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Discrimination and maze learning

7.1. Discrimination-Background

IN the literal sense discrimination refers to the capacity of the organism to detect differences. Traditionally, discrimination studies have been concerned with an animal's ability to respond differentially to items or places in the environment. In some studies the interest lies in the limits of the sensory/perceptual systems, as in the determination of thresholds, or acuity. More often the psychologist's emphasis is on the learning based on the ability to form discriminations: how animals come to identify the relevant aspects of an environment, and how they choose adaptive behaviours.

The logic of discrimination learning usually stresses some association between reward and one value of a variable dimension, e.g. the brighter panel, the leftmost door, and so on. Most such studies utilize items rather than places, for reasons to be discussed shortly. None the less, this type of learning occurs within a spatio-temporal context, and the role played by this context has proved of some interest. The importance of temporal contiguity between the relevant discrimination response and the reward has formed a large part of experimental psychology in recent decades, though work with taste-aversion learning (cf. Kalat and Rozin 1973) suggests that such contiguity is not always essential to learning. On the other hand, the importance of spatial contiguity between the discriminandum and the site of response and/or reward, though well documented, has neither been thoroughly explored nor explained. Munn (1950, p. 115 ff.) has described how, early in animal experimental work, apparatus was designed to circumvent the difficulties introduced by spatial discontinuity. Thus, the Lashley jumping stand and the Yerkes discrimination box forced animals to respond directly to the discriminanda. Now, it is standard procedure to 'shape' animals to respond at the appropriate site before discrimination training begins.

These techniques enable the experimenter to focus directly on the discrimination process but prevent any examination of the role of exploratory place learning. An animal introduced for the first time into a discrimination situation will respond as it does in any other new environment, with exploration and the construction of cognitive maps. The

elimination of this place learning from the concern of the experiment does not mean that it fails to occur; considerable recent work attests to the importance animals attach to locations. However, this has not been reflected in theories of discrimination learning to date (cf. Mackintosh 1974).

The debilitating effects of cue-response spatial discontinuity and the similar, though lesser, effects of cue-reward discontinuity were documented by Miller and Murphy (1964) and are discussed at length by Cowey (1968). The basic problem introduced by such discontinuities is clear; animals are faced with a conflict in deciding *where* to focus their attention. The site of the cue, the response, and the reward are all important; to which should the animal attend?

In some discriminations strong approach behaviour can be seen to develop once the animal has identified the relevant cues. For example, in a study by Grastyan and Vereczkei (1974) cats were trained to approach food in one part of a straight alley or T-maze. Subsequently, a signal (buzzer) was introduced, correlated with the availability of reward, either in the start area or in the 'incorrect' arm of the T-maze. Animals began to orient to the source of the signal rather than to the reward site, leading ultimately to a complete breakdown in appropriate goal-directed behaviour. Here, the conflict between a cue and a place led to maladaptive behaviour; as the authors point out most learning situations involve the superposition of relevant cues and places, and conflicts such as the above are rarely seen. *Sign tracking* or *auto-shaping* (e.g. Hearst and Jenkins 1974) offers an example of the synergistic action of place and guidance hypotheses. A number of different behavioural paradigms fall into this category, sharing a common feature; animals respond to an item correlated with reward (or avoid one correlated with punishment) even though these responses are not necessary in obtaining reward (or avoiding punishment). Indeed, after a certain amount of training such responding survives punishment, either by direct shock or by the indirect loss of rewards as in Grastyan and Vereczkei's study.

It is clear from these data that discrimination situations elicit strong hypothesis behaviour, and that animals are quite sensitive to conflicts between relevant places and guidances. Any understanding of the effects of hippocampal lesions upon discrimination learning demands a careful analysis of the types of hypotheses used by intact animals.

7.1.1. HYPOTHESIS BEHAVIOUR IN DISCRIMINATION LEARNING

We have already described a variety of hypotheses that animals can use to solve problems. Place hypotheses were postulated to involve the functioning of different neural systems than those involved in taxon hypotheses, and this difference held to underlie the divergent behavioural properties of these classes of hypotheses. The foregoing description of place learning in

discrimination situations suggests that place hypotheses might be unusually important, and the particular properties of the locale system thus become critical to an understanding of discrimination learning. Evidence from a variety of studies indicates that place hypotheses are used preferentially if the situation allows. Thus, in a T-maze place learning takes precedence if sufficient information is available to sustain it. This is particularly important at the onset of training; subsequent to this it appears that animals learn to respond on the basis of other information. That is, after reaching a learning criterion and with continued training intact animals seem to make increased use of a taxon hypothesis (typically an orientation hypothesis), even when they had previously been using a place hypothesis (Hicks 1964, Mackintosh 1965).

This tendency to utilize response routines with well-learned habits leads to stereotyped behaviour patterns which are often quite difficult to alter; this is related to the property of persistence already described for the use of taxon hypotheses, especially those involving the repetition of exactly the same responses. A similar effect is produced by insoluble or highly stressful situations (Maier 1949). Here, behaviour becomes quite stereotyped, even in the face of non-reward. It is noteworthy that once such fixations appear they often cannot be broken by the subsequent introduction of rewards contingent upon other responses. This lack of variability in behaviour is not limited to the molar level of the animal's choice behaviour. Maier points out that 'even the manner of jumping and types of escape behaviour become highly specific' (p. 30). This extreme rigidity in behaviour, based on the repeated use of particular responses, is a regular feature of hippocampal behaviour in general and normal behaviour in those situations completely eliminating the participation of the locale system.

The normal animal, in most situations, does not easily fall into fixated response routines. The hippocampal animal, on the other hand, manifests such routines quite often. In the absence of any distinct external item, and lacking a locale system, the hippocampal animal must utilize an orientation hypothesis to solve spatial tasks in particular and other tasks where spatial factors play a disguised role. This tendency manifests itself in a variety of experiments, and could provide the basis for an understanding of 'response perseveration' in these animals; we discuss this possibility later (p. 340).

These observations suggest that one of the primary aspects of discrimination learning concerns an appreciation of the relevant *places* in the situation. The normal animal, we assume, initially learns *where*, and not necessarily to *what*, to respond. This is an important distinction within the framework of our model. Learning about places is a function of the hippocampal cognitive-mapping system, and the animal without a hippocampus would be expected to approach a discrimination problem in a fundamentally abnormal way.

In the absence of a system directing attention to places, the hippocampal animal is forced to attend to items or to associate rewards with particular responses. A brief look at several studies demonstrates this point:

- (1) Stevens and Cowey (1972) tested rats on a lever-press alternation task; the rats were provided with a light cue telling them which of two levers to press on any given trial. In one condition there was cue-response contiguity; that is, the light cues were mounted within the manipulanda (panels). Both hippocampal and normal rats solved this task easily. In a second condition the light cues were spatially separate from the levers. Hippocampals solved this task at about the same rate as in the first condition; normals, on the other hand, took significantly longer to learn. This suggests that, for the hippocampal rats, the locations of cue and response site, and their spatial relation, was irrelevant. Presumably the normal animals, for whom the spatial relation between cue and response was important, were faced with a conflict; attention could be directed to the place containing either the cue or the response object. In order to solve this relatively simple problem the normal animal would have to ignore places.
- (2) Gambarian et al. (1972) tested hippocampal cats on several simple conditioned reactions. In order to obtain food the cat had to approach and press a lever upon presentation of a non-directional conditioned stimulus. When two levers were available at opposite ends of the testing box, and a different conditioned stimulus used to signal food for each lever, hippocampal cats performed roughly at chance level. That is, though they reacted appropriately to a conditioned stimulus by approaching and pressing a lever, they failed consistently to approach the lever in the correct place.
- (3) In an experiment by Karmos and Grastyan (1962), cats were placed in a box containing a food well on a ledge and a speaker mounted beneath it. A series of clicks, delivered through the speaker, signalled the availability of food. The authors describe the behaviour which persisted in their hippocampal cats as follows:

'if the conditional stimulus was delivered at a time when the food tray just happened to be in the visual field of the animal, a quick reaction as in a normal animal resulted. When at the time of delivery of the conditional stimulus the animal was sitting with its back to the food tray, long-lasting, searching, sniffing orienting movements ensued. The special conditional act only appeared when the animal caught sight of the feeding device during this searching behaviour elicited by the conditional stimulus' (p. 219).
- (4) Finally Molnar (1973) trained cats on a two-phase conditioned reaction which had both place and cue components. The testing box

was rectangular with three identical feeders, one on each of three walls. A small cage with a pedal was attached to the fourth wall. Food was always delivered to the feeder opposite the small cage and never to the other feeders. Non-directional auditory cues came from a loudspeaker on the top of the box, directional cues from a loudspeaker over the correct feeder. On each trial, the animals were required to sit quietly in the centre of the box (place) and to run to the small cage and press the pedal when a non-directional stimulus was sounded from the overhead speaker (place?). The pedal press delivered food to the feeder, and initiated one of three conditions: either the sound went off and was not replaced, or it was replaced by a different non-directional sound from the same overhead speaker, or it was replaced by a directional sound from above the correct feeder. Only in this last of the three conditions could the second sound act as a guidance. The first two conditions required place hypotheses for solution. The cats were trained on all phases of the task before hippocampal lesions were made. After the lesion, they failed on all place components but were as good, if not better, on the cue-guided component. Instead of sitting quietly at the beginning of the trial they paced about the box incessantly. The first sound no longer produced a directed response to the cage but instead the cats continued to wander and search in the manner described by Karmos and Grastyan above. If a cat chanced upon the pedal in the cage and initiated the second phase there was an interesting difference in its behaviour depending on which of the three conditions obtained. If the directional sound came on, the animal ran to the correct feeder, in some cases with a shorter latency than before the lesion. In either of the non-directional conditions, however, the cat continued its hyperactive wandering which included visits to the two nonrewarded feeders.

These examples show quite clearly the difficulty that hippocampal animals have in the simple problem of knowing *where* to respond. No difficulty is apparent in responding to an item or cue, however, as shown by their immediate reaction upon sighting the food tray or hearing the directional sound.

The hypothesized absence of this fundamental place learning in hippocampal animals should have profound effects on all their discrimination behaviour. Even the simplest of tasks might be solved in an abnormal way. Of course, discrimination problems favouring the use of place hypotheses should be quite difficult for hippocampal animals. They must adopt an alternative hypothesis in order to solve such tasks, if possible.

7.2. The effect of hippocampal lesions on discrimination

7.2.1 SIMULTANEOUS DISCRIMINATION

The most commonly used discrimination task, and the one to which much of the foregoing discussion applies most directly, involves the simultaneous presentation of two choices, with the animal being rewarded for responding to one but not the other. Mazes of various types, as well as operant chambers, can be used, and discrimination might be required between places, or any perceivable dimension of items.

Such discrimination tasks can be readily split up into two categories, depending upon whether or not they involve a spatial variable; that is, involve the consistent association or reward with a location in either egocentric or non-egocentric space. Table A16 presents the results of those studies concerned with simultaneous spatial discrimination, while Table A17 presents the results of the remainder of the simultaneous discrimination studies. Aside from these two categories one could mention those few spatial studies which strongly biased animals towards the use of place hypotheses; that is, reward was associated most simply with a location in locale, or non-egocentric, space. We shall discuss these studies separately.

It is clear from Tables A16 and A17 that no obvious generalized deficit is seen in hippocampal animals in most types of simultaneous discrimination learning. However, deficits are sometimes reported, and even in the absence of a changed rate of learning there are indications that hippocampal and normal animals solve such problems in different ways. A close analysis of these sometimes subtle differences offers strong evidence for the assertion that hippocampal animals lack the ability to utilize place hypotheses. However, before considering these studies we shall discuss in some detail those few experiments which directly tested locale function.

7.2.1(a). *Spatial discrimination-locale dependent.* There are few studies in the literature which tested the ability of hippocampal rats to learn discriminations requiring place hypotheses. This is, no doubt, due to the difficulty of devising such a test; locations are often defined in terms of the stimuli at or near them, and a guidance hypothesis based on approaching (or avoiding) one of these stimuli is almost always available to the animal.* Seven studies, two of them from our laboratory, did severely bias the situation towards the use of place hypotheses and against the use of taxon hypotheses.

Rabe and Haddad (1969b) placed thirsty rats on one table of a Maier three-table apparatus** and allowed them to drink water for a short time.

* Pohl (1973), for example, devised a 'landmark' discrimination task which he assumed measured allocentric, or extrapersonal, space. The correct food well in this Wisconsin General Testing Apparatus (WGTA) task was marked by an adjacent item. It is clear that this task is not entirely locale dependent and could be solved by responding to the well near the landmark.

** This is basically a Y-maze with platforms at the end of each arm.

The animals were then removed from the rewarded table and put on another one; their task was simply to return to the table where they had just received water. The position of reward varied from trial to trial, as did the subsequent placement of the rat, so that proper performance depended upon remembering where the water was on any given trial. Although a particular cue might be associated with reward during the course of the rat's initial exposure to the water, it is much more likely that the normal rat would utilize its cognitive map of the situation and, by making a slight change in the map on each trial, obtain reward. It is not surprising that only 6 of 21 hippocampal rats reached the minimum criterion necessary for showing better than chance performance in this study.

Olton (1972a) tested rats on a task similar in several ways to that used by Rabe and Haddad. Thirsty rats were given a discrimination task in a plus-maze, with considerable extra-maze information available. A single discrimination problem consisted of five trials. On the first trial the rat was forced to go from the start arm (which remained the same on all problems) to one of the other three arms; on the second trial the animal was forced to go to a different arm. One of these forced choices led to water; the other did not. Thus, after these two trials the rat had information about two of the choice arms. On the remaining three trials free choices were allowed. Each new problem provided different information about the location of water or no water. All rats were tested extensively pre-operatively and performed much as one would expect; on the initial free-choice trial they approached the water arm most often, the no-information arm sometimes, and the no-water arm rarely. On the third free-choice trial they almost always chose the water arm. After receiving 48 problems all rats were subjected to sham operations and given an additional 12 problems; these operations did not affect their performance. Following this, all rats received bilateral hippocampal lesions and, after recovery, an additional 48 problems. Hippocampal damage had a marked effect on performance. Basically, the lesioned rats chose randomly on the initial free-choice trials and began to show a preference for the water arm by the final trials. This random choice on the initial trials indicates that the hippocampal rats could not rapidly learn about the location of water as they had been able to do pre-operatively. The learning that was seen over the free-choice trials presumably reflects learning the correct turn on the given problem. It is clear, as in Rabe and Haddad's study, that hippocampal animals cannot utilize information about the location of water in determining subsequent behaviour under free-choice conditions.*

Plunkett, Faulds, and Albino (1973) compared hippocampal and normal rats in two tasks using a plus-maze. In one case the animals had to learn

* As Olton (1972a) points out, his results are incompatible with the Douglas-Pribram (1966) hypothesis that the hippocampus is solely involved in error evaluation.

to make a particular turning response, regardless of where they started; in the other case they had to go to the same place. Hippocampal rats learned the response task as rapidly as did normal rats, but had a marked deficit on the place task. A total defect was not seen in this study, perhaps because, as the authors point out, 'place learning and response learning are not isolated in the two tasks' (p. 80). This result has been replicated by de Castro (1974).

In the first of our studies (Riches 1972) thirsty rats were required to go to the same arm of an elevated Y-maze when started from either of the other two arms; the starting arm was varied randomly from trial to trial. Normal rats learned this task quite rapidly; the median number of trials needed to reach a 9/10 criterion for seven normal subjects was 14. As expected, the hippocampals were quite poor at this task. Of the nine rats in this group, two failed to reach criterion in 100 trials. The other seven had a median score of 52 trials to criterion. No hippocampal rat learned the task faster than any normal rat. Those lesioned rats which learned the task were given a series of probe trials in an attempt to determine which cues they were using. These probe trials consisted of trials run in the total darkness, or with distal visual cues at the start and/or choice obscured by black curtains. In pilot studies we had found that almost all animals initially learn this discrimination using visual information, and the probe trials were therefore limited to variations in this modality. Figure 31 portrays the probes and the order in which they were given to the rats. The essential findings were that the performance of both groups fell to chance in the total darkness, but that the type of visual information used by the two groups was different. All of the normal animals but one performed perfectly when either the start arm or the choice arms were blocked with curtains. Further, relatively few errors were made when the entire maze was surrounded by curtains, leaving only the differential lighting on the ceiling as possible location information. It seems likely from these data that the normal rats were not dependent on any single source of information, but rather could respond on the basis of virtually any aspect of the visual environment; that is, they had some kind of 'map' of the situation. On the other hand, the lesioned rats virtually all made mistakes under either the start-curtains or choice-curtains condition. Their performance under the all-curtain condition was no better than chance. This pattern suggests that each hippocampal rat had solved the problem by responding to a limited sample of cues, possibly only a single cue, and that they had no idea of the total arrangement of the situation. These conclusions were strengthened by further probe trials, luring which the animals were started from the goal arm itself with curtains around that arm on two trials and no curtains on a third. Under these conditions every normal animal turned around in the start (goal) arm at least twice, suggesting that they 'knew' that this was the place where reward was normally found (water was

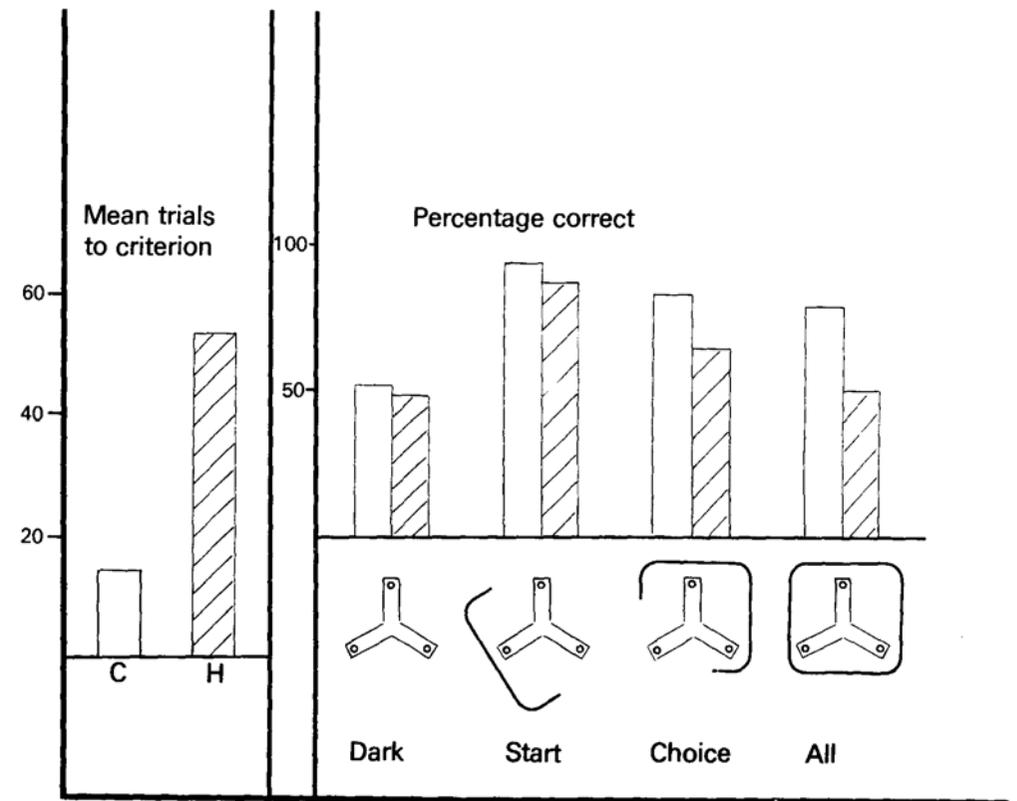


FIG. 31. Performance of controls (C) and hippocampal (H) rats on Y-maze task where the goal arm remained constant and the start varied randomly between the other two arms: left, median performance of the controls and hippocampals which learned the task; right, the performance of the two groups on different probe trials given after criterion was reached.

not available on these trials). Only four turn-arounds were recorded for the entire group of lesioned animals. They clearly had no idea that this was the place where reward was situated.

Our second experiment (O'Keefe *et al.* 1975) was run to preclude the objection that the lesioned rats failed on the Y-maze (as well as in the T-maze used by Plunkett *et al.* and de Castro) because of an inability to inhibit inappropriate body turns. Rats were tested on a circular runway located in the centre of a room and there were many extra-maze cues available, though none of these were close to the runway. There were eight wells sunk into the runway, at equal spacings, and water could be delivered to any of these through polythene tubing and a hypodermic system from underneath the wells and runway. Two tasks were used, differing in the means by which the rats (with fornix or control lesions)

could find the water. In one task water was always to be found in the well located in the same place in the room. In the second task the correct well was 'marked' by a small light. In the place task the light was present but irrelevant; in the light, or cue, task the correct well varied in location from trial to trial. Between trials the maze itself was rotated, the water wells changed, and the starting position varied. This had the effect of preventing the use of intra-maze cues, other than the light, or specific responses. During a preliminary training stage rats were allowed to find water associated with either the place or the cue. After this learning the formal testing stage began. Now, water was available only after the rat responded at the correct well. A response was defined as prolonged sniffing at the well and was registered automatically by an electric circuit incorporating metal plates on the floor of the maze, the rat, and the brass water well. Rats received water on every trial, even if they had responded at incorrect wells first. Criterion for learning was 9/10 trials during which a response was made only to the correct well. The results of this study are shown in Fig. 32; fornix-lesioned rats failed on the place task and were better than normal on the cue task.

As we argued in the paper reporting this study, the defect seen in the lesioned rats could not be attributed to changes in such things as

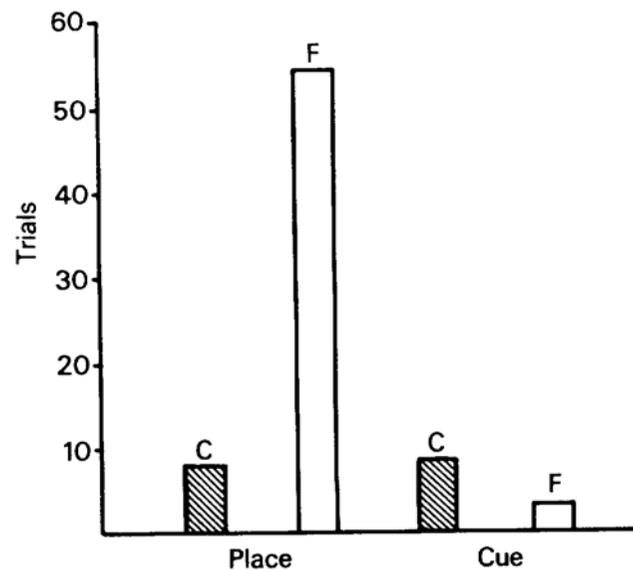


FIG. 32. Circle maze. Median trials to criterion of controls (C) and fornix-lesioned (F) rats on two water-finding tasks: left, results when the well where water could be obtained was always situated in a particular part of the room (place); right, results when the well was marked by a strong light (cue). (After O'Keefe *et al.* 1975.)

motivation or general learning ability. We also argued that a response-inhibition defect could not account for these data. Rather, this study seems to show a highly selective failure of place learning.*

Recently Olton, Walker, and Gage (1977) have tested lesioned rats on their eight-arm spatial memory task (see p. 69). In this task the rats are allowed to retrieve food from each of eight arms of a radial maze in any order that they choose. Normals usually choose seven or eight baited arms before re-entering a previously visited arm. The choices appear to be on the basis of the spatial locations of the arms as defined by the extra-maze room cues. The performance of animals previously trained on this maze was reduced to chance levels by lesions in the hippocampus, entorhinal cortex, or fornix. Some of these animals fell into obvious orientation hypotheses such as successive 90° turns or running straight ahead. The choice patterns of others appeared to be random. In a subsequent study (Olton, personal communication) cue groups formally similar to the light cue groups in the O'Keefe *et al.* (1975) study described above were run. For these animals a drawbridge into each of the baited arms was open at the start of the trial and was closed by the animal as it crossed it into an arm. Thus a closed drawbridge provided a non-spatial cue as to which arms had been entered. As in the O'Keefe *et al.* study lesioned animals did not show any deficits in this condition.

These studies show the place-learning deficit in hippocampal animals quite clearly. A final study, which was not intended primarily as a discrimination study by its authors, points up the way in which place hypotheses may operate in tasks which have no obvious spatial component and can thereby influence hippocampal performance relative to normals. Douglas and Pribram (1969) tested monkeys on a task in which different numerals were projected onto panels; the monkeys had to press these in a certain order to obtain reward. First, one numeral (5) was presented in the lower right-hand panel of the 4 x 4 panel array (the DADTA apparatus). When the monkey depressed this panel the second numeral (0) was presented in the upper left-hand panel; a press on this panel was rewarded. Hippocampal monkeys seemed to learn this sequential task more rapidly than normal animals. Following learning, on a few trials within a session, a distractor stimulus (1) was presented in one of four locations simultaneous with the presentation of the second stimulus. This distractor initially affected the latency to respond to the correct stimulus to about the same extent in all the monkeys. However, hippocampal monkeys had a higher probability of actually responding to the distractor. While the normal (and amygdalotomized) monkeys habituated this increased latency effect, speeding up their correct responses on the distractor trials, the hippocampal monkeys continued

* The published paper includes a thorough discussion of the notion that place learning in this situation was merely a form of distal cue learning, and concludes that this could not have been the case.

to be distracted, as measured by their prolonged latencies to respond to the correct stimulus. However, hippocampals, like the others, virtually ceased pressing the distractor panel. At this point the same distractor (1) was presented at a new location for four trials, and then new distractors (2, 4, 6, 8) were each presented once at this new location. Both of these conditions increased the latencies of the normal and amygdalotomized monkeys again, while only the new distractors affected the hippocampals, who were virtually unaffected by the change in the location of the old distractor.

We think these results show that the hippocampals had learned the initial task in a way completely different from the other monkeys. These others appear to have learned the location of the relevant panels and could rapidly learn to ignore distracting stimuli appearing in the wrong place. Thus, they habituate both responses to the distractor and the increased latency effect. The same distractor, put in a new location, increases their latencies again. Hippocampal monkeys do not appear to have learned the location of the stimuli to which they must respond. Over the first 32 distractor trials they responded to the distractor almost as often as to the correct stimulus. This suggests that they had learned initially merely to press the second panel, which lit up wherever it was, and had then to learn a discrimination between the correct stimulus and the distractor when the two were presented simultaneously. The fact that they ceased responding to the distractor indicates that they learned this discrimination. However, the fact that their latencies were always longer on the distraction trials means that they *had to* attend to both stimuli in order to know which panel to press. In other words they could not discriminate between these two stimuli on the basis of their location, as could the other monkeys. Once having learned this discrimination, the lesioned monkeys would not be disturbed at finding the same distractor in a new location. A new distractor, however, would affect them, as this would require another discrimination. This lengthy analysis offers a particularly nice example of the different modes of learning in hippocampal and normal animals when measures of the rate of initial learning indicate that little or no difference exists. Experiments such as this, using simple learning situations followed by various probe trials, are the best means for bringing out these crucial differences.

7.2.1(6). *Spatial discrimination—locale or taxon.* In simultaneous spatial (or *position*) discriminations the animal is rewarded for consistently responding to the alternative in a particular part of egocentric space. Thus, the right arm of a T-maze, or the food-well on the left in an operant chamber, can be associated with reward. We have already noted that several hypotheses could be used to solve such tasks but that the normal animal uses a place hypothesis during initial learning if possible. Means (1969a)

and Means and Douglas (1970) tested the usage of particular information by normal and hippocampal rats in this situation. Rats were trained on a T-maze spatial task and were then subjected to a set of cue-utilization probe trials.* In agreement with earlier work, normal rats used place hypotheses during initial learning, switching to others with continued training. Hippocampal rats, on the other hand, did not use place hypotheses at any stage of learning.

The dependence of the lesioned rats on taxon hypotheses could lie at the root of the difficulties they sometimes have with these simple spatial tasks. When a deficit is reported in these animals in simultaneous spatial discriminations it is usually a reflection of prolonged responding to the incorrect choice, that is, an inappropriate persistence on an orientation hypothesis. For example, the deficit reported by Means *et al.* (1972) for hippocampal rats was a direct consequence of the fact that

'individual animals would make one or more long sequences of incorrect responses. The effect was all-or-none. Either the animal made a long sequence of errors (10 or more) or it did not. The frequency of response sequences of intermittent length is no different than that found in other groups of animals' (p. 462).

Those hippocampal animals not producing such long sequences learned the problem at a normal rate.

This result suggests that spatial discriminations which bias animals towards incorrect orientation hypotheses could routinely elicit deficits in hippocampal animals. Thus, in a typical spatial task animals have an initial preference for one of the two choices; if lesioned animals are trained against this preference a deficit results (e.g. Samuels 1972). On the other hand, training the animal towards its preference might, in the absence of any tendency to explore the other arm, lead to better than normal performance in the hippocampal animal. When initial preferences are not taken into account a mixture of these could be expected, such that the group scores would be the same for lesioned and normal animals. Of course, there are other factors determining the likelihood of an orientation hypothesis being used, as distinct from a guidance hypothesis. The topography of the situation, for instance, will affect the ease with which orientation sequences are utilized; thus, the presence of barriers or obstructions biases against the chaining of response sequences. Additionally, the use of correction or non-correction techniques is important. The correction technique involves allowing the animal to respond appropriately on every trial; the non-correction technique involves terminating a trial

* This procedure involved the use of a plus-maze. By starting the animal from different sides and by interchanging the stimulus patterns it was possible to put into opposition the use of place, guidance, and orientation hypotheses. Several such trials enable one to define fairly accurately which of these an animal is using.

upon commission of an error. It is clear that correction militates against response chaining, while non-correction can foster it (cf. Sutherland and Mackintosh 1971, pp. 26-7).

If we consider the effect of correction *versus* non-correction we note that in all but 1 of the studies listed in Table A16 using correction no deficit was reported for hippocampal animals. Thus, the technique which limits the use of persistent orientation hypotheses tends to prevent a deficit in the lesioned animals. On the other hand, not all studies using non-correction techniques report deficits. Within this category the question of initial preferences seems to be crucial. In the two studies where rats were trained by non-correction techniques against their initial preference deficits were reported (Samuels 1972, Means *et al.* 1972); we have already noted that in the latter study the deficit was directly related to the adoption of persistent orientation hypotheses in some of the lesioned rats. In the remaining studies on rats no account was taken of initial preference and learning typically appeared to proceed at a normal rate. However, in two studies, one of them on rats and the other on monkeys, the data suggest that this normality might be an artefact of group statistics. In the Means and Douglas (1970) study one subgroup of hippocampal rats was impaired; the authors point out that by chance there was a preponderance of rats trained against their preference in this subgroup. More tantalizing is the observation in the Mahut and Zola (1973) study that, of the six lesioned monkeys, three were significantly better than normal while three were significantly worse. As a group the lesioned animals did not differ from controls.

The results of spatial discrimination studies suggest the following conclusion: in those situations either allowing for or fostering the use of orientation hypotheses hippocampal animals will show a deficit when trained against their initial preference. This deficit results from the particular persistence of orientation hypotheses, as discussed earlier. The normal animal, in the same situation, uses a place hypothesis and thereby avoids persistent choice of the wrong arm.

The importance of orientation hypotheses, with their attendant rigidity, in hippocampal animals is seen in several situations related to spatial discrimination. We shall discuss a number of these in subsequent sections. Three examples are worth mentioning here.

- (1) In a probability learning situation two discriminanda are associated with reward in a certain ratio, say 70:30. The normal animal in this situation tends to maximize his rewards by responding predominantly to the most-rewarded choice. Stevens (1973c) reported that hippocampal rats learn spatial probability tasks at a faster than normal rate; this could reflect the use of a persistent orientation hypothesis. More recently, however, Stevens and Cowey (1973) and Nonneman *et al.* (1974) have reported deficits in this task in hippocampal

animals. These latter studies investigated probability learning after the animals had been trained on position or alternation tasks in the same maze. Reward in the probability task was maximized to the side that was previously non-rewarded. Thus, these studies actually constituted a complex form of reversal learning, which almost inevitably produces strong deficits in animals with hippocampal lesions (see p. 282). In contrast to this, Stevens (1973c) assessed preferences in a simple choice test and trained his rats against this preference; this does not constitute a reversal problem. If the probability task is non-spatial the tendency to choose an orientation hypothesis could lead to slower maximization in the hippocampal animal (e.g. Douglas and Pribram 1966, study. 1).

- (2) Hsiao and Isaacson (1971) tested rats on a Y-maze, with water being available in one goal arm and food in the other. On alternate days the animals were food or water deprived and had to make opposite responses to gain the appropriate reward. Hippocampal rats were retarded in learning this task, primarily because they made the same turning response on both food and water days.
- (3) Bauer (1974) trained rats on a Y-maze discrimination of brightness; half of the rats in each group were pre-trained on the maze without the brightness cues. These rats fell into position habits during pre-training as they had no basis for predicting which arm would contain reward. This experience hindered subsequent learning of the brightness task, but most severely in the hippocampal rats. Kimble (1975) confirmed this result, though his control rats were not impaired by the pre-training.

7.2.1(c). Non-spatial discriminations. In non-spatial discriminations the relevant stimuli are typically spatially separate; in simultaneous discriminations they must be, while in non-simultaneous discriminations they need not be. We shall discuss some examples of this latter category later (pp. 331-5). In order to prevent the use of spatial information in the simultaneous task the stimuli are interchanged in some random sequence, such that spatial hypotheses (either place or orientation) would afford 50 per cent correct performance at best. None the less, it is clear that spatial information represents a powerful irrelevant cue in these situations and that the adoption of spatial hypotheses can constitute a source of considerable error in performance.* Our analysis of spatial tasks suggests that when forced to adopt inappropriate orientation hypotheses hippocampal animals will show deficits. On the basis of this one might expect

* Irrelevant cues might constitute strong sources of error in spatial discriminations, but they are rarely used in such studies. Samuels (1972) has shown that such irrelevant cues are not as powerful in interrupting spatial tasks as in the reverse case, but more data are needed here.

that those non-spatial discriminations fostering the initial use of orientation hypotheses could similarly elicit deficits.

The data presented in Table A17 demonstrate that in a wide variety of situations hippocampal animals learn non-spatial discriminations at a seemingly normal rate. However, there are exceptions; further, in some of those studies reporting normal learning rates there are hints that hippocampal and normal animals are learning in different ways. In a study of brightness discrimination in a Y-maze (Kimble and Kimble 1970) data were presented on the use of hypotheses by the rats during learning; a hypothesis was defined as three or more successive choices to the same feature (bright, dark, left, right); with at least two of these involving an alternation along the non-chosen dimension. Although hippocampal rats, as a group, learned this task at a normal rate, there were differences between the groups in the use of particular hypotheses. The mean length of orientation hypotheses (left or right turns) was significantly greater in the lesioned rats than it was in the control rats.* **

An experiment by Olton (1972b) provides more direct evidence for the assertion that, in situations fostering the initial use of irrelevant position hypotheses, hippocampal animals might be impaired. Rats were trained on a pattern discrimination in a two-choice box. Both normal and hippocampal rats rapidly began to respond almost entirely to their preferred side, even though reward was correlated with the shifting patterned stimuli. Within four to five days both groups of rats began to show an increase in latency to respond when the negative patterned stimulus was presented on the preferred side, though still ultimately responding to that side. At this point the two groups diverged. Normal rats, within three days, broke their position habit and reached criterion on the visual task. All but 1 of the 10 lesioned rats failed to reach criterion within 13 days, continuing to respond almost entirely to their preferred side even though they took longer to respond to the negative stimulus on that side. These data attest to the difficulty hippocampal rats have in breaking orientation routines, even in the face of knowledge that the response is inappropriate. This is reminiscent of Maier's (1949 p. 41 ; see p. 267) description of normal rats forced into response routines. Upon

* The fact that, as Isaacson and Kimble (1972) stress, these prolonged runs were seen only with position and not brightness hypotheses must not be over-emphasized. An incorrect position hypothesis is partially rewarded, and this is not true for an incorrect brightness hypothesis.

** Kimble (1975) has re-analysed these data and pointed out that the hippocampal rats fell into two subgroups: those which learned very rapidly, and those which took considerably longer to learn. Thus, the bi-modality seen with position tasks is evident in non-position tasks as well. It is likely that the slow learners in the hippocampal group were those who adopted an incorrect orientation hypothesis. In a separate experiment published for the first time, Kimble (1975) demonstrated that the tendency to adopt fewer overall hypotheses, more and longer orientation hypotheses, also holds for lesioned rats tested in a Y-maze brightness discrimination where reward was given on every trial, regardless of the animal's choice. This confirms the notion that hippocampals are less flexible in their choice behaviour and more likely to persist in orientation hypotheses whether they are 'right' or 'wrong'.

introduction of punishment associated with the negative visual stimulus his rats began to show a resistance in jumping to that stimulus. Nevertheless, most of his rats failed to break out of their persistent habits, in the same way that Olton's hippocampal rats increased their latencies to the negative stimulus but could not switch their responses.*

Thus, the development of persistent response habits by hippocampal rats can, as in normal rats, impair the animals' ability to learn non-spatial tasks. What distinguishes the hippocampal animal in this regard is the relative ease with which such persistent habits are adopted. Of the remaining studies on non-spatial discrimination, those reporting deficits seem amenable to the interpretation that the hippocampal deficit was a function of either prolonged position hypotheses (e.g. Andy, Peeler, and Foshee 1967, Duncan and Duncan 1971) or other stereotyped behaviours interfering with proper discrimination (e.g. Woodruff and Isaacson 1972, Woodruff, Schneiderman, and Isaacson 1972). We return to a fuller discussion of persistent habits in hippocampal animals later (p. 337ff).

7.2.1(d). *The reversal of simultaneous discrimination.* When an animal has learned to discriminate between two stimuli, or places, so as consistently to choose the positive and avoid the negative, the situation can be altered so that the previously positive choice becomes negative and *vice versa*. This constitutes a discrimination reversal problem; it involves giving up a previously correct hypothesis and switching to a new one. Superficially, this switch might seem quite easy to accomplish, in that the same stimuli (or places) remain relevant in the reversal task. Thus, overtraining on the initial task often has the effect of facilitating reversal; this overtraining reversal effect (ORE) can be explained by assuming that with increased training the animal is more likely to choose a new hypothesis based on the same stimuli (cf. Sutherland and Mackintosh 1971, pp. 252 ff.). However, the ORE is rarely seen in spatial tasks; in fact, a number of studies have reported the opposite effect, prolonged reversal after overtraining on a spatial task (e.g. Krechevsky and Honzik 1932). As we have pointed out, most spatial tasks are initially solved by normal animals with place hypotheses but added training causes a shift towards the use of orientation hypotheses. Further, we have suggested that these are unusually prone to persistence. The absence of an ORE in many spatial tasks might be attributable to this shift with overtraining, a possibility also noted by Sutherland and Mackintosh (1971, p. 283). A number of studies demonstrating an ORE in spatial tasks were so constructed as to prevent the building up of smooth response sequences (e.g. Capaldi 1963, Ison and Birch 1961), the condition essential to the development of

* Olton's study shows that hippocampal rats can obtain information about stimuli which are not controlling their choice behaviour. This is incompatible with any attention-shift dysfunction theory, as is the study by Harley (1972) using compound cue discriminations.

strongly persistent orientation hypotheses. The reader is referred to Sutherland and Mackintosh for further discussion of this point. It is worth noting one further study here, as it will come up in our later analysis of the lesion data; Mackintosh (1965) has shown that the mere inclusion of a barrier which slowed rats down could lead to faster spatial reversals.

These considerations are important in view of the unusually crucial role orientation hypotheses play in hippocampal animals. Our previous discussion of discrimination learning, in conjunction with the above data from normal animals, would suggest that hippocampal animals should be particularly deficient at spatial reversals, in that they typically solve spatial tasks through the use of orientation, rather than place, hypotheses. No particular prediction is offered concerning the reversal of non-spatial tasks; however, those situations fostering the use of inappropriate orientation hypotheses could elicit deficits in reversal, in the same way they do in initial learning.

Spatial reversals. The results of those experiments concerned with the reversal of spatial discriminations are shown in Table A18. As suggested above, hippocampal animals show profound deficits in most of these studies. The few exceptions to this seem to involve procedures which either prevent the use of smooth response sequences or provide the animals with a means of breaking such sequences; that is, an alternative hypothesis. In a series of experiments Cohen and his co-workers have tested rats on a variant of T-maze spatial reversal (Cohen, LaRoche and Beharry 1971, Cohen and LaRoche 1972, 1973). A plus-maze was used, with only three arms open at any time. After learning an initial spatial habit rats were started from the previously unused arm (180° from the initial start arm) and required to go to the same place for reward. Thus, for rats using place hypotheses this new task does not involve a reversal in the standard sense of the term, while for those using an orientation hypothesis a reversal is required. Under this simple condition the hippocampal rats had a deficit in learning the new task. However, the addition of brightness cues at the start of the second task eliminated the deficit (Cohen *et al.* 1971). Presumably the animals could use these cues as an alternative to the orientation hypothesis, in effect treating the second task as an entirely new problem. Similarly, the presence of doors at the choice points also eliminated the deficit (Cohen and LaRoche 1972, 1973).

In several studies Stevens (1971, 1973b) explored the relationship between reversal and inter-trial intervals. An unusual procedure was used in these studies; the animals were minimally trained (either 6 or 10 trials without a learning criterion). Under these conditions hippocampal rats showed a deficit only when reversed to their initially non-preferred side, and then only when the inter-trial interval was 4 min. With a 5 second

inter-trial interval reversal proceeded at a normal rate. These data are only suggestive, and further studies of the relation between inter-trial interval and reversal are needed, but they are consistent with the view that orientation hypotheses can be altered when they are repeatedly nonrewarded at a rapid rate. This point has already been raised in our discussion of habituation and will be discussed at length in the chapter on extinction (pp. 344-5).

Essentially, then, spatial reversals provide a measure of the extent to which an animal relies upon orientation hypotheses; the difficulty in reversal seems related to the use of these persistent habits. Hippocampals are deficient in this situation because they typically cannot use alternative hypotheses.

Non-spatial reversals. The results of studies using non-spatial reversals are given in Table A19. A split appears in these data between different species. Deficits are seen in most studies using hippocampal rats and cats, while hippocampal monkeys reverse at a normal or faster than normal rate. All of the studies reporting deficits in hippocampal rats and cats are unanimous in indicating that these animals do *not* have unusual difficulty in giving up their responses to the previously positive non-spatial stimulus;* most of the deficit results from the adoption of, and subsequent persistence in, an inappropriate (50 per cent rewarded) orientation hypothesis. Thus, Isaacson *et al.* (1968) note that

'hippocampally damaged animals do not perseverate the old response, they give it up and reach a plateau of 50% correct responses due to a fixation of an approach response to one side or the other' (p. 74).

The only exception to this pattern was seen in a part of the Isaacson *et al.* (1968) study where correction techniques were used. As we have already seen, this technique tends to prevent the use of persistent orientation hypotheses; hippocampal cats tested in this way reversed at a normal rate.

Reversal studies in monkeys extend this analysis. Zola and Mahut (1973) have carefully analysed data from both visual and tactile reversals in monkeys with fornix lesions or hippocampal damage. Lesioned animals gave up their responses to the previously correct object as rapidly as did normal monkeys. In contrast to what has been reported for rats and cats, Zola and Mahut showed that lesioned monkeys did not adopt persistent orientation hypotheses which could retard reversal. This was particularly apparent in the group tested on visual reversals. In this case the lesioned monkeys reversed *more* rapidly than did the intact monkeys, a result we

* This point has been made in a different way in an experiment by Riddell, Malinchoc and Reimers (1973). Rats were initially trained on a brightness discrimination and then shifted to a position discrimination. Hippocampals accomplished this shift as rapidly as did normals.

discuss below. In the tactile reversals the animals did occasionally use orientation hypotheses, but no difference was seen in the rate of reversal between the various groups.

Zola and Mahut showed that the facilitation in visual object reversals in the lesioned monkeys was related to their achieving criterion more rapidly once they had given up their responses to the previously correct stimulus; both groups took about the same number of trials to reach this stage. We have no simple explanation for this paradoxical facilitation of reversal; it might be related to the fact that orientation hypotheses are not used by monkeys in the WGTA to any great extent. This is consistent with the observation that normal reversal follows the use of either correction or non-correction techniques in this apparatus. Further, in one study reporting reversal deficits in hippocampal monkeys (Douglas and Pribram 1966) a different apparatus was used (the DADTA). We have already discussed one study using this multi-panel apparatus (pp. 275-6) and have seen that orientation hypotheses might play an important role in it. While no data were given in the Douglas and Pribram (1966) study concerning the use of orientation hypotheses, much of the deficit in the hippocampal monkeys appears related to prolonged responding at the 50 per cent correct level; this is suggestive of the use of such a hypothesis.

Thus, we can conclude that the reversal of non-spatial discriminations proceeds normally in hippocampal animals except when they adopt maladaptive orientation hypotheses. Situations constructed to prevent such strategies allow for normal reversal; situations allowing for such hypotheses typically produce deficits. Normal monkeys might use place hypotheses in the latter case, but these are easily dropped if proved incorrect.

7.2.2. SUCCESSIVE DISCRIMINATION

Another type of discrimination task that has been used with hippocampal animals involves presenting only one stimulus on any given trial, with the proper response depending upon which stimulus is presented. For example, if both arms of a T-maze are white the reward would be on the right, while if both are black it would be on the left. This task, termed successive discrimination, is typically more difficult for the normal animal than is the simultaneous task.* Most authors agree that there are two ways in which the normal animal can solve this task (cf. Lovejoy 1968, Sutherland and Mackintosh 1971, Mackintosh 1974). The animal could learn to make a particular response given a particular stimulus (i.e. if black, turn left; if white, turn right), or it could learn a compound discrimination (i.e. approach white on the right or black on the left, but avoid white

* This successive discrimination task should be differentiated from another task involving separate presentation of stimuli. In this latter case a single stimulus is either presented or not, and the animal is rewarded for responding in its presence and not in its absence. This task, termed successive go-no-go discrimination, will be discussed later.

on the left or black on the right). The former alternative does not appear to involve place learning and also does not seem to be used by normal animals except in rare cases. One such case, it should be noted, occurs when the stimuli are separate from the place where the response is to be made. Here, of course, the locale system would be at a disadvantage. The latter alternative, involving a compound discrimination solution, could be facilitated by the use of the locale system as the animal can learn to go to a stimulus in one place but not in another. Given this, it is likely that hippocampal animals would have deficits in such tasks. Four studies have tested hippocampal rats on successive discrimination (Kimble 1963, Lash 1964, Seidenstadt and Hagstrom 1970, Isaacson, Schmaltz and Douglas, 1966) and deficits were seen in all cases. The nature of the deficit seems analogous to that seen in simultaneous discrimination.

Lash (1964) tested rats on successive discrimination in three different mazes. These mazes differed in the extent to which the responses made in them were discrete and easily discriminable. Hippocampal rats tend to adopt more pronounced orientation hypotheses in those mazes allowing for the most discriminable responses; their performance on these three mazes was inversely related to response discriminability. The more likely they were to adopt an orientation hypothesis, the poorer the performance. A study of the post-operative retention of a pre-operatively acquired successive discrimination provides data consistent with this view. Isaacson et al. (1967) trained rats on two mazes, a Y-maze and an arrowhead maze. Responses on the latter are more discriminable, and this maze was easier to learn pre-operatively by all the rats. Post-operatively, the hippocampal rats had deficits on the successive task; they showed pronounced orientation hypotheses on the arrowhead maze in particular.

Isaacson and Kimble (1972) and Isaacson (1974) have re-analysed the data from Kimble (1963). They suggest that animals solve this task as though it were two separate problems, using what we described above as 'learning a response to a particular stimulus'. The data they present, however, fail to support their analysis. If normal animals did, in fact, treat this situation as two separate problems, learning first one (if white, go right) and then the other (if black, go left), one would expect criterion performance on one task combined with random performance on the other. This pattern was seen in only one of the six normal animals tested (Isaacson and Kimble 1972, Table 2). Two of the animals showed a pattern involving criterion performance on one task (e.g. if black, go left) combined with total failure on the other. In other words, these animals responded on the basis of a place or orientation hypothesis, always going to the same place or making the same turn. The remaining three normal animals seemed to learn both components of the task concurrently, indicating the use of the compound discrimination discussed above. It is worth noting that these three rats had the fastest learning rate. Hippocampal

rats (Isaacson and Kimble 1972, Table 5) were more likely to fall into an orientation hypothesis; three of the five hippocampals showed turning hypotheses and the other two showed a pattern of responding consistent with the use of an hypothesis like that described by Isaacson and Kimble, that is, solution of one problem combined with random responding on the other. None of these animals learned both tasks concurrently.

These data, then, demonstrate that normal animals learn either by the use of a compound discrimination or a two-component orientation hypothesis, and that the former solution is faster. Hippocampal animals, on the other hand, use only the latter solution, or a one-component orientation hypothesis yielding maladaptive behaviour. They seem incapable of utilizing the compound discrimination strategy.

7.3. Maze learning

The use of complex mazes has had a long history in experimental psychology since their introduction by Small (1901). We have already referred in a general way to some of this work (pp. 50-2). Here we shall want to look more carefully at the factors which early experimenters identified as contributing to the rat's ability to 'solve' the maze. Much of the relevant literature is summarized by Woodworth (1938) and Munn (1950 pp. 181-226, 255-65). The reader's attention is especially directed to the classic article by Dashiell (1930). Before Dashiell's work, it had become generally accepted that one factor involved in maze learning was what Hull (1932) called the *goal gradient* factor. Animals tended to eliminate errors at choice points near the goal end of the maze earlier in training than those at the start of the maze. Hull postulated that the effect of reinforcement was strongest at the goal and diminished progressively the further one went backwards through the maze.

It was clear, however, that other factors were also involved. Dashiell's important contribution was to identify a *goal-direction* factor. He had noticed a curious improvement in the performance of a group of rats trained on a set of maze problems which were the forerunner to the Hebb-Williams maze. The maze was a rectangular box into which partitions in various configurations could be set. Different problems were made up from different configurations of barriers but the start box was always located somewhere along one side of the box while the goal was always on the opposite side. The rats showed a steady improvement across mazes suggesting that, in addition to the specific route for each problem, they were acquiring some general knowledge of the direction of the goal from the start and other parts of the box. Further evidence for this goal-direction factor was a marked reduction in their willingness to enter blind alleys which pointed away from the goal and a greater difficulty in avoiding blinds which pointed towards the goal. This latter

observation was confirmed in a multiple-T, six-choice point maze in which the blind alley entered most pointed towards the goal and the three alleys entered least pointed away from the goal. Similarly, in an elegant little maze with one blind pointing forward and the other backward, animals run in a configuration in which the goal was located forward made more entries into the forward-pointing blind while animals with the goal backward entered the backward blind more often. Similar analyses of the relative difficulty in eliminating goalward-pointing blinds were done by Tolman (1932), Spence (1932), and Hull (1952), the latter two in a pseudo-numerical fashion which added little to the original observations.

Dashiell's final demonstration of the goal-direction factor involved the maze which now bears his name. This is a checkerboard pattern of alleys and blocks which offers the rat numerous alternative paths to the goal. In such a maze rats do not repeatedly choose the same path but vary their route from trial to trial. They learn not an S-R routine but the direction of the goal.

In addition to the goal-direction and goal-gradient factors, other less important factors contributing to the rat's maze performance were listed by Woodworth (1938): (a) the entrance or start-box area is important in orienting the animal; often when a rat is placed in the middle of a familiar maze, it will head back to the start and then turn around and make a successful run; (b) anticipatory errors occur when the rat prematurely makes the last turn before the goal; for example, in a linear maze with the correct response sequence RRRRRRRL, the most difficult choice point is the final right turn (Spragg 1933); (c) egocentric predilections such as a tendency to continue forward after a detour, wall hugging (thigmotaxis), or a preference for left or right turns.

According to the theory we are advancing, there are two ways that the cognitive map would be useful to an animal running a maze. First, it locates the animal's position in the maze, and second it points the direction of the goal from that position. The second type of information can be used to generate the hypothesis 'go towards the goal' and is entirely responsible for the goal-direction factor. The first type of information makes available a set of place representations which can be incorporated into place hypotheses about the individual choice points: 'go from place A (first choice point) to place B (second choice point)'. While there is no obvious difference as far as we can see amongst various maze configurations in the usefulness of place hypotheses concerning individual choice points, the same is not true about the goal-direction hypotheses. Mazes with many choice points where one alley runs in the direction of the goal and the other away from it will be more sensitive to goal-direction hypotheses than those in which all or most of the choices have both alleys perpendicular to the goal direction (such as in linear mazes).

Clearly, then, the theory predicts that animals with hippocampal lesions will be impaired on all mazes. Further, in contrast to normals, hippocampals should be insensitive to goal-direction factors such as whether blinds point towards or away from the goal. Finally, since the lesioned animals must rely on routes (concatenations of guidances and/or orientations) to solve the maze, they will be at least as sensitive as normals to these factors. For example, their performance should improve if they are provided with a set of cues at choice points or given a trail to follow. If there is a goal gradient (and the data are by no means unequivocal) then hippocampals should show it in a pure form, learning the choices at the end of a maze more quickly than those at the start.

7.3.1. HIPPOCAMPAL LESIONS AND MAZE LEARNING

Table A20 lists studies concerned with complex maze learning in hippocampal animals. Deficits were reported in 18 of 20 studies. We searched through this literature for studies which provided information on the nature of the deficit in order to test the more specific predictions of the theory. Six gave information about the performance of the animals on individual choice points or on mazes of different configurations: Kimble (1963), Kveim, Setekleiv, and Kaada (1964), Jackson and Strong (1969), Winocur and Breckinridge (1973) Myhrer 1975a, and Myhrer and Kaada 1975. Kimble, Kveim et al., Myhrer 1975a, and Myhrer and Kaada 1975 used the Hebb-Williams maze.* Kimble chose two problems, one which he considered easy (no. 1) and the other difficult (no. 6). The easy problem requires the animal to run directly from the start to the goal, while the more difficult one is solved by a twisting route which at one point requires the rat to turn away from the direction of the goal. The first is clearly aided by a goal-direction factor while solution of the second is hindered by it. The unoperated controls in Kimble's study made an average of three times as many errors on the difficult maze as on the simple one, in spite of the fact that the method of scoring errors afforded almost twice as many opportunities for making errors in the simple maze. The hippocampals were significantly impaired on both mazes, but made twice as many errors on the simple maze. In view of the differences in possible errors in the two mazes (see above) this probably represents equally poor performance on both mazes. Thus, unlike the normals, their behaviour seemed not to reflect a sense of the goal direction; Kimble describes the hippocampals as running back and forth in the side alleys of both mazes and failing to enter the centre of the maze as the control

* The Hebb-Williams maze (see Rabinovitch and Rosvold (1951) for the configurations) is a successor to the Dashiell maze described above. There are actually only 12 configurations; the mirror images of these make up the additional 12 problems. The difficulties in scoring errors and the inequality of errors at different points in this type of maze which prevented our using the Kveim et al. data were amongst the reasons for the original abandonment of the predecessors to the Hebb-Williams maze.

animals did (see also Hughes 1965). Myhrer 1975a found essentially the same results but also had a large deficit in his neocortical controls.

We tried to extend this type of analysis to the Kveim *et al.* study which used all 24 problems of the Hebb-Williams maze and presented the data for each problem separately. If all the problems could be rated as reliably in terms of their sensitivity to the goal-direction factor as nos. 1 and 6, we would predict that the hippocampals, although impaired on all problems, would be relatively less impaired on problems where the goal-direction factor hindered the normals (as in no. 6) and relatively more impaired on problems where it helped them (as in no. 1). Kveim *et al.* did find that some problems were relatively easier for the hippocampals than others, but we have not been able to convince ourselves that these are different from the rest in terms of the goal direction factor. It should be noted that the Hebb-Williams maze does not lend itself to this type of *a priori* analysis in the way that the multiple-T non-tracing mazes used by Dashiell, Tolman, and other earlier workers do. Furthermore, the use of a dome over the maze by Kveim *et al.* would tend to militate against the goal-direction factor. Finally, the rank-order correlation of 0.78 between the scores of the normals and the hippocampals suggests that the hippocampals found all mazes equally more difficult and that there was no interaction between problems and the lesion.

Jackson and Strong (1969) used a six-alley, twelve-cul Lashley-III maze. In this maze the rat runs along each alley roughly at right angles to the direction of the goal until it comes to an opening in the wall in the direction of the goal. Correct performance requires the animal to turn through the wall in the direction of the goal and then to make another 90° turn so as to head along the new alley in the direction opposite to which it had just been coming. Jackson and Strong point out that two different types of error are possible in this maze. The first (called a door error) occurs when the rat fails to turn into the wall opening and continues into the cul at the end of the alley. This error is sensitive to goal direction and should be selectively biased against the lesioned animals. The second type of error (an alternation error) is committed when the animal goes through the opening but turns in the wrong direction in the new alley. Since the new alley is perpendicular to the goal direction, alternation errors are insensitive to this factor and should not distinguish between the two groups. This is exactly what Jackson and Strong found. Confirmation that the Lashley-III maze is sensitive to the goal-direction factor comes from a study by Zack (1968). He showed that normals, but not hippocampals, were disturbed by rotation of the maze in the room after they had learned.

Winocur and Breckinridge (1973) used a six-choice linear maze in which each choice point consists of a pair of doors both roughly parallel to the direction of the goal, rendering the task relatively insensitive to the goal-direction

factor. The order of the correct doors was LRLRRL. They found that the hippocampals were impaired on all choice points but more so on choices 3 and 5. We can offer no theoretically motivated explanation for this selective impairment. Perhaps the fifth door proved difficult because the rats were using an LR alternation hypothesis. In an important series of attempts to improve the performance of the lesioned animals, Winocur and Breckinridge added guidance cues to the doors at each choice point in one experiment or to just the fifth door in another. Adding cues to all the doors improved the performance of both groups by about 50 per cent but the significant difference between them remained. When the cues were subsequently removed, the performance of the hippocampals but not the normals deteriorated. Provision of a guidance at the fifth door alone was also beneficial for both groups and furthermore erased the selective difficulties of the lesioned animals at doors 3 and 5.

A study by Leaton (1969) also demonstrates the reliance of lesioned rats on guidances and/or orientations. He forced rats, over a series of trials, to run the correct path in a six-unit multiple U-maze by blocking off the incorrect alleys. After this initial training the animals were tested with the blind alleys opened. Leaton found that when the blind alleys were quite similar to the correct alleys the hippocampal rats made considerable cul entries. When the blinds were obviously dissimilar, the hippocampals avoided them as well as the normals.

The performance of hippocampal rats has been tested on the Dashiell maze in two experiments (Niki 1966, Ellen and Bate 1970). As predicted, Niki found not only a deficit but also less flexibility in the number of routes used by the lesioned animals. In the Ellen and Bate study the pathways through the centre of the maze were of a different brightness from those on the outside, providing the animals with a guidance trail to follow. Both normals and lesioned animals showed little variation in routes and there was no difference between them.

In summary, several points can be made. First, there is a universal deficit in maze learning in animals with hippocampal lesions. We attribute this to the absence of place information which would support decisions at choice points where no guidance cues are available. In the absence of either guidance or locale hypotheses these animals must rely on orientation hypotheses such as LR turn alternations or left turns at all doors. Provision of guidances helps hippocampals as much as normals. Second, although strong evidence on the insensitivity of lesioned animals to goal-direction factors is lacking, what there is, is consonant with the prediction. We suggest that future studies of maze learning in hippocampals be designed to test different hypotheses about why these animals fail. As a test of the goal-direction hypothesis derived from the cognitive-map theory, we recommend variants of the simple two blind maze used by Dashiell (1930, see above).

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