9

Operants: the limited role of the locale system

In the previous chapters of this section of the book evidence was marshalled in support of the view that hippocampal animals lack exploratory mechanisms and the ability to construct locale space; consequently they cannot utilize place hypotheses. In the absence of the locale system hippocampal animals solve problems with taxon hypotheses, and their behaviour reflects the properties of the taxon systems. Certain experimental situations will primarily reflect the operations of the taxon systems; some examples of this are classical conditioning and most operant training procedures. In these and other taxon-biased situations we would expect the hippocampal animal to perform at least as well as the intact animal, though perhaps in a different manner. In this chapter we consider a variety of experimental procedures which extend this analysis.

9.1. Classical conditioning and incentive effects

What little evidence is available suggests that hippocampal lesions do not affect the learning of classically conditioned responses. Thus, Allen (1940) showed that hippocampal dogs acquired an olfactory conditioned forelimb response normally, while Isaacson and Douglas (cited by Douglas 1972) showed that hippocampal dogs acquire a forelimb flexion response quite rapidly. Schmaltz and Theios (1972) have shown that hippocampal rabbits acquire a nictitating membrane response more rapidly than do normal rabbits. Finally, Pigareva (1974) reported normal acquisition of a conditioned alimentary reflex with either 100 per cent or 50 per cent reward.* **

A variation of classical conditioning techniques involves what has been termed *incentive motivational* conditioning. When an initially neutral stimulus is paired with reward (or punishment) this stimulus acquires general motivational properties and can then function as an incentive (cf. Bindra 1968). Such incentive stimuli, when introduced into a new situation, often have marked effects upon an animal's behaviour. We have already discussed the way in which stimuli associated with pain exert effects upon an animal's behaviour in other situations; this is one example of an incentive effect. The fact that incentives transfer from one environment to another indicates that the locale system is not essential to their effects; this suggests that hippocampal animals should show incentive effects.

Available data support the view that stronger than normal incentive effects are seen in hippocampal animals. Morey and Brown (1972) measured the effect of positive incentive conditioning on general activity and goal-directed behaviour. During the conditioning process hippocampal rats were significantly more locomotor in response to the incentive stimulus than were intact rats; they did not, however, show more goal-directed behaviour. Antelman and Brown (1972), in the course of a study on two-way active avoidance described above (p. 309), tested the effect of the avoidance CS on licking behaviour in another situation. They found that this negative incentive stimulus suppressed licking behaviour to a greater extent in the hippocampals than it did in the controls. These studies indicate that there is no basic defect in the response of hippocampal animals to incentive stimuli, either positive or negative.

On the other hand, Micco and Schwartz (1971) presented evidence which suggested to them that reactions to conditioned incentives could be defective in hippocampals when inhibition was required. Rats were trained on a lever-press Sidman avoidance task. Following this, in a separate apparatus, positive and negative incentive stimuli (tones) were established. The effects of the introduction of these tones upon avoidance performance were then assessed. In both intact and hippocampal rats the negative incentive stimulus (previously paired with shock) led to an increase in the rate of lever pressing; the positive incentive stimulus decreased lever pressing in the intact, but not the hippocampal, rats. The results summarized in the previous paragraph plus studies involving CER conditioning (see pp. 304-5) indicate that the explanation offered by Micco and Schwartz is highly unlikely; in other experiments hippocampal animals could inhibit responding quite well when confronted with negative incentive stimuli. One possible source of the discrepancy lies in the nature of the behaviour involved. Micco and Schwartz used an operantly trained response, while Antelman and Brown (1972) and Nadel (1968) used a consummatory response (licking at a spout).

9.2. Operant tasks

In the typical operant task the animal is placed in a relatively restricted environment containing one or more manipulanda; responses to these manipulanda are rewarded in some fashion. A typical operant chamber for rats, the Skinner box, is simply an enclosed box containing a lever and a recessed food well in most cases. Presses on the lever are rewarded by

* Deficits were seen when reward was only given on 33 or 25 per cent of the trials. We shall discuss the partial reinforcement effect in the next chapter.

** Hippocampal lesions can affect the retention of classically conditioned responses (Gralewicz and Strumillo 1971, Gralewicz and Zdankiewicz 1973). The problem of retention is discussed later (pp. 374-7).

delivery of a food pellet through a food magazine. Similar apparatus can be devised for other species. It is important to note that the responses required of the animal in most of these situations are of a very low initial probability of occurrence and the animal must be 'shaped', or specially pre-trained, to perform them.

By their nature most operant tasks minimize the role of the hippocampus in the control of the animal's behaviour, though they do not eliminate it. The impoverished sensory environment of the Skinner box is designed to elicit only a limited amount of exploration. Initially this might help the animal locate the significant features of the box, such as the lever and food well, but very quickly the reward contingencies should strengthen the taxon hypothesis 'press the lever' and locale involvement should be drastically reduced.

It is worth digressing here to describe how the relative insensitivity of operant tasks to hippocampal function is a direct and ineluctable result of Skinner's scientific methodology. We have it on his own word (Skinner 1959) that he is guided in his work solely by the search for order or lawfulness in behaviour:

'the notes, data and publications which I have examined do not show that I ever behaved in the manner of man thinking as described by John Stuart Mill or John Dewey or as in reconstructions of scientific behaviour by other philosophers of science. I never faced a Problem which was more than the external problem of finding order. I never attacked a problem by constructing a Hypothesis. I never deduced Theorems or submitted them to Experimental Check . . . Of course, I was working on a basic Assumption–that there was order in behaviour if I could only discover it– but such an assumption is not to be confused with the hypothesis of deductive theory. It is also true that I exercised a certain Selection of Facts, not because of relevance to theory but because one fact was more orderly than another. If I engaged in Experimental Design at all, it was simply to complete or extend some evidence of order already observed' (p. 364).

Since Skinner seeks order not in a theoretical model but rather in surface behaviour, he constantly redesigns his experiments not with a view to understanding behaviour but rather to eliminating the reasons for its variability. This stems from one of his unstated assumptions: that all intra-individual variation in behaviour is due to environmental noise, a chance response to a stimulus. Similarly, inter-individual variation is due to biological and cultural noise. One of the main tenets of our model is that this thesis, underlying so much of present-day psychology, is completely wrong. Instead, we submit that one of the major brain systems controlling behaviour, the hippocampus, is specifically designed to produce variability in behaviour. On this model behaviour cannot be wholly explained on its own level but must be shown to depend upon law-abiding neural systems.

Skinner recognizes this alternative:

'It is the function of learning theory to create an imaginary world of law and order and thus to console us for the disorder we observe in behavior itself. Scores on a T-maze or jumping stand hop about from trial to trial almost capriciously. Therefore, we argue that if learning is, as we hope, a continuous and orderly process, it must be occurring in some other system of dimensions—perhaps in the nervous system, or in the mind, or in a conceptual model of behavior' (p. 375).

but rejects it.

'When we have achieved a practical control over the organism, theories of behavior lose their point. In representing and managing relevant variables, a conceptual model is useless; we come to grips with behavior itself. When behavior shows order and consistency, we are much less likely to be concerned with physiological or mentalistic causes. A datum emerges which takes the place of theoretical phantasy. In the experimental analysis of behaviour we address ourselves to a subject matter which is not only manifestly the behavior of an individual and hence accessible without the usual statistical aids but also 'objective' and 'actual' without recourse to deductive theorizing' (p. 375).

It is little wonder, then, that Skinner moved very quickly from his original studies on exploratory behaviour to reflexes and ultimately to operant tasks. Although one of his stated principles of research is

'when you run onto something interesting, drop everything else and study it' (p. 363),

without a theory or preconceived notion of how animals function he had no means of deciding which things were interesting. One instance is particularly illuminating within the context of our theory. During an alley study Skinner tried to save himself some leg work by getting the animal to return by itself to the start of the alley after each trial. The modified apparatus was essentially a rectangular maze with food always given in one corner (C) after a complete circuit. It worked in principle, but

'there was one annoying detail, however. The rat would often wait an inordinately long time at C before starting down the back alley on the next run. There seemed to be no explanation for this' (p. 365).

Having approached so close to the precipice, the quest for explanation, he safely jumps back:

'When I timed the delays with a stop watch, however, and plotted them, they seemed to show orderly changes. This was, of course, the kind of thing I was looking for' (p. 365).

The alleys eventually became Skinner boxes, the delays smoothed out,

and the important question—why did they delay?—finessed.*

The Skinner box, and most operant procedures employed therein, consequently put few demands upon the locale system. We can now look at the results of studies of operant behaviour in hippocampal animals. In this chapter we shall be concerned primarily with the performance of animals on various operant schedules as such; in the next chapter we shall take up the question of the effects of changes in reward conditions upon behaviour, and the problem of shifts in operant schedules will be considered within that context.

Hippocampal animals have been tested on a wide variety of operant schedules; the results of these studies are given in Table A24. Before considering these in more detail it would be worthwhile to consider the grosser aspects of the behaviour of animals in the operant situation. As we noted above, lever pressing is a low-probability response, at least in rats, and special 'shaping' techniques must be used to generate appropriate performance. Typically, these involve first training the animal to eat or drink, in conjunction with the noise from the reward magazine. Following this, animals are shaped, often by a method of successive approximations, to press the lever for reward. Only when this has been accomplished can the effect of various reward schedules on performance be assessed.

Those few reports which comment upon this early stage all suggest that hippocampal animals react abnormally to the shaping procedures. In the rat, for instance, Schmaltz and Isaacson (1966a) note that

'the initial reinforcements have highly differential effects on the animals. The hippocampally lesioned rats take up a position close to the food cup after several reinforcements. The normal and decorticate rats, on the other hand, continue to explore the operant chamber and require many more reinforcements until they are magazine trained' (p. 180),

while Warburton (1972) notes that

'during shaping the hippocampal animals showed a marked tendency to remain close to the water nozzle after the first few reinforcements' (p. 351).

Warburton found that this tendency made it difficult to shape lever pressing, while Schmaltz and Isaacson state that

'in the majority of cases, the hippocampectomized rats, once magazine trained, were easily shaped to the bar press response. This was due chiefly to the

* Why, indeed, did Skinner's rats delay their running? This task appears to be an appetitive counterpart to the two-way active avoidance task (p. 298). There, the situation allows for a conflict between two hypotheses: (1) avoid a dangerous place, and (2) run to avoid shock. In Skinner's situation the conflict lies between similar place and response hypotheses. In a similar study Brown (1946) failed to find any effect of a common start-finish locus on maze performance. However, in this study there was little indication that the rats were utilizing place hypotheses, as both maze rotation and a substantial lateral shift of the maze had little effect upon performance. We would predict that in a properly constructed situation, allowing for conflict between hypotheses, hippocampal animals would perform 'better' than normal animals, failing to show the delay.

repetitive nature of much of their behavior. Once reinforced for a response, they tended to repeat this response over and over again until another reinforcement was given. In a few instances, however, the repetitive behavior of hippocampectomized animals interfered with the shaping process. Responses became so rigid that it was very difficult to use the successive approximations technique' (p. 180).

Similar findings were reported for the monkey by Jackson and Gergen (1970). They noted that:

'during hand training, attempts to use successive approximations became difficult because responses that were initially reinforced were hard to extinguish. These responses quickly became stereotyped, and the animals would frequently perform certain of these responses repetitively in a ritualistic sequence' (p. 544).

Thus, reward appears to have a strong effect upon the hippocampal animal in this situation, leading to repetitive responses to the lever and food or water dish. The intact animal, on the other hand, is more variable in its behaviour, rarely repeating responses. The importance of this difference will become clear in our discussion of the various operant schedules.

9.2.1. CONTINUOUS REINFORCEMENT—CRF

The foregoing discussion of shaping effects applies to an operant schedule where the animal is rewarded for each response to the lever; this is termed a continuous reinforcement (CRF) schedule. In line with the above discussion it is not surprising to note that hippocampal rats can acquire CRF responding more rapidly than can control rats (Schmaltz and Isaacson 1966a, Means, Walker, and Isaacson 1970) and tend to respond more frequently, though this difference is rarely a significant one (cf. Rabe and Haddad 1968, Haddad and Rabe 1969). An important difference between hippocampal and normal rats in the CRF situation was brought out in a recent study by Van Hartesveldt (1973). Her rats were trained with either a large or small reward (0.08 ml or 0.01 ml water); hippocampal rats acquired the response at an equal rate under both reward conditions, while control rats acquired the response as rapidly with the large reward, but were reliably slower with the small reward.*

9.2.2. FIXED RATIO—FR

On this schedule the animal is rewarded for making a fixed number of responses: thus, reward rate and response rate are directly related. Four studies of performance on FR schedules in hippocampal animals have been

* This difference in acquisition rates does *not* imply that the hippocampal rats are insensitive to differences in reward magnitude. In this study, as well as in several others (e.g. Franchina and Brown 1971, Gaffan 1972, Freeman *et al.* 1974) their response rates vary with reward magnitude in a normal way. There is no evidence to suggest that the hippocampus is fundamentally involved in evaluating reward magnitude. We suspect that under the low-reward condition control rats were more likely to explore and thus slower to learn.

reported. Van Hartesveldt (1973) concluded that the data from her study and two earlier ones (Rabe and Haddad 1968, Carey 1969) indicate normal performance by the lesioned rats on FR so long as there is a gradual increase in the FR requirement. Thus, Rabe and Haddad started their rats on CRF and then shifted them to FR-20; they found increased responding in their hippocampal rats, beyond that seen in the control rats. However, Carey (1969) and Van Hartesveldt (1973) shifted their rats from CRF to FR-5, then FR-10, and only gradually increased the response requirements; in these cases the hippocampal rats responded at normal rates. Consistent with this, Rabe and Haddad found that the response rates of hippocampals increased normally when the rats were shifted from FR-20 to FR-30. Finally, a more recent study (Schmaltz, Wolf, and Trejo 1973) also found that FR performance was normal when the ratio was gradually increased. Thus, shifting from CRF to FR-5, FR-10, FR-20, and FR-40 yielded normal response rates. However, shifting to FR-80 and then FR-160 produced abnormal increases in response rates in the hippocampal rats, though they eventually adjusted their response rate to a normal level on the final FR-160 sessions. Thus, FR performance can be normal in hippocampal animals, except when they have been shifted from a schedule with markedly smaller demands. The meaning of this over-reaction will be discussed shortly.

9.2.3. FIXED AND VARIABLE INTERVAL - FI AND VI

On these schedules the animal is rewarded once during a given interval (either fixed or varying about a mean), regardless of the number of responses made during that interval. The FI schedule generates a particular pattern of responding, often referred to as the FI scallop (because of its appearance in cumulative recorder records). Typically, the animal shows a post-reward pause in responding, then starts responding more rapidly as the end of the interval approaches. This pattern does not appear with the VI schedule, which has consequently been of less experimental interest. In the only study utilizing VI with hippocampal animals Jarrard (1965) found increased response rates in his pre-operatively trained lesioned rats.

Four studies of FI performance in hippocampal animals have been reported. Ellen and Powell (1962) reported relatively normal FI performance in their hippocampal animals, with a tendency towards decreased responding. Their lesioned rats developed an FI scallop but responded less frequently during the period just before reward than did controls. On the other hand, it took longer for the hippocampals to develop a marked post-reward pause. Both Beatty and Schwartzbaum (1968) and Haddad and Rabe (1969) report mostly increased response rates for hippocampal rats on FI. Haddad and Rabe included two lesion groups in their study: one with small anterior lesions similar to those used by Ellen and Powell,

the other with larger anterior-posterior lesions. The group with small lesions performed normally, in accordance with Ellen and Powell, the group with large lesions had increased response rates.

Analysis of the temporal patterning of responses reveals several differences between hippocampal and control rats. Haddad and Rabe found that their lesioned rats developed a more pronounced FI scallop than did control rats; that is, they responded at an increased rate just prior to the reward. However, they apparently showed no abnormality in the development of a post-reward pause.* Beatty and Schwarzbaum (1968), on the other hand, found a significant retardation in the development of the post-reward pause in their lesioned rats, combined with a less marked increase in terminal rates. In a separate group of lesioned rats these authors investigated FI performance under conditions of non-deprivation. The pattern of increased post-reward responding and normal terminal responding was also evident in these rats, performing for sucrose.

These discrepancies are not easily accounted for. Such factors as the reward employed (Beatty and Schwartzbaum used sucrose, the others water) and the extent of prior CRF training might have been involved in their production. In any case, all of the studies show a disruption of FI performance related in some temporal fashion to the reward, either its prior or its anticipated occurrence.

9.2.4. DIFFERENTIAL REINFORCEMENT OF LOW RATES—DRL

The seeming abnormalities of hippocampal animals on FI schedules, involving aberrant temporal patterning of responses, have been explored more thoroughly using another schedule presumed to require precise patterning of responses. In the DRL schedule the animal must withhold its responses for a fixed period of time before reward becomes available. Responses during this delay interval reset the delay; thus, high rates of responding, or an inability to pattern responses, lead to low rates of reward. A large number of DRL studies have been reported for hippocampal animals, with often confusing results. Before considering the performance of lesioned animals in detail it is worth discussing the nature of normal performance. The DRL schedule is a difficult one for the normal rat. Typically, no more than 50 per cent of the available rewards are obtained, and reward/response ratios rarely go beyond 40 per cent. In the intact rat responses are patterned as follows: there is an immediate post-reward burst, followed by a decline in responding, then by a build-up towards the end of the delay interval. With continued training there is a decrease in short-latency responses which partly accounts for observed improvements. It is clear that it is quite difficult for normal rats to perform well in the standard DRL situation. This difficulty is related to the multiple hypotheses that can be used in this situation.

* Jackson and Gergen (1970) report the same pattern for the hippocampal monkey.

Responses to the lever are both rewarded and punished; thus, the tendency will exist both to approach and avoid the lever. The intact animal resolves this conflict by using a place or orientation hypothesis to mediate lever pressing and a different hypothesis to avoid the lever during the delay interval. We have already seen that cats in this situation move to the opposite side of the box and lie down during the delay (Bennett 1975, see p. 185). In discussing the 'collateral' behaviour which develops to bridge the DRL delay, Kramer and Rilling (1970) indicate that pigeons, as well, utilize the strategy of moving away from the lever at the inappropriate time. Laties, Weiss, and Weiss (1969) have studied the collateral behaviour of rats, showing that any behaviour which takes the animal away from the lever and keeps it busy will improve DRL performance. The introduction of a cue signalling the termination of the delay period makes such collateral behaviour unnecessary. If we can judge by the change in hippocampal EEG patterns, such a cue alters the cat's delay behaviour (Bennett 1975). In both cat and rat the cue vastly improves DRL performance, yielding up to 70 per cent rewarded responses. Hippocampal animals should be able to generate some form of adequate collateral behaviour, though they could not use a place hypothesis taking them away from the lever. Further, they should benefit from the introduction of the cue.

However, most DRL experiments are preceded by extensive training on CRF. This would have the effect of increasing the strength of the orientation hypothesis mediating lever pressing, perhaps more so in hippocampal than in control animals, as we have seen. As a consequence, such pre-training would make it much harder for the hippocampal animal to find adaptive collateral behaviours strong enough to compete with the hypothesis established during CRF training. In the absence of any possibility of using a place hypothesis, this condition should maximize the hippocampal animal's difficulty with the DRL task. There are two ways in which the lesioned animal could be helped to overcome this difficulty: (1) through the introduction of a cue; (2) through the opportunity to develop strong taxon-based collateral behaviour.

While hippocampal animals are often deficient at DRL there are conditions under which they perform normally. Ellen *et al.* (1973) showed that both extensive lesions *and* extensive pre-training on CRF are necessary for persistent impairments in this task. Earlier studies reporting normal DRL performance in hippocampals utilized either small lesions (e.g. Ellen, Wilson, and Powell 1964) or minimal CRF pretraining (e.g. Schmaltz and Isaacson 1966a). There is a consistent, though apparently not inevitable, relationship between response rate and performance in the DRL situation, and the fact that CRF schedules can elicit increased response rates in hippocampal animals provides a basis for understanding the effect of CRF pre-training on subsequent DRL performance. There are conditions, however, when response rates and performance (in terms of the number of rewards obtained)

do not co-vary. Thus, Schmaltz and Isaacson (1968) demonstrated that blinding hippocampal rats reduced response rates but did not noticeably increase reward rate. Schmaltz *et al.* (1973) showed that hippocampal rats trained initially on FR and then switched to DRL did not respond significantly more than did intact rats, but nevertheless received fewer rewards. On the other hand, Nonneman and Isaacson (1973) showed that a deficit in DRL in neonatally lesioned rats only occurred in combination with high CRF rates. Lastly, the addition of a cue signalling the end of the delay interval both decreases response rate and increases reward rate, such that hippocampals perform as well as do normals (Pellegrino and Clapp 1971, Rickert *et al.* 1973) whether or not they have received extensive CRF pre-training.

9.2.5. A SYNTHESIS

The overall picture provided by these operant studies suggests several conclusions: (1) the lever pressing response is one that hippocampal animals acquire rapidly and execute repetitively; (2) this repetitive responding can interfere with performance on certain schedules, particularly those requiring precise temporal patterning of responses; (3) hippocampal animals seem abnormally sensitive to abrupt shifts in reward contingencies; (4) to some extent the deleterious effects of repetitive responding can be ameliorated by the addition of an external cue guiding the animal's responses.

These conclusions suggest to us the following analysis of hippocampal performance in operant situations. Lever pressing itself is easily supported by an orientation hypothesis. This, coupled with the absence of exploration, leads the hippocampal to acquire the basic lever-press routine faster than will the normal and can produce over-responding without loss of rewards in both CRF and FR schedules. Increased responding would not result in fewer rewards in the FI schedule but could result in abnormal temporal patterning of responses. Here, as in the DRL schedule, alternate hypotheses can take the animal away from the lever during those times when responses are either ineffective or actually punished (through an increase in the delay period). That is, we feel that rats cannot 'count time', but rather bridge temporal intervals by engaging in any of a variety of behaviours which fill the required interval. The normal rat can call on behaviours based on place (go to the other side of the box), guidance (do not press unless light is on), or orientation (engage in a sequence of collateral displacement behaviours) hypotheses. The hippocampal rat is restricted to guidance or orientation hypotheses.

We have seen that the provision of a guidance in the DRL schedule enables the hippocampal animal to bridge the delay as well as can the normal animal. Promoting the use of collateral behaviours based on orientation sequences should similarly improve the performance of hippocampal animals.

Preliminary evidence (Van Hartesveldt, personal communication) supports this prediction. There is some evidence available on the use of orientation sequences by lesioned animals in situations other than the DRL. While several early studies suggested that hippocampal animals were deficient at learning such sequences (Kimble and Pribram 1963, Gross, Chorover, and Cohen 1965), later work has demonstrated that these animals learn sequences more rapidly, and better, than do normal animals. For example, Jackson and Strong (1969) have shown that hippocampal rats are superior to intact rats at learning to press up to three levers in various sequences to obtain reward.

We can now turn to a discussion of a mixed group of studies which combine certain features of operant and discriminative behaviour. In some of these tasks locale mechanisms play an important role, while in others they are of miminal importance.

9.3. Delayed response

In this task the animal is typically confronted with several identical food wells, but temporarily prevented from approaching them. One of these wells is then baited with reward and, after some delay, the animal is allowed to respond. Delayed response tasks are seemingly dependent upon locale mechanisms; that is, a food well is baited in sight of the animal, and proper performance requires that the animal remembers the location of that well which was baited and then, when given the opportunity, responds to it. In other words, the animal must use information about *where* to direct its response, rather than to what kind of object it must respond.

There is little doubt that hippocampal damage causes deficits in delayed response; Table A25 gives the results of those studies which have used this task. The suggestion of a deficit was present in early work with monkeys (Mishkin 1954, Orbach, Milner, and Rasmussen 1960). Later work with cats and rats showed profound impairment of delayed response (Karmos and Grastyan 1962, Ungher and Sirian 1970, Niki 1962). However, more recent work, again in monkeys, showed no deficit in delayed response (Mahut 1971). There is little doubt that hippocampal animals remember that *some* food well has been baited for they respond rapidly after the delay interval. Deficits which are reported presumably reflect the animal's inability to distinguish between several identical objects solely in terms of their spatial location. Karmos and Grastyan (1962) tested cats in a situation with food wells on each of three walls of a box, the animal being restrained in a waiting box (with glass wall) attached to the fourth side of the box. A tone presented through the speaker mounted over a food well signalled the availability of food in that well. Hippocampal cats were deficient at delayed response primarily because they responded to the first well that caught their sight upon entering the test area after the delay.

Similar results were reported by Ungher and Sirian (1970). Their fornical cats made errors primarily by responding to the wells which were closest to the restraining box.

In the absence of an ability to remember where the correct well is located, the hippocampal animal could perform adequately by assuming a posture during the delay which 'told' it the location of the correct well. Ungher and Sirian report that fornical cats which used this strategy did manage occasionally to perform adequately. They state that:

> 'after being presented the meat bowl, some cats with fornicotomy and sometimes the controls maintained, over the delay interval, while still in the cage, the bowl-watching posture. This facilitated the delayed response performance in the damaged cats; they seemed to have memorized the cues. If during the delay interval the damaged cat was made to shift from this posture the erroneous responses multiplied ... Diverting maneuvers in controls rarely resulted in erroneous responses' (pp. 177-179).

Mahut (1971) has also suggested that her hippocampal monkeys solved the delayed response task by using a strategy which could override their spatial defect. It seems likely, then, that the spatial component in the delayed response situation is responsible for such defects as are observed in hippocampals.

9.4. Alternation and go–no-go

There are a variety of tasks which involve alternating or interchanging responses in some fashion. We have just discussed one variant, that involving the performance of a sequence of responses, with a complete sequence leading to reward. Available evidence indicates that hippocampal animals are quite capable of learning these sequences. Another, somewhat different, class of tasks typically limits response alternatives to two, and requires that the animal alternate between these in some way. Thus, on successive trials reward could follow a right turn in a T-maze, then a left turn, then a right, and so on. This is simply a rewarded counterpart of the spontaneous alternation task. Similarly, in a two-lever Skinner box successful performance could involve pressing the left lever for reward, then the right lever for another reward, then the left, and so on. In one version of this task cues are not provided, and the animal must alternate on the basis of its memory of the preceding response. In a second version cues are provided as to which lever is to be pressed, and alternation can be achieved simply by responding to the cues. These tasks have typically been labelled *spatial delayed alternation,* as they involve changing responses over time in terms of space.

A third class of tasks, often called *non-spatial alternation,* involves emitting or withholding one particular response. Thus, on one trial reward is obtained by responding, whereas on the next trial there is no reward and

proper performance involves withholding the response. This alternation pattern can be tested in either the Skinner box or the alley. It is *not* a true non-spatial analogue of the spatial alternation task noted above; such an analogue would involve the presentation of two items, with reward alternating between the two from trial to trial while the items shifted location in some random fashion. Such an item alternation task has not, to our knowledge, been used with lesioned subjects.

The non-spatial alternation task is a special case of a broader category of tasks labelled *go–no-go:* here, responses are sometimes rewarded, sometimes not. The availability of reward is typically signalled by a guidance; in the special case of alternation the guidance is replaced by the memory of the previous trial.

9.4.1. SPATIAL ALTERNATION

Most experiments involving spatial alternation in hippocampal animals have employed operant chambers; a few studies, in rats, have used two-choice mazes. The results of these studies are given in Table A25. In the studies using a T-maze or Y-maze deficits have generally been noted, even when inter-trial intervals are quite brief (e.g. Racine and Kimble 1965).* As in tests of spontaneous alternation (see p. 260) hippocampal animals find it quite difficult not to repeat responses. The deficit seems related in some way to the fact that the type of maze typically used restricts choices to two markedly different turns. Hirsch (1970) tested rats in a modified Thompson box** with four doors. Reward followed any choice which was not a repetition of the previous choice. In this situation rats with hippocampal lesions obtained a normal number of rewards; however, they tended to alternate between two choices, while the control animals spread their responses more evenly over the four choices.

Though deficits are often reported in alternation tested in an operant chamber there are exceptions, in monkey (Waxler and Rosvold 1970), cat (Brown, Kaufman, and Marco 1969), and rat (Stevens and Cowey 1972, 1973). In the Waxler and Rosvold study data were presented for individual monkeys. Some hippocampal monkeys were normal while others were deficient, and these differences could not be attributed to any difference in the size of the lesion, as had been suggested by an earlier study (Rosvold, Mishkin, and Szwarcbart 1964). The authors suggested that there are several ways to learn this task, and that some of these might require the hippocampus, while others would not. For example, they noted

* Jarrard (1975) has shown that pre-operatively trained rats perform a Y-maze spatial alternation following hippocampal lesions, even with inter-trial intervals as long as 10 mins. This atypical result could be a function of any of several procedural differences between the various studies: (1) the pre-operative training; (2) the use of correction or non-correction procedures; (3) the use of a heterogeneous maze providing cues to alternation.

** This apparatus typically is rectangular, with partitions dividing it into a start area, a choice area containing doors, and a goal area.

that some monkeys tended to respond to one manipulandum and then immediately switch to the other one to await the next trial; this strategy correctly 'tells' the animal where to respond and, if used by a hippocampal monkey, could lead to normal performance. Other monkeys tended to respond to one manipulandum, await the next trial, and then switch to the other side. It is likely that a hippocampal animal using this strategy would be impaired in that it would respond immediately to the nearest manipulandurn upon starting the next trial. This being the case, one is surprised that most other studies have reported such clear-cut deficits in spatial alternation learning in hippocampal monkeys. Mahut (1971) also presents individual data and again there was a split in the hippocampal group: two failed completely while two learned, though at a retarded rate. The total failure of both monkeys with amygdala lesions in Mahut's study may partially explain the total deficits reported in the early studies; the lesions in these latter studies often included some damage to the amygdala.

Thus, while the story is not clear as yet, it does seem likely that the monkey without a hippocampus can sometimes find a way to solve this task, perhaps along the lines suggested by Waxler and Rosvold. In the only cat study reported, that by Brown *et al.* (1969), the hippocampal animals were slightly, though not reliably, worse than were the intact animals. The authors did not comment upon the way in which the animals solved the task. We already have noted in our discussion of delayed response that lesioned cats can learn to take up postures which overcome their spatial defect, and this might have happened in the Brown *et al.* study.

Four operant spatial alternation studies have been reported for the rat; two of these found deficits in hippocampal rats (Niki 1966, Riddell, Malinchoc, and Reimers 1973), while two found either normal or better than normal performance in the lesioned rats (Stevens and Cowey 1972, 1973). There were some important procedural differences between these studies which might account for the different results they obtained. Stevens and Cowey (1972) report four studies, all using the same basic paradigm. Rats were placed in a Skinner box with two levers (or panels) on either side of a recessed well in which a food cup was located. In some of the studies cues were presented, either on the panel or above and to the side of the lever, while in others there were no cues to the alternation pattern. Among the results reported in this series of studies were the following.

(1) Both control and hippocampal groups performed reliably better when a relevant cue was provided, whether on the panel or to the side of the lever. This improvement was limited, in Stevens and Cowey (1973), to rats with dorsal but not ventral hippocampal lesions.

(2) The availability of an irrelevant cue (unrelated to the position of the 'rewarded' manipulandum) also improved performance, though to a lesser extent than did the relevant cue.
(3) Hippocampal rats performed equally well when the cue was spatially contiguous with the response site (lit panel) or when it was separate (light to the side of lever), while the control rats were as good as the hippocampals with the spatially contiguous cue, but significantly poorer with the separate cue.
(4) Contrary to the claims of the authors, there is little evidence that the rats learned the alternation task in the absence of the cue.

Performance of all the non-cued groups peaked at between 60 and 70 per cent. Random initial choices, combined with a 'lose-shift' strategy would generate 'learning' scores of roughly 65 per cent. The 'learning' seen in these animals, then, seems to involve the adoption of such a strategy.

Much the same thing was seen by Niki (1966), whose normal rats achieved only 70 per cent correct responses after 10 days of training without cues, and by Riddell, Malinchoc, and Reimers (1973), who set their criterion at 50 per cent correct responses in the absence of cues. The deficit in Niki's study was related to the fact that

'bursts of responding on the same bar were frequently observed in the hippocampal animals' (p. 4).

Thus, a major difference in these studies might be the extent to which they fostered the adoption of a 'lose-shift' strategy; this is consistent with procedural differences between the studies. Niki gave his animals 50 rewards per day, regardless of how long this took, while Riddell, Malinchoc, and Reimers gave their animals 20 correction trials each day. Stevens and Cowey, on the other hand, tested their animals for a fixed period of time and the number of rewards that could be obtained was inversely related to the amount of time spent responding to the incorrect lever. In this sense the rats in the Stevens and Cowey studies were under pressure to avoid perseverative errors, while the same was not true in the other studies. This analysis is consistent with data concerning the rate at which the animals decreased perseverative errors in the various experiments. In both the Niki and Riddell, Malinchoc, and Reimers studies the decrease was relatively slow, normal rats achieving 50 per cent only after five to six days, while in the Stevens and Cowey studies 50 per cent performance was achieved by the fourth day. The deficits reported by Niki and Riddell, Malinchoc, and Reimers, then, could relate to the low cost of perseverative responding in their situations, in conjunction with the established tendency of hippocampal animals to engage in bursts of incorrect responses. *

* The massive defect in Riddell, Malinchoc, and Reimers is certainly related to the fact that the rats had just previously been performing a position task in the same apparatus. This prior experience could only exacerbate the difficulties of the hippocampal rat.

The most interesting aspect of these data is the abject failure of all the animals to acquire the alternation pattern in a remotely successful way in the absence of cues in the operant chamber, as compared with the relative ease with which alternation is acquired in the T-maze. In the latter case there are two distinct locations containing food and the normal animal can adopt a place hypothesis involving alternation between the two. In the operant chamber the food is often in the same place regardless of which lever is to be pressed, while the proximity of the two levers and the restricted overall environment minimize the usefulness of place hypotheses. As in the DRL task, the provision of a guidance improves normal as well as hippocampal performance.*

9.4.2. GO–NO-GO AND NON-SPATIAL ALTERNATION

The essential feature of the go-no-go situation is that sometimes a particular response is rewarded while at other times the identical response goes unrewarded. The cue to the availability of reward can be either external (e.g. a tone signalling the fact that a response will be rewarded, the S^+), or internal, as in temporal discrimination, or through the use of a patterned sequence of discrete reward and non-reward trials.

The results from studies of go–no-go are presented in Table A25, separated into those which provided cues and those which utilized temporal or patterned-trial procedures. In the standard go–no-go procedure a confused mixture of results has been reported. In two early studies, which were not adequate tests of go–no-go (Niki 1965, Swanson and Isaacson 1967), hippocampal rats were extensively pre-trained on a CRF lever-pressing task and then a discriminative stimulus (S^-) was introduced signalling the non-availability of reward. In both studies the hippocampal rats failed to decrease their responding during the S^-. The fact that there was extensive CRF pre-training, however, limits the generality of these results.

Schmaltz *et al.* (1973) have reported that rats with hippocampal lesions are deficient in go–no-go, and that this deficiency involves over-responding to the S^- and, during the later stages of the study, the S^+ as well.** Similarly, Wild and Blampied (1972) and Woodruff, Means, and Isaacson (1973) report that hippocampal rats are impaired both on retention and acquisition of go–no-go. On the other hand, Schwartzbaum, Thompson, and Kellicutt (1964) showed that hippocampal rats could retain a preoperatively acquired go–no-go discrimination, the only abnormality in

* We have already discussed the fact that when the cue is at a remove from the lever normal animals perform less well than do hippocampals (p. 268).

** In this study the hippocampal rats did not make more S^- responses than did a control group which received bilateral hippocampal injections of sodium sulphadiazine, a drug assumed not to elicit seizures. Another group of rats given bilateral injections of penicillin, an epileptogenic drug, were significantly *better* than either of the above two groups. This set of results is extremely difficult to interpret (see Chapter 12 for a discussion of chemical injection studies).

their behaviour being an increase in responding during the S^+ beyond that seen in normal animals. This pattern of adequate go–no-go performance coupled with high S^+ response rates has also been reported by Gaffan (1973) in the absence of pre-operative training. Freeman, Kramarcy, and Lee (1973) trained rats on a go–no-go tone discrimination using either the presence or absence of tone as the S^+. Hippocampal rats performed normally when the presence of tone was the S^+ (and its absence the S^-) but were deficient when these conditions were reversed.* Further, Freeman and Kramarcy (1974) report normal S^+/S^- learning when either tone or light serve as the S^+.

In two other studies, using hippocampal cats and dogs respectively, Buerger (1970) reported deficient go–no-go performance while Mering and Mukhin (1973) reported normal go–no-go in their hippocampal animals.**

In the midst of this confusion we can only suggest the following conclusions: (1) there is no general deficit in go–no-go discrimination in hippocampal animals; under certain circumstances they can perform adequately on this task; (2) while not necessarily performing in a deficient fashion, hippocampals tend to over-respond to the cues; (3) this indicates that in this situation the lesioned animals are, as in other situations we have already noted, unusually dependent upon guidances.

As regards the use of external cues, in both Schwartzbaum *et al.* (1964) and Gaffan (1973) separate tones were used as S^+ and S^- and normal performance was seen in both cases. In all the other studies only one cue was used, with the exception of Mering and Mukhin (1973) who also reported normal performance. Thus, it appears that hippocampal animals have difficulty in so far as they cannot rely upon a cue telling them when responses will be rewarded. It is possible to suggest that their difficulty resides in their use, in the absence of places or guidances provided by the experimental situation, of an orientation hypothesis that carries with it over-responding and stereotyped behaviour.

These studies do not support the conclusion that the hippocampal animals failed to appreciate the significance of an S^-. In five of the studies (Schwartzbaum *et al.* 1964, Wild and Blampied 1972, Gaffan 1973, Freeman *et al.* 1973; Freeman and Kramarcy 1974) go–no-go training was followed by tests of the *generalization gradients* established to the discriminative

* This deficit might relate to the difference seen in intact animals between feature-positive and feature-negative tasks. When the S^+ is a discrete stimulus learning is faster than when this stimulus is the S^-. This relates to the autoshaping and sign-tracking phenomena we discussed earlier (p. 266), which represent the utilization of guidances. The added deficit of hippocampals on the feature-negative task is consistent with their presumed dependence upon guidances.

** Buerger used an unusual procedure. Cats were rewarded for responding during S^+ and for not responding during S^-, but were punished for incorrect responses or non-responses. They had extensive damage to piriform cortex and some damage in amygdala as well. Mering and Mukhin used more confined lesions and got normal go–no-go behaviour except in the case where the S^+ was simply the time since the previous trial. Again, the importance of a salient guidance is noticeable.

stimuli; that is, following training the animals were tested with a range of stimuli varying in similarity to the original S^+ and S^-. In all these cases, with the exception of Wild and Blampied (1972), the lesioned animals showed good gradients, both of excitation and inhibition. Thus, tones which were similar to the S^+ elicited responding, while those similar to the S^- elicited considerably less responding.

The results of go–no-go alternation studies are presented in Table A25. With the exception of Franchina and Brown (1970) and Brunner, Haggbloom and Gazzara (1974), all studies have used an operant chamber. In the former runway study reward was available on alternate trials and good performance consisted in a particular pattern of latencies: long after reward and short after non-reward. A deficit was seen in the hippocampal rats in this situation; they started running rapidly on almost all trials, while control rats showed longer start latencies on the trials following reward. On the other hand, Brunner *et al.* reported normal performance on this task in rats with X-ray-induced hippocampal dysfunction.

A series of studies by Walker, Means, and their colleagues has investigated the effects of hippocampal lesions on an operant analogue of this task; rats were given discrete trials in an operant chamber with reward and non-reward trials alternating in a fixed sequence. The results of these studies seem to suggest that lesioned rats can be either better or worse than are normals at this task, depending upon the inter-trial interval. Our previous discussion of performance in operant situations would certainly suggest that the lesioned rats should be deficient at this task; in the absence of specific cues they should over-respond during non-rewarded trials, at least during the early stages of training. Thus, the facilitation reported with brief inter-trial intervals is unexpected. In order to account for this facilitation we must consider the nature of the task more closely. Good performance in this situation consists in either or both of two things: a long latency to respond on the non-reward trials and fewer responses on those trials. Anything in the experimental situation which contributes to these would improve performance. For instance, the location of the levers relative to the food cup might influence latency to respond, as might the amount of food obtained on the previous reward trial.

In the first two experiments in this series the food cup was located across the box, opposite the levers. After a reward trial, upon retraction of the lever, the rat would have to move across the box to eat its pellets. Upon resumption of the trials the lever is re-inserted but no other cues given. Latency to respond on this (non-reward) trial would clearly depend upon several things, including the probability that the animal would be waiting for the lever to reappear or aware of its location in the box. We have already described, in discussing Karmos and Grastyan (1962), how the hippocampal animal fails to respond in similar circumstances unless it

actually detects the triggering object (see p. 268). It is possible that in this operant alternation situation the hippocampal animal is at an advantage because it does not know where the lever is located. This is consistent with the fact that changes in the location of the lever can have powerful effects upon the picture just outlined; both Warburton (1969) and White (1974) have found slight deficits at brief inter-trial intervals when the lever was located adjacent to the reward site.

Walker, Messer, and Means (1970) reported that hippocampal rats were normal with 10 s intervals but deficient with longer intervals. Means (personal communication) notes that in this study the food cup was adjacent to the lever, as it was in subsequent reports. Walker *et al.* (1972), varying inter-trial interval, found facilitation at 10 s, normal performance at 20 s, and deficits at 40 and 80 s. Walker and Means (1973) report normal performance at 10 s inter-trial interval, and Means (personal communication) now suggests that there is a slight facilitation for the hippocampal rats at this interval.

In addition to changing the location of the food cup relative to the lever, the later studies simultaneously altered one other feature of the task, the reward schedule used during the go trials. In the two early studies, with the food cup and lever on opposite sides of the box, presses were rewarded on an FI-2 schedule to eliminate multiple presses. Thus, given a 10 s trial, rats could obtain at best five pellets per trial. In the later studies, with food cup and lever adjacent, responses during go trials were rewarded on a CRF schedule, vastly increasing the number of pellets the animals could obtain. The number of pellets obtained on go trials could affect latencies on subsequent no-go trials. Where data are given (Means *et al.* 1970) a clear-cut relationship emerges between the number of rewards obtained and the increase in no-go trial latencies both for normal and for hippocampal rats. This relationship did not hold as clearly for no-go trial responses, particularly for the normal rats. The latency measure, however, appears to be the more sensitive one for dissociating normals from hippocampals, and one could suggest that 'learning' in this situation depends indirectly upon the rate at which rewards are obtained. Facilitation observed in the lesioned rats could simply indicate that they obtain more rewards at the start of training. This would be expected on the basis of their performance in any operant situation. Means (personal communication) occasionally observed his rats in this situation and noted that the hippocampals spend more time near the lever and food cup, and less time grooming and exploring. This pattern is consistent with what we have seen for CRF performance and with the idea that these rats obtain more rewards.

The results of the latest study in this series confuse matters somewhat further. Walker and Means (1973), using adjacent lever and food cup and a CRF schedule on go trials, investigated the effects of interpolating a

different lever during the inter-trial interval. Rats were first trained with a 10 s interval and then switched to a 30 s interval. As noted above there was no facilitation in the hippocampal group at the 10 s interval in this study. At the 30 s interval the hippocampals were impaired, but primarily in relation to intact controls. Cortically lesioned controls also had some difficulty with this task. At this point a new lever was introduced (on the other side of the food cup) during the middle 10 s of the inter-trial interval and responses to it were rewarded on a CRF schedule. This hindered the performance of both hippocampals and cortical controls, though only temporarily. The hippocampal rats responded considerably more frequently to this lever than either of the control groups.

In sum, hippocampals appear to be basically deficient at the go–no-go task, as one might expect, though at short inter-trial intervals certain features of the apparatus, combined with the properties of the reward schedule, can act to overcome this deficit. Without further data concerning the actual behaviour of the rats in this situation it is not worth speculating any further. It is worth pointing out an inaccuracy in a report by Woodruff et al. (1973). They stated that go–no-go brightness discrimination is impaired while go–no-go alternation is facilitated. They further state that when visual cues are available to the hippocampal rat in the alternation situation they are not used, and this would argue against our notion that hippocampals pay particular attention to such guidances. However, this statement is misleading. Visual cues were used in only one study of go–no-go alternation (Walker, Means and Isaacson 1970) and then they were added after rats had reached criterion. We would predict that such cues, if available during learning, should ameliorate any defects observed in hippocampal rats at long inter-trial intervals.

9.5. Summary

Summarizing this section is difficult, for there are a number of situations in which the effects of hippocampal lesions remain unclear. Situations requiring, or favouring, place hypotheses, such as delayed response and delayed spatial alternation, usually produce deficits. Situations clearly requiring taxon hypotheses, such as classical conditioning, appear to produce mostly normal behaviour. Problems of interpretation arise particularly with those situations requiring behavioural flexibility. Abrupt shifts in reward characteristics or response requirements usually elicit deficits, though these can often be overcome by the presence of appropriate guidances. Finally, processes such as generalization seem intact in hippocampal animals.

Part of the problem in providing a clear picture for most of these situations lies in the interaction between locale and taxon mechanisms directing behaviour. For many of the tasks discussed in this chapter

the locale system plays a minor role. However, there are exceptions; the lay-out of an environment can often be crucial in determining behaviour, as seen in the ostensibly non-spatial lever-press go–no-go studies. Further, exploration is a basic aspect of the intact animal's response to any change, including that inherent in shifting operant schedules. The failure of hippocampal rats to adjust to such shifts is most marked when the shift is abrupt. In the following chapter we consider this problem in detail, in the context of an examination of the reactions of hippocampal animals to the removal, or change, of the reward features of a task. Our discussion will directly confront the central problem of *perseveration,* or *persistence,* in hippocampal animals, and the conclusions reached in that discussion will help to make sense of the somewhat confused picture presented in this chapter.
