be a major determinant of behaviour. We shall see shortly that the distinctiveness, or *salience*, of the threatening item strongly influences the choice of a coping hypothesis.\*\*

According to the above analysis, the responses of animals in threatening situations should depend upon whether the threat comes from the place or some specifiable item. There is some evidence from the work of the Blanchards and their colleagues concerning the way in which animals initially identify and respond to threatening places and items. Blanchard, Dielman, and Blanchard (1968a, b) have shown that shock will cause rats to crouch or freeze, and that this behaviour is linked to the place in which shock had been received. Blanchard and Blanchard (1969a) extended this analysis by demonstrating that rats shocked in one place will not crouch if immediately moved to another, neutral, place. When subsequently returned to the original, dangerous, place the rats crouched. Thus, postshock crouching was not a response to pain *per se*, but rather to the place in which pain had been received.\*\*\* Much the same thing is seen when

\* Analogously to the autoshaping seen in appetitive situations (p. 263), the locations of stimuli associated with threat become aversive. That is, the site of a light which signals the imminence of shock is avoided; lever pressing to avoid shock is more easily learned if the light is distant from, rather than near, the lever (Biederman, D'Amato, and Keller 1964).

\*\* A salient CS in a fear-conditioning situation tends to reduce the magnitude of place fear, as animals learn that threat is specifically linked, either spatially or temporally, solely with the CS (cf. McAllister *et al.* 1974).

\*\*\* The question of the time-course of changes in crouching after shock is an interesting and involved one. In most of their studies the Blanchards measured the change in crouching over time, during which the animal was left in the threatening situation. Thus, they were actually measuring the extinction of crouching. Blanchard and Blanchard (1969a) did compare crouching either immediately or one hour after shock, with the latter group kept outside the shock situation for the shock-retest interval. Crouching was approximately equivalent for the two groups for the first hour they spent in the shock situation, independent of the shock-retest interval. This result suggests that crouching does not change, at least over one hour. However, there is a large body of data concerned with the fact that certain aspects of behaviour do change as a function of time after shock, in particular that freezing can increase—the so-called *incubation effect* (e.g. McMichael 1966). In this case the animal spends the shock-retest interval in a different place and the typical finding is that the ability of the threatening place or item to elicit freezing increases monotonically with time. In addition to this there is the *Kamin effect* (Kamin 1957). Here, a U-shaped relearning function is displayed after initial training in avoidance. Some recent work by Pinel and Mucha (1973a,b) has suggested that the incubation effect represents a change in *activity* in response to threat, while the Kamin U-shaped function is based on changes in reactivity to shock over time. As with the Blanchards' results it appears that the incubation effect is linked to the particular threat; there is no suggestion that an animal's activity decreases independently of the presence of threat on retest. The extent to which the Kamin effect is dependent upon re-establishing the original shock situation is unclear. Brush (1971) reviewed much of the incubation and Kamin-effect literature; he also quoted an unpublished

a threatening item is put into an otherwise neutral place. A rat confronted with a cat for the first time will spend a proportion of its time crouching (Blanchard and Blanchard 1972b). Over time an increase in crouching develops, even though no contact with the cat has been made. Some of this freezing persists after removal of the cat, indicating that the rat has identified the place as threatening.\* Blanchard and Blanchard (1969b) have shown the same thing with an electrifiable prod which had previously been used to administer shock in another place. Thus, evidence from several studies attests to the relative ease with which places are identified as threatening, either through the receipt of pain or through association with threatening items.\*\*

A somewhat different picture emerges when one considers reactions to threatening items, separately from the places within which they occur. Blanchard and Blanchard (1970a,b) have shown that highly discriminable threatening items elicit some increase in crouching, but a much more specific avoidance of the particular item itself. Thus, as a result of discriminating and identifying a specific threatening item the animal's behaviour becomes relatively tied to that item. This ability to separate out specific threatening items lies at the root of hypotheses based on approach or avoidance of items rather than places.\*\*\*

The above discussion indicates that animals rapidly learn to identify threatening places and seek to discriminate those items within the place which are specifically dangerous. The seeming predominance of place learning suggests that, as in appetitive learning and primarily at the onset of learning, place hypotheses might be most effective in coping with threat.

#### 8.1.2. COPING WITH THREAT

The forms of coping behaviour elicited by threat fall into a few simple categories. In fact, it has been suggested that the limited behavioural repertoires evidenced in the face of threat are of some special theoretical

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experiment by Brush and Sakellaris which suggests that the Kamin effect is *not* based on changes in reactivity to shock. Thus, the nature of the time-dependent changes in retention of aversive contingencies remains a confused issue. We do not feel that these time-dependent changes basically affect the argument we are making here. Recently, Klein, Murphy, and Freeman (1975) have shown that the Kamin effect is intact in rats with hippocampal lesions.

A different set of issues arises when one considers the effect of multiple inescapable shocks upon subsequent behaviour (e.g. Anisman and Waller 1973). Here, too, there is considerable confusion, and controversy, concerning arguments that are peripheral to our focus.

\* Blanchard, Mast, and Blanchard (1973) have studied the factors controlling the rats reaction to the cat. Neither the smell, nor the sight, nor the vocalizations of the cat are in themselves enough to elicit crouching. Movement of the cat is critical. In fact, movement of non-predator items also elicits some crouching.

\*\* A threatening place, in our terms, is obviously related to what has been called *situational* fear. It differs in so far as we attribute quite different properties to it, relative to those associated with items, or *discriminated* threats.

\*\*\* There is an interesting but as yet untested possibility that putting a neutral item into a dangerous place results in that item being identified subsequently as threatening.

significance (e.g. Bolles 1970, 1971); we shall discuss this position shortly. When confronted with a dangerous place animals attempt to flee; this appears to be the highest-priority hypothesis. When flight is not possible animals freeze. In studying the rat's reaction to threatening places this importance of flight has been repeatedly emphasized. Thus, Bolles (1970) asked:

'Why is a change in geographical location such a particularly effective stimulus change?' (p. 42).

The foregoing would suggest that one highly likely hypothesis in response to threat is: 'get out of this place'. Further, it seems likely that animals would preferentially escape to places previously identified as non-threatening.

Behaviour in response to a threatening item is somewhat more complex. Again, flight would appear to be a likely possibility. Blanchard and Blanchard (1971) have shown that, in response to a cat, rats will flee if possible. They conclude that

'the availability of escape is a principle determinant of the relative dominance of these reactions' (p. 361)

referring to flight and freezing. The failure of a flight hypothesis does not, in this case, automatically lead to freezing. The animal can attempt to manipulate the situation so as to make the threat 'disappear'. Thus, animals can learn to press levers to turn off a threatening buzzer. Another possibility is to move to some part of the environment which is not associated with threat, as in the case of the avoidance of an electrifiable prod, or shocked water dish, or cat. Finally, depending upon the topology of the situation and the character of the threatening item, animals will sometimes engage in attack. The crucial determinants of attack would seem to be the distance between the animal and the threatening item. In practice this shows up in the fact that animals attack more frequently in small enclosures and when confronted with threatening items which move, thereby making it difficult to maintain some critical safe distance (see Myer (1971) for a review of some of these studies).

The above suggests that various kinds of hypotheses are possible when an animal is confronted with threat. A threatening place can be coped with by 'going to a safe place' or simply 'leaving the dangerous place'. A threatening item can be coped with by 'fleeing the item', or 'approaching items distinguishable from danger', or 'making a response which temporally or spatially decreases the impact of the item', or, lastly, 'attacking the item'. In some situations more than one of these hypotheses would be appropriate and we would suggest that, to the extent that conflict exists, place hypotheses would have precedence, if only because animals seem to learn more rapidly about places than about items. This overview

of behaviour in threatening situations can best be evaluated by comparing it with other, more traditional, views in its ability to account for some common varieties of aversive learning.

### 8.1.3. AN ANALYSIS OF BEHAVIOUR IN RESPONSE TO THREAT

There are a great many behavioural paradigms based on the use of aversion. These can be classified in ways which are parallel to those used in the classification of threats. Thus, there are tasks related to places or items, to innate or learned threats, to escapable or inescapable threats, to random or stimulus-contingent or response-contingent threats, and so on. The appropriate combination of these factors gives rise to the paradigms known as *escape*, *conditioned fear*, *punishment*, *avoidance*, and others. It is not our intention here to discuss the entire range of aversively motivated behaviours. There exist numerous reviews in this field for the interested reader (e.g. Mackintosh 1974). Rather, we shall concentrate upon avoidance, as much of the work, both with normal and lesioned animals, has utilized variants of this paradigm. Where necessary we shall extend the analysis to other paradigms.

Some writers have attempted to classify avoidance tasks in terms of the nature of the response required, in particular separating out so-called *active* and *passive* avoidance tasks. This tendency has been particularly strong within physiological psychology. In so-called active avoidance animals can avoid pain only through some active behaviour, while in passive avoidance the animal can easily avoid pain by remaining immobile. This distinction is unfortunate for two reasons. First, it carries with it the implicit assumption that animals are actually learning responses, and we shall see that this is only one way in which active avoidance can be mastered. Second, it implies that animals solve passive avoidance tasks by remaining immobile. Again, there are reasons to doubt this conclusion. In our discussion of the lesion literature we shall partially maintain the use of this active-passive distinction, merely as a means of classification, without any assumptions about the way in which animals solve these tasks. Our main discussion centres around active avoidance in general, and the variety known as shuttle-box avoidance in particular.

*8.1.3(a). Active avoidance in the normal animal.* The standard active avoidance paradigm is deceptively simple. A rat is placed in one side of a two-compartment box (A). After some time a neutral stimulus (the conditioned stimulus CS) such as a tone is presented and several seconds later an electric shock (the unconditioned stimulus, UCS) is delivered through the grid floor of side A. After its immediate reflexive reactions to the shock the rat will eventually escape to the other side of the box (B) where there is no shock; the CS and UCS are typically terminated by this response. After a fixed interval (the confinement period or inter-trial

interval ITI) the rat is removed from B and replaced at the start (A) for another trial or, alternatively, given a further ITI in a neutral place before starting another trial. Within a relatively small number of such trials the rat learns to move from A to B when the CS is presented, thus avoiding rather than escaping the shock. This behaviour is then maintained in the absence of further shocks.

Two problems are presented to the theorist by this task, termed *one-tray active avoidance*. First, there is the question of the types of hypotheses animals use to solve it. Second, there is the issue of the factors which maintain avoidance behaviour in the absence of any obvious reinforcement. For various historical reasons most of the work in this field has concentrated on the second issue, and conclusions about the first must be inferred from theories built primarily to account for the paradoxical maintenance of avoidance. We can begin our analysis of avoidance learning by looking at the traditional approach, two-factor theory, its recent modifications, and an alternative scheme proposed by Bolles (1970).

*Two factor theory.* The essence of traditional two-factor theory, as noted already, is that avoidance behaviour involves two main processes: the Pavlovian conditioning of fear to the CS, and the instrumental learning of an adequate avoidance response. Experimental work in support of this model attempted to show that something called fear could be conditioned to neutral stimuli and that responses leading to the reduction of fear were learned. These mechanisms could account for both the acquisition and maintenance of avoidance behaviour.

However, it is now clear that the ability of the CS to elicit fear is not necessarily maintained during the course of stable avoidance behaviour (Kamin, Brimer, and Black 1963, Linden 1969); these findings, and others concerned with the abnormal persistence of avoidance under extinction conditions (cf. Seligman and Johnston 1973, for a discussion of the two-factor model in this context), pose a serious problem for two-factor theory. The traditional model has recently been revised, typically so as to expand the role of Pavlovian conditioning during avoidance to include the development of a response-produced inhibitory feedback which both reduces fear and reinforces behaviour (e.g. Weisman and Litner 1969a,b, 1971, 1972).

The same problem has been addressed by Denny and his colleagues in a somewhat different way. In a series of studies (e.g. Denny and Weisman 1964, Weisman, Denny, and Zerbolio 1967, Denny, Zerbolio and Weisman 1969, Denny 1971) they have provided evidence in support of a relaxation model of avoidance behaviour. Stimuli which signal punishment elicit fear, and their removal is followed by relief and relaxation which act as reinforcers for the responses leading to these

states. It is clear that relaxation is, in most essential respects, similar to the conditioned inhibition of fear postulated by revised two-factor theory. Both depend upon events subsequent to the avoidance response. As we shall see shortly, a number of experiments done within the relaxation framework have provided evidence relating to the question of the kinds of hypotheses animals use in solving avoidance tasks. In particular, these data point to the importance of place hypotheses.

*Species-specific defence reactions (SSDR's).* Bolles (1970) has pointed out that an animal's choice of responses in aversive situations is hardly random. He suggests that

'What keeps animals alive in the world is that they have very effective *innate* defensive reactions which occur when they encounter any kind of new or sudden stimulus. These defensive reactions vary somewhat from species to species, but they generally take one of three forms: Animals generally run or fly away, freeze, or adopt some type of threat, that is, pseudo-aggressive behaviour' (p. 33).

The strongest evidence in support of the view that SSDR's play an important role in avoidance learning is the fact that those tasks requiring as responses either SSDR's or slight modifications of these are learned quite rapidly, while those which require responses incompatible with SSDR's are learned more slowly or with great difficulty (Bolles 1970). Thus, one-way active avoidance, as described above, is learned rapidly as it can involve flight. On the other hand, learning to press a lever to avoid shock can take an agonizingly long time.

Bolles has also offered an explanation for *two-way active avoidance*, which is a variant of the one-way task with a crucial procedural difference. Upon completion of a trial (be it escape or avoidance) the animal is *not* removed and returned to the start. Rather, after an inter-trial interval the CS is presented again and the animal must 'shuttle' in the other direction (i.e. from B to A) to avoid shock. This task is considerably more difficult for the normal animal than is the one-way task, and most investigators attribute this to the fact that the animal must re-enter areas where punishment had previously been received. Bolles suggests that the conflict inherent in this situation promotes the SSDR of freezing, which is incompatible with the shuttling (or flight) responses necessary for appropriate avoidance. This invocation of conflict between flight and freezing is a constant feature of SSDR explanations in avoidance, both in the active case, as seen here, and in the passive case, as discussed already for the work of the Blanchards (p. 293). Bolles supposes that specific stimuli, such as the CS or a feedback safety signal, become increasingly important when such conflicts exist. In a series of studies Bolles and Grossen (1969) showed that such stimuli were important in the learning of two-way, but not one-way, active avoidance. Thus, SSDR's such as flight and freezing suffice by

themselves in one-way avoidance and most varieties of passive avoidance, while two-way avoidance and such tasks as lever-press avoidance require the mediation of specific stimuli supporting the learning of non-SSDR responses.

*'Cognitive' theory.* Dissatisfaction with two-factor theory has coincided with the general rebirth of interest in cognitive approaches to behaviour. Recently, Seligman and Johnston (1973) have elaborated such an explanation for avoidance learning. Their model rests on the 'cognitive' notion that animals have preferences and expectancies, and that the combination of these can, in any situation, influence behaviour. Classically conditioned fear remains in the theory as a source of motivation, but its reduction is no longer seen as essential in either the learning or maintenance of avoidance. Basically, then, this model exchanges instrumental acts for preferences and expectancies, and eliminates the reinforcing role of fear or safety. It remains a fundamentally associationistic, two-factor theory. The confirmation of expectancies acts to reinforce those behaviours predicated on these expectancies.

Unfortunately, this model fails to go any further. It is easy to see that animals would prefer no shock to shock, or safety to danger. But, how are these latter identified? As a description of what goes on *after* an animal has figured out its environment the model succeeds. As an explanation of how animals learn about the safe and dangerous aspects of their environment it is reduced, it seems, to the trial-and-error strengthening of expectancies, biased perhaps by something akin to SSDR's.

*A synthesis.* None of these models, in our view, provide a completely satisfactory account of avoidance behaviour.\* One is left wondering about the circumstances under which the conditioned inhibition of fear, or relaxation, occur. The nature of flight, and the factors determining its occurrence, are not adequately spelled out (though Blanchard *et al.* 1975 have begun the process of spelling out some of the stimulus factors controlling freezing). It remains possible that if these factors were elucidated they might point to something like 'relaxation in a safe area', leaving us with the essential problem of determining just why an animal feels safe when he performs an avoidance response. In other words we have not gone very far beyond a description of what the animal actually does. Similarly, the cognitive model of Seligman and Johnston fails to go beyond a description of behaviour to an analysis of its antecedents.

A common thread working through all these difficulties has been the refusal of traditional theorists to distinguish between threatening places

\* There are other approaches to aversive learning not discussed here. One could, for instance, mention Herrnstein's (1969) attempt to account for such learning simply in terms of shock density. Mackintosh (1971) effectively refutes this argument, while Seligman and Johnston (1973) subsume it.

and cues. Though the literature is rife with hints that the 'discriminability' of the source of threat is an important variable and that quite different results obtain when 'situational' rather than 'discriminated' threat is involved, theorists have so far refused to examine the implications of this for their theories.\* To suggest that place learning is at the root of all avoidance behaviour is not our aim; however, it is clear that such learning can be important, perhaps crucial, in many avoidance situations, and that a consideration of such learning could provide a means of extending current views of avoidance behaviour.\*\*

We have already specified what we mean by a threatening place, and how it is to be distinguished from a threatening item. Further, we have seen that this distinction enables one to demonstrate that animals react differently to places and items. This framework can be used to examine the ways in which the locale system might influence avoidance behaviour. First, we can consider the question of flight. Neither Bolles (1970) nor Blanchard and Blanchard (1969a) specify the variables controlling flight. While it is clear that these authors cannot mean that flight exists in an environmental vacuum, they have not managed to elucidate those aspects of the environment towards which, or away from which, flight is directed, except in the limited case of flight from a well-specified item. The Blanchard and Blanchard (1971) study suggests that

'such factors as availability of escape and discriminability of the eliciting stimulus largely determine whether freezing or avoidance will be the principal response to threat' (p. 361).

However, what is meant by the availability of escape? We have assumed that this depends on the animal's ability to find a place which it considers safe. Given this, one can suggest that flight is a function of several factors: (1) a tendency to move away from threatening places or items; (2) a tendency to move towards safe places. The importance of a change in geographical location lies in the fact that such a change usually involves going to a different place, and that in itself can reduce the threat that confronts the animal. We do not deny the potential validity of the relaxation concept; a new place, given that it is known to be safe, will provide a situation in which the animal can relax. What is crucial, however, is not the relaxation *per se*, but the attainment of safety.

Thus, when confronted with a threatening place or item, animals, as a first hypothesis, seek out a safe place. The predominance of flight reactions in threatening situations is a function of the rapid learning about

\*Testa (1974) has discussed the importance of locations in avoidance learning, but in a way we find both incomprehensible and empty of theoretical significance.

\*\* We have attempted a limited redefinition of the avoidance and punishment literature, particularly as it applies to studies of animals with hippocampal damage, in a recent paper (Black et al. 1977). Our discussion there focuses on the same data in a somewhat different way than in the present chapter.

places and the subsequent rapid availability of place hypotheses. If a safe place can be found avoidance will be rapidly acquired. One-way active avoidance provides a situation in which a relatively safe place exists. We have already noted that neither CS termination nor a feedback safety signal play much of a role in either the learning or maintenance of this type of avoidance in the normal animal (Bolles and Grossen 1969). If, however, we consider the role of place learning, we can see that animals are sensitive to those features of the task situation which affect the use of place hypotheses. Thus, any manipulation which increases the discriminability between the safe and dangerous areas in the avoidance box, or increases the safety or danger of one or the other, can lead to more rapid learning (e.g. Knapp 1965, Moyer and Korn 1964, Reymerse and Rizley 1970).\* The inter-trial interval also seems to be important in determining the rate of learning. With a short interval the animal could fail to learn that the 'safe' side of the box was indeed safe; responses to that side are rapidly followed by placement in danger again. This importance of safe time in the shuttle-box situation can be contrasted with the effects of increasing inter-trial interval in a situation where safe-place learning is clearly unimportant. Thus, several studies have shown that lever-press avoidance deteriorates, rather than improves, with increasing intervals (Pearl and Fitzgerald 1966, Cole and Fantino 1966, Morris 1973). In this situation avoidance behaviour does not involve going to a safe place; rather, it rests on a response hypothesis.

Two-way active avoidance provides a situation in which there is no safe place; punishment is received in both parts of the box and there are only temporarily safe time periods. The fact that normal animals learn this task with difficulty could reflect their tendency to adopt initially a maladaptive place hypothesis, as seen in a study by Theios and Dunaway (1964). In contrast to the one-way task any manipulation which increases the discriminability of the two sides of the box retards two-way avoidance learning, as does increasing the shock level beyond a certain point (e.g. Denny *et al.* 1969, McAllister, McAllister, and Douglass 1971). These manipulations presumably increase the likelihood that place hypotheses will be used and sharpen the conflict between flight and freezing. Lastly, normal animals initially learn the two-way task in an imbalanced way. That is, they learn to go in one direction rapidly (e.g. A to B), but in the other slowly (B to A). This initial imbalanced learning is quite sensitive to variations in inter-trial intervals spent in the two parts of the box (Weisman *et al.* 1967), but does not seem related to the CS in the situation (Morris 1973). Thus, it would seem to reflect safe-place tendencies which must be overcome before adequate two-way avoidance can be manifested.

\* Differentiating the safe and dangerous areas in a one-way escape task also facilitates learning (Franchina et al. 1973).

In sum we are suggesting that safe-place hypotheses are predominant in normal animals and that the ease with which they learn tasks favouring the use of SSDR's such as flight or freezing reflects this predominance. Learning in situations where such hypotheses are adaptive is sensitive to those environmental variables which enhance the ability of the animal to differentiate the safe place from dangerous items or places. On the other hand, learning in situations where safe-place hypotheses are not adaptive requires the mediation of other hypotheses and the concomitant influence of other variables, such as the salience of the CS, is seen.

Both place and taxon hypotheses can involve either flight or freezing. The use of a place hypothesis in an avoidance situation cannot be determined by the form of the behaviour chosen, but rather by its flexibility and the nature of the variables to which it is sensitive. In order to determine precisely how an animal solves a given avoidance task one must go beyond the rate of learning to a consideration of the variables in the learning situation which affect performance.

This analysis of avoidance, based almost entirely on an examination of one-way and two-way shuttle avoidance, provides us with a view of the various strategies open to animals in threatening situations. We can now turn to a discussion of the effects of hippocampal lesions upon reactions to various threats and subsequent coping behaviours. We shall extend our analysis of normal performance to other aversive learning situations, including passive avoidance, in the context of this discussion.

## 8.2. The effect of hippocampal lesions on responses to threat

### 8.2.1. IMMEDIATE REACTIONS TO PAIN AND THREAT

Hippocampal rats react to shock in much the same fashion as do normal rats. The immediate (unconditioned) reaction includes a rapid flinching response (the flexion reflex), followed by somato-motor responses varying in nature and extent with the intensity of the stimulus (cf. Myer 1971). At low intensities shock elicits primarily flinching behaviour (Muenzinger and Mize 1933), as intensity increases jumping becomes prevalent (Kimble 1955, Trabasso and Thompson 1962), while at even higher intensities (beyond 1.0 mA) locomotor activity, particularly running, becomes probable (Campbell and Teghtsoonian 1958, Goodman et al. 1966). While the occurrence of these reactions is influenced by features of shock other than its intensity, such as its consistency, we limit our discussion here to intensity primarily because this is the only parameter of shock that has been studied in hippocampal animals.

Thresholds to the initial reaction to shock have been reported to be unchanged in hippocampal rats (Schlosberg, Johnson, and Lash 1969), as have changes in heart rate consequent upon moderate shock (Caul

*et al.* 1969).<sup>\*</sup> However, hippocampal rats over-react to intense shock, both behaviourally (Schlosberg *et al.* 1969) and in terms of heart-rate changes (Jarrard and Korn 1969). The latter effect likely depends on the former (e.g. Obrist, Sutterer, and Howard 1972), and one could characterize the changes in hippocampal animals as involving abnormally strong somato-motor reactions, particularly running, in reaction to intense aversive items.<sup>\*\*</sup> Of course, we have already noted that much the same exaggerated responsiveness is seen in these animals with ostensibly neutral stimuli (pp. 257-9), and these phenomena could represent an underlying hyper-responsiveness of all sensory systems.

The reactions of hippocampal animals in the period after shock and/or in the face of threatening items, have been studied in several experiments. In Blanchard, Blanchard, and Fial (1970) rats were shocked with a prod, and their reactions to its subsequent re-introduction (without shock) were assessed. Both control and hippocampal rats decreased their activity after being shocked when confronted with the prod; the decrease in the control rats was greater than that seen in the lesioned rats. However, the latter actively avoided this threatening item significantly *more* than did the former. Thus, reactions to threatening items are not reduced in any simple way in hippocampal animals. In a subsequent study in the same paper the authors tested the reactions of rats to shock in an environment devoid of any discriminable item and from which escape was not possible. In this situation hippocampal rats froze less than normal rats. In so far as freezing reflects a response to a threatening place in this task, the deficit in hippocampal rats implies that fear of dangerous places is diminished or absent in these animals. Though comparisons between studies are to be made with caution, one can take, from a study by Blanchard *et al.* (1968a), a non-shocked control group tested in virtually the same fashion as the hippocampal group in the Blanchard, Blanchard, and Fial (1970, experiment 2) study. This control group demonstrated freezing scores quite similar to those seen in the hippocampal rats, and this suggests that the lesioned animals were simply not responding to the dangerous place.

Both the Kim *et al.* (1971b) and the Blanchard and Blanchard (1972b)

<sup>\*</sup> Both Blanchard and Fial (1968) and Eichelmann (1971) purport to show that hippocampal rats are more sensitive to low-level shock than are normal rats. However, neither study clearly supports its claim. In the first study the hippocampal lesion group *did* have a lower jump threshold than its control group. However, this control group had a higher threshold than all the other groups in the study, including two other control groups with cortical damage only. The hippocampal lesion group differed only from its own, seemingly aberrant, control. In the second study the lesion group had a jump flinch threshold that was significantly lower than that for normal animals but was not different from that of cortically damaged control animals.

<sup>\*\*</sup> These observations are of some importance because shock is often used in behavioural studies, and an exaggerated reaction to intense shock could form the basis for 'deficits' in lesioned animals. Thus, hippocampal rats can fail on certain problems when shock avoidance is used as the motivation, while succeeding on the same problems when food reward is used. Similarly, hippocampal rats have been shown to fail on a pattern-discrimination task at high shock levels while succeeding at lower shock levels (Musty 1970). The exaggerated reaction to shock in these studies typically manifests itself in fixated response strategies which interfere with discrimination.

studies were concerned with the reaction of hippocampal rats to cats. In the first study hippocampal rats were found to move about more in the presence of an inescapable cat than did normal rats; they also ate and drank significantly more than did the normals.\* Blanchard and Blanchard included a condition in their study in which the rats could escape the cat. They replicated the Kim *et al.* result of increased movement in the face of the inescapable cat, but also showed that the hippocampal rats would escape *more* rapidly than would the normal rats if given the chance to do so. Thus, the greater activity of hippocampal rats in the presence of an inescapable cat cannot reflect decreased fear *per se*, as Kim *et al.* suggested.

In both studies the hippocampal rats were less active in the presence of the cat than they were in its absence. As we have already noted, the immediate immobility elicited in normal rats by a cat tends to increase over time, and some immobility persists after removal of the cat. In hippocampal rats, on the other hand, immobility scores do not change during the time the cat is present (Blanchard and Blanchard 1972b). There does not appear to be a development of the notion of a dangerous place through association with the cat.\*\*

It is noteworthy that flight from the cat in this study, and from the shock prod in Blanchard, Blanchard, and Fial (1970), was greater in hippocampal than it was in normal rats. Blanchard and Blanchard (1971) suggested that the conflict between flight and freezing diminishes the ability of normal animals to flee. The absence of that part of immobility related to the threatening place could account for the superior flight performance of the hippocampals.

Additional evidence bearing on the problem of reactions to threatening items comes from studies of conditioned fear (cf. McAllister and McAllister 1971, for a review of the normal data). Estes and Skinner (1941) reported an aversive conditioning procedure which involved superimposing a CS and an unavoidable shock upon a stable appetitive behaviour, in their case lever pressing for water. The normal animal in this situation rapidly inhibits its appetitive behaviour during the CS preceding the shock and typically freezes instead; this immobility in response to an inescapable threatening item has been termed *conditioned suppression* or the *conditioned emotional response (CER)*. A number of investigators quote Brady's (1958) assertion that hippocampal damage causes deficits in the CER and assume that there is a basic defect in fear conditioning (e.g. Olton and Isaacson 1969). However, in that report Brady specifically

\* Nonneman and Kolb (1974) have reported reduced fear reactions in hippocampal cats in the presence of another, threatening, cat. The lesioned cats mostly ignored the other cat, going directly to food. If chased, however, the lesioned cats showed flight.

\*\* A study by Glickman and Morrison (1969) showed this absence of place fear in an elegant way. Control and hippocampal mice were put into single cages with the doors open, such that they had access to an area containing a predator (owl). The lesioned mice were significantly more likely to be eaten than were the controls, as well as being more active.

mentions that his result should be interpreted with caution, as histology was not yet available for his lesioned rats. No further mention of these data has appeared, and in view of subsequent demonstrations that other limbic lesions can lead to deficits in the CER (e.g. the amygdala, Goddard 1964) we feel that these data are insufficient. Several later studies of the conditioned suppression of drinking, a paradigm related to the lever-press CER, demonstrated adequate learning in hippocampal rats (Kaplan 1968, Nadel 1968, McGowan, Hankins and Garcia 1972).\*

Another method of testing conditioned fear involves measuring flight from a CS previously associated with punishment in a different situation. McAllister and McAllister (1971) point out that this technique provides an

'uncontaminated index of fear and allows a clear distinction to be made between the conditioning and the measurement of fear' (p. 108-109).

That is, punishment is not received in the testing situation, and any flight from the CS must be a result of the fear-conditioning procedure. Goldstein (1965) tested hippocampal rats in such a situation and found that they learned the test response of jumping a hurdle to escape the CS almost as well as did control rats. Finally, in an escape-from-fear paradigm, where fear was established in the same test chamber as escape was assessed, rats with hippocampal damage escaped quite well when confronted with the CS previously paired with shock (Haggbloom, Bruner, and Bayer 1974).\*\*

These studies confirm the impression that the hippocampal animal treats threatening items in a relatively normal manner—fleeing or freezing in accordance with the utility of these behaviours in the particular situation. Contrary to what has been suggested by numerous writers, there is not a unitary decrease in freezing; that portion elicited by threatening items seems intact in hippocampal animals. However, freezing is not seen in threatening places. A 'freezing deficit' model makes sense only when viewed in conjunction with the separation between places and items; both elicit freezing in the normal animal while only the latter does in hippocampals.

As we have noted, animals sometimes react to painful stimulation with aggression; there is evidence that hippocampal lesions affect these behaviours. There is a clear-cut reduction in shock-induced fighting after hippocampal lesions in rats (Blanchard and Blanchard 1968b, Blanchard, Blanchard, and Fial 1970, Eichelman 1971, Kim *et al.* 1971b, Kolb and

\* McGowan *et al.* found deficits with ventral, but not dorsal, lesions. Nadel found normal learning with either lesion. See Freeman, Mikulka, and D'Auteuil (1974) and Molino (1975) for partially conflicting reports.

\*\* Escape in the damaged rats was better than normal, which might reflect the fact that normal rats, during fear conditioning, tend to freeze, and this conflicts with subsequent escape. Similarly, pre-shock can retard acquisition of one-way active avoidance in normal, but not hippocampal, rats (Haggbloom *et al.* 1974).

Nonneman 1974, De Castro and Marrone 1974)\* and this seems related to the fact that these animals less often assume the 'boxing stance' typical of fighting between rats (Blanchard, Blanchard, and Fial 1970).\*\* However, this latter study also showed that aggression aimed at a moving electrified prod was *increased* in hippocampal rats. Blanchard, Blanchard, and Fial suggest that their results

'offer little support for any hypothesis that hippocampal lesions either enhance or attenuate a unitary aggression mechanism' (p. 101).

Rather, they feel that changes in aggression after the lesion relate to a basic effect of the lesion upon the ability of the animal to remain immobile. While hippocampal rats fight less, hippocampal gerbils fight *more* than do normal gerbils, even though they have difficulty adopting the side-by-side inactive posture which often precedes fighting in this species (Glickman *et al.* 1970). Taken together, these findings indicate that hippocampal lesions do not directly influence aggressive behaviour but can affect various behavioural components often involved in aggression. Depending upon the topology of the particular aggressive behaviour under study these changes could result in either more or less fighting.

The results of all those studies concerned with reactions to threatening places and items suggest that fundamental mechanisms underlying what has been called fear are not disrupted by hippocampal lesions. Rats with such damage flee threatening items if possible, and crouch in their presence when escape is not possible. Thus, the *reaction to threatening items, whether it involves an inactive or active behaviour, remains intact in hippocampal rats*. On the other hand, *there is evidence that these animals do not react to threatening places*. This distinction between threatening places and items is also seen in avoidance learning situations, to which we shall now turn our attention.

## 8.2.2. LEARNING BASED ON AVERSION

8.2.2(a). *Active avoidance*. We shall discuss three types of experiments under this heading: (a) one-way active avoidance; (b) two-way active avoidance; (c) active avoidance involving some manipulation within the situation.

*One-way active avoidance*. The results of experiments concerned with one-way active avoidance are given in Table A21; in about one-third of

\* De Castro and Marrone (1974) showed that shock-induced fighting was diminished in fornix-lesioned rats, but only if they had not had pre-operative experience in the aggression situation. Unfortunately, they did not comment on the behaviour of pre-operatively trained rats.

\*\* Peters and Brunner (1976) have shown that rats with hippocampal granule cell loss, induced by X-irradiation, 'box' more than controls when intact intruder rats were placed into their home cages. They did not, however, fight more often. This study differs from the others cited above in that fighting was not shock induced.

these studies deficits were seen in the lesioned animals. The observed pattern of results might reflect procedural differences between the studies involving manipulations of parameters to which the lesioned and normal animals were differentially sensitive. In particular, various manipulations of the CS seem to effect these animals differently.

With a few exceptions the studies listed in Table A21 conform to a pattern; those studies using a CS failed to produce a deficit, while those not using a CS produced a deficit. This implies that the hippocampal animals were uniquely dependent upon specific cues in this situation; this would be expected if one assumed that they could not use place hypotheses. Two studies by Olton and Isaacson (1968a, 1969) provide evidence for these assertions. In the first study the effects of pre-habituation to the CS were measured; in the second the effects of prior CS-UCS (inescapable) pairings were measured. In both cases the performance of the hippocampal, but not the normal, animals was markedly affected by these treatments. Pre-habituation to the CS retarded learning while prior CS-UCS pairings profoundly improved it. Plunkett (personal communication) has shown that hippocampal rats tested in this situation develop a sharp generalization gradient to the CS; that is, they are under strong stimulus control.

These observations suggest that one-way active avoidance can be learned with the use of either place or taxon hypotheses, and that normal and hippocampal animals could solve the task in different ways. We have completed a study which directly tested this possibility (Oetliker 1972). Rats were trained on a one-way active avoidance task in a box with transparent plastic side walls and wooden end walls which could accommodate cardboard (black or white) inserts. There was no specific CS and the UCS, electric shock through the grid floor, was delivered through an automatic programme set to give a brief shock every 5 s. Rats were trained to a relatively weak criterion of learning (8 correct avoidances out of 10 trials) in the hope that this would maximize their chances of using a place hypothesis. Both control and lesioned rats reached this criterion within 20 trials, and there was no reliable difference between the groups on this measure. At this point a series of probe trials was instituted. On each day rats received six trials; the first two and last two were 'normal' trials, identical to those given during initial learning, while the middle two constituted the probes. On each probe trial some change was made in the situation. Either the rat was started in the previously safe area, or the black and white cardboard inserts were interchanged, or the entire box was rotated, and so on. In some probe conditions several changes were made simultaneously. The results of these trials were clear; normal animals behaved almost entirely on the basis of where they were put in the box. When put on the safe side they stayed put; when started on the dangerous side they ran. Thus, they seemed to be using a place hypothesis which

could be fulfilled with either an active or a passive response.\* In fact the only probe condition which altered this pattern of performance involved completely surrounding the apparatus with a black curtain, effectively removing almost all of the extra-apparatus cues. Under this condition the normal animals froze on both sides of the box. This result suggests that they were using extra-box cues to support their place hypothesis, and that in the absence of this information they were unable to determine the safe place and froze *in situ*.

Lesioned rats, on the other hand, did not respond in a way which could be characterized as dependent upon place hypotheses. They often ran when put on the safe side and equally often remained still when put on the dangerous side. It was not possible in this study to determine exactly which cues the lesioned rats were using, though it seems likely that they were not using extra-box information. When the entire box was surrounded by curtains and the apparatus rotated by 180°, these rats ran from 'safety' and remained in 'danger' as defined by the position of these areas in the room. This behaviour, however, was completely appropriate in terms of the intra-box cues available to the animals, which had been reversed during the rotation.

The results of this study, in conjunction with earlier work, indicate that hippocampal animals can solve one-way active avoidance tasks, but that they cannot use place hypotheses to do so. Deficits should appear when normal animals are favoured through their use of a safe-place hypothesis.

*Two-way active avoidance.* As Table A22 shows, hippocampal animals are usually superior to normal animals at two-way active avoidance. At first glance this facilitation following hippocampal damage can be associated with the absence of place hypotheses. Such hypotheses, as we have noted, are inappropriate in the two-way task, and the animal must disregard them in order to find the correct solution. Lacking such hypotheses, the hippocampal animal would have an immediate advantage in this situation. This is consistent with the fact that CS manipulations, which strongly affect normal performance in two-way active avoidance, have little effect on hippocampal performance (Olton and Isaacson 1968a, Ackil *et al.* 1969). Further, Plunkett (personal communication) has shown that hippocampal rats have a flat generalization gradient to the CS in this task, in contrast to what is the case in one-way active avoidance. While normal rats use the CS to help overcome their reliance on place hypotheses, the hippocampal rats can ignore it. Finally, it has been shown that normal animals learn to go in the two directions at an unequal rate, while hippocampal animals learn to go in both directions at about the same rate

\* The distinction between active and passive avoidance breaks down in the face of results such as these. The normal animals seek out a safe place and will use either active or passive behaviours to fulfill this quest. This becomes important when we consider so-called passive avoidance tasks (pp. 311-15).

(Papsdorf and Woodruff 1970, in rabbits, Olton and Isaacson 1968a, in rats). This was shown by computing correlations between avoidances in the two directions: normal animals had low correlations; hippocampal animals had quite high correlations.

There is one particular aspect of hippocampal performance in this situation which does require discussion. A number of studies have shown that lesioned animals are considerably more active between trials than are normal animals. This increased rate of inter-trial responding could be responsible for the facilitation seen after lesions. Thus, Schlosberg *et al.* (1969) have shown that hippocampal rats have an abnormally strong tendency to run in response to unsignalled shocks, while Lovely *et al.* (1971) have shown that hippocampal rats run more to stimuli which predict shock, even in the absence of an avoidance contingency. The latter authors conclude that the

'facilitated CAR performance is simply a consequence of this altered responsivity to electric shock' (p. 349).

The idea that facilitation in two-way avoidance after hippocampal lesions is due to an increased responsiveness to the CS, or shock, would make it unnecessary to postulate the absence of place hypotheses. While it is clear that increases in inter-trial responding often correlate with superior performance in hippocampal animals there are reasons for assuming that this activity change is not fundamentally responsible for the superior performance, but might instead result from the action of the same underlying change.

The basic question concerns why hippocampal animals run more in response to shock or to stimuli which have been paired with shock. This is the case not only in the two-way avoidance studies, but also in the various studies by the Blanchards and their colleagues discussed above. This increase in running appears related to a shift in the normal flight/freezing continuum, a shift we have identified with the loss of that part of freezing related to threatening places. While it seems certain that normal animals freeze more in most two-way avoidance studies than do hippocampal animals, it is not the case that this indicates a higher level of fear on the part of the normal animals. Antelman and Brown (1972) reported that hippocampal animals were, if anything, more afraid of the CS than were normal animals. If the CS from their two-way situation was introduced into a new situation, where the animals were engaged in an appetitive task, the hippocampal rats suppressed their ongoing behaviour to a greater-than-normal extent.\* In fact, Antelman and Brown suggest that

\* This result suggests that hippocampal animals learn something about the CS, in opposition to Plunkett's data on generalization (p. 308). Such data demonstrate the need for multiple measures in assessing the importance of procedural factors.

'animals with lesions of the hippocampus were more fearful than control animals' (p. 15).\*

Thus, the decreases seen in freezing, and the concomitant increases in inter-trial responding, cannot be due simply to a decreased fear of the CS. We would suggest that it is possible that hippocampals move more in this situation because of the absence of place fear. Thus the increase in inter-trial responding rests directly on the absence of place hypotheses. It shows up because the animals have no reason to inhibit it. On the other hand, it cannot be the cause of the facilitation in two-way avoidance learning; while this facilitation is usually associated with increased responding this association is not inevitable. Ackil *et al.* (1969) have shown that pre-habituation to the CS decreases the number of spontaneous running responses in the hippocampals to a relatively normal level but does not remove their superior learning. Similarly, Ross, Grossman, and Grossman (1975) have dissociated the two in fornical rats. We conclude from this that the hippocampal superiority in the two-way avoidance situation is due to several factors, but that the basic underlying cause is the absence of place hypotheses. Given the absence of place fear hippocampal animals are more likely to be active and consequently more likely to 'find' the correct hypothesis.\*\*

*Active avoidance requiring non-flight manipulations.* The final category of active avoidance tasks to be considered concerns those in which flight is not a useful hypothesis. Avoidance of shock demands the acquisition of some other response, such as lever pressing. As we have noted, such tasks are acquired only with considerable difficulty in normal animals.

Perhaps the most common variety of such avoidance tasks is the so-called *Sidman avoidance*. Here, the animal is placed in an operant chamber containing a lever or other manipulandum. Each response to the manipulandum delays the onset of shock for a fixed period of time. This task can be set up in a number of ways: the presence or absence of a CS signalling the oncoming shock is one important variable; the prior experience of the animals in similar situations seems to be another.

Acquisition of operant avoidance can be normal in hippocampal rats (Ellen and Wilson 1963, Micco and Schwartz 1971) or under some

\* We have already discussed certain aspects of this abnormally strong fear of items related to shock in hippocampals (pp. 303-6). It is worth noting further that in most of these situations the effect of the threatening item was assessed in a previously safe place. Normal animals might initially regard such an item with less trepidation than if it were presented in its original context. Hippocampals, on the other hand, do not seem to be affected by the context within which threat occurs. This failure of context effects in the lesioned animals suggests that the transfer of incentive effects from one situation to another might consistently appear stronger in lesioned rats.

\*\*A report by Lover (1975) concerning two-way active avoidance would not have been predicted by this interpretation. He showed that hypophysectomy removed the facilitation elicited by hippocampal damage (see our discussion of the pituitary-adrenal system (pp. 357-62)).

circumstances better than normal (Duncan and Duncan 1971, Schmaltz and Giulian 1972). In these latter studies there was the suggestion that the superiority of the hippocampal rats involved their being relatively more likely to respond to the CS with a lever press. Again, we find the hippocampal animals to be unusually tied to the threatening cue.

The only report of a deficit in hippocampal animals in an operant avoidance situation concerns the case where the animals had prior training on a task which required a response that competed with the avoidance response. Thus, Ellen and Wilson (1963) showed that pre-training on a lever-holding shock-escape task interfered with subsequent learning of the lever-pressing shock-avoidance task. This interference from prior operant training is a common feature of hippocampal behaviour in these situations, as we shall see in the next chapter (pp. 320-1). It does not appear to be related specifically to the avoidance contingencies in the Ellen and Wilson study.

*8.2.2(b). Passive avoidance.* Passive avoidance is a term applied to a class of tasks in which animals must refrain from making certain experimenter-defined responses; failure to refrain results in punishment. The use of the term *passive*, as we have already noted, carries with it the implicit assumption that the best solution in such situations lies in immobility or simple non-responding. Thus, Blanchard and Blanchard (1969b) state that

'a "one-trial conditioning" hypothesis for crouching can predict one-trial passive avoidance without any assumption that the S has learned to inhibit a specific response' (p. 374).

While it is clear that rats can learn to remain immobile in order to avoid punishment (e.g. Brener and Goesling 1970), it is not at all clear that immobility *per se* is the preferred mode of solution in most commonly used passive avoidance paradigms. Several investigators (Liss 1968, Olton 1973) have pointed out that animals do not necessarily solve such tasks in a particularly passive way.

We feel that the distinction between active and passive avoidance in the literature is an insignificant one in comparison with the differences between paradigms requiring the use of specific behavioural hypotheses. As our study of one-way active avoidance suggests, animals which have learned actively to avoid places or items will passively avoid them as well (pp. 307-8). What appears to be important is the identification of the threat, rather than the particular response requirement. Thus, prior training on passive avoidance can facilitate subsequent active avoidance (Bresnahan and Riccio 1970), a result that would be impossible if the learning of particular responses were essential in either task. Only when the situation is so constructed as to eliminate the use of either place or guidance hypotheses will an animal resort to the simple motor-response inhibition

learning which the passive avoidance terminology implies.

These 'passive' avoidance paradigms require that the behaviour to be punished be one with a reasonable probability of occurrence. This can either be the result of some prior training or of some inherent tendency on the part of the animal. A number of paradigms based on the use of these kinds of behaviours have been devised, and it is surely the case that they do not all reflect the action of the same underlying mechanisms. In particular, tasks vary in the extent to which they depend upon the avoidance of threatening places or items. Further, within a given paradigm performance can usually be assessed in any of several ways, each of which might reflect the action of different mediating factors. Most passive avoidance tasks can be viewed as situations in which place hypotheses are not essential. One would expect, therefore, that hippocampal animals would have no specific difficulty with such tasks. Before turning to the evidence from lesion studies we shall briefly describe some of the more commonly used paradigms.

*Procedures for passive avoidance.* One major class of passive avoidance paradigms can be labelled *approach-avoidance*. In such tasks the animal is initially trained on an approach task, such as running to obtain food or water, and is subsequently punished for making that response. In most cases this involves the use of a runway or similar apparatus, leading to a goal box with a food or water dish. Punishment in this situation typically involves giving the animal a grid shock while it is consuming the reward; alternatively, shock can be administered through the dish containing the reward. Thus, punishment is usually associated both with the place and the item. Passive avoidance can then be measured in several ways: latency to contact the item; latency to enter the goal area; latency to leave the start area. These measures might reflect the action of different systems. Another variant in this situation concerns the number of punishments. In most cases shock is applied only once, and learning of passive avoidance is assessed under what are essentially extinction conditions. Once the animal returns to the source of punishment (and is not shocked) the situation has changed and one is no longer measuring passive avoidance. In other cases shock is applied on several trials, and the number of shocks taken is a more valid measure of avoidance behaviour.

A related class of passive avoidance tasks involves the use of essentially untrained response tendencies which are highly likely for the species being tested. These typically rely on placing the animal in a situation which is inherently fearful and then punishing its attempts to withdraw. Thus, most animals placed on a raised platform in the middle of an exposed field will step down from the platform in an attempt to move towards the perimeter. This step-down response can be punished and passive avoidance measured as a function of subsequent step-down latencies.

Similarly, animals put out on a perch with a considerable drop to the floor, or in a large, open box, will rapidly move into a smaller box if possible. This tendency can be punished and subsequent step-through latencies measured as a reflection of passive avoidance. These tasks involve something like an approach-avoidance conflict, where one component is learned and the other unlearned.

Another commonly used paradigm involves training animals on one-way or two-way active avoidance and then punishing these active responses. In other words, when placed in the start area the animal must now stay put to avoid punishment; running to the other side will lead to shock. This task has been called *shock-shock* passive avoidance. There are other variants that one could mention here; the reader is referred to Black *et al.* (1977) for further discussion of these and for a more detailed analysis of the performance of hippocampal animals in these situations.

*Hippocampal lesions and passive avoidance.* The results of those studies involving passive avoidance learning in hippocampal animals are given in Table A23. The most striking aspect of these data is that deficits in these tasks, often assumed to be invariably associated with hippocampal damage, have actually been demonstrated in less than half the published studies. Those paradigms which can be described as independent of place hypotheses almost invariably produce no defect in hippocampals. This includes such paradigms as step-down and step-through passive avoidance, as well as the punishment of some consummatory response. Mixed results have been reported for many of the other paradigms. In large measure this confusion can be attributed to differences in the way passive avoidance was measured in the various studies. The data are consistent with the view that hippocampal animals do not passively avoid places devoid of distinctive items, while they do avoid items.

Nonneman and Isaacson (1973) tested cats on an approach-avoidance task. Their animals were trained to approach food and were then shocked for touching the food dish. On subsequent trials their hippocampal cats showed a passive avoidance deficit in terms of their latency to start running towards the area containing the food dish. However, these cats did not, in fact, touch the dish itself more rapidly than did the control animals. This split between immobility in the face of a threatening place and avoidance of a previously punished item was seen in nearly all of the studies performed in this manner. When the measure of avoidance was the latency to move into a dangerous place the hippocampal animals appeared to be retarded; when the measure was contact with the threatening item no defect appeared. Such results were reported by Kimble, Kirkby, and Stein (1966), Andy *et al.* (1967), Brunner and Rossi (1969), and Fried (1971).

A more direct test of the place-item distinction stressed here is available in the study by Blanchard, Blanchard, and Fial (1970). In their Experiment

2, rats were tested for the passive avoidance of what was described as either a highly discriminable stimulus (an electrifiable metal box) or a poorly discriminable stimulus (a portion of the grid). This latter condition was biased towards the use of a place hypothesis. Hippocampal rats avoided the metal box as well as did normal rats but tended to receive more shocks from the grid, though this difference was not statistically reliable. In Experiment 3 of this paper the same rats were tested on another passive avoidance task involving a threatening place and in this case the hippocampals were significantly impaired.

The authors of this report took the position that the hippocampal defect in passive avoidance, and indeed in all avoidance situations, was a function of altered defensive crouching behaviour. At a descriptive level this notion contains a good measure of truth. After raising the question

'What function of the hippocampus, disrupted by hippocampal damage, is normally involved in the elicitation or maintenance of defensive immobility' (Blanchard, Blanchard, and Fial 1970, p. 101),

they proceeded to rule out the possibility that lesioned rats have higher pain thresholds, as well as the possibility that the hippocampus is involved in the association between neutral and painful stimuli. They then pointed out that avoidance of a specific aversive item might be controlled by brain processes different from those controlling immobility, and that these two reactions (flight and freezing) could be elicited by differentiable conditions.

We have previously discussed the question of flight and freezing (pp. 294-302) and feel that the analysis given by Blanchard, Blanchard, and Fial is correct up to a point; however, it is important to extend their account to distinguish those different conditions responsible for flight and freezing. Freezing is most often a response to an inescapable place, though it can occur in the presence of an inescapable threatening item. Most studies focus on the former, so that there has been a conflating of freezing and place-dependent threats that is misleading. The fact that immobility reactions seem to be defective in hippocampal animals in most of the studies reported to date could mean either that they cannot react appropriately to threatening places or that they cannot emit immobility responses. We believe the former interpretation is more likely and predict that lesioned animals would freeze appropriately when such behaviour was necessary for avoidance of an object.

Analysis of the passive avoidance data in terms of the place-item distinction imposes regularity on what otherwise appears to be a rather messy set of data. It is difficult to extend this analysis any further, as it is often impossible to know from the published reports the extent to which different behavioural strategies are tapped by different paradigms. Only in those situations requiring place hypotheses, or with the use of measures

reflecting place-learning mechanisms, will a deficit appear in hippocampal animals. The passive avoidance of threatening items is intact in these animals.

One further paradigm, conditioned taste aversion, supports this analysis. This task involves poisoning a novel food and measuring the animal's subsequent avoidance of that food. We noted earlier (p. 292) that the learned aversion and learned safety seen in this situation represented clear examples of the way in which items are tagged with some motivational valence through experience. The effects of hippocampal lesions on this type of learning have now been assessed in eight studies (Table A23). Miller, Elkins, and Peacock (1971) reported that rats with extensive hippocampal ablations failed to show conditioned aversion, but the effect was quite small in their control animals as well. Best and Orr (1973) reported deficits only after dorsal hippocampal lesions, while McGowan *et al.* (1972) reported no deficits with either dorsal or ventral lesions. Five subsequent studies all reported no deficits in hippocampal animals, in terms of the acquisition, magnitude, and extinction of conditioned aversion. Taken together, these studies indicate that the hippocampus is not integral to this type of passive avoidance learning.

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