

6

Exploration

6.1. Novelty

THE ongoing activity of any animal is a complex mixture of numerous separate activities, including such things as walking, eating, drinking, sniffing, grooming, sleeping, and so on. Each species engages in a mixture of activities that is, to some extent, unique to that species. Similarly, reactions to particular forms of external stimulation may vary from species to species. However, within this broad range of genetic variability there are patterns of behaviour that remain constant across species. Thus, in the face of threat most animals seek to flee to safety, or remain immobile, or engage in some form of attack. Similarly, in the presence of food, water, or a sexual mate, most animals (assuming a state of need) engage in some form of approach and consummatory behaviour. Lastly, when confronted with biologically neutral stimuli most animals tend to ignore these stimuli and attend to something, or somewhere, else.

These patterns, however, all refer to classes of external stimulation about which the animal has knowledge (innate or acquired). Reactions to stimulation, the significance of which is uncertain, follow a different course. Initially, there is usually a cessation of overt responding during which the animal prepares itself for, and engages in, the registration of information; only then is some overt response emitted which could involve approach or avoidance. This pattern of behaviour is, to some extent, dependent upon the occurrence of genuine *novelty*, that is stimulation never before encountered, but portions of this behaviour pattern can reflect the occurrence of any transitory change in the external environment. In this chapter we discuss the nature of novelty and change, the course of an animal's reactions to these, the role played in these reactions by the locale and taxon systems, and the ways in which the hippocampal animal's reactions differ from those of the normal animal.

6.1.1. NOVELTY AND NOTICEABILITY

It is important to distinguish between two different properties items or places can have for an organism. We shall define *novelty* as a property of those items or places which have not been experienced before. *Noticeability* refers to a property of those items or places which attract attention.

Part of the confusion between these two arises from the fact that in the intact organism novelty almost always implies noticeability as well, though the converse is not the case.

Few items or places are completely novel; novelty typically consists in new configurations of familiar elements. New pictures hide old lines, old colours; the novelty of the wife in the best friend's bed lies neither in the wife, nor the friend, nor the bed, but in the unfamiliar conjunction of the three. Novelty 'wears off' rapidly with several exposures; repeated exposures to items or places *with the opportunity to explore* leads to a growing sense of familiarity. On the other hand, temporal parameters *per se* do not seem to be important; an event recurring after a year is no more novel than when it recurs after a day. Novelty, then, would seem to depend on a long-term memory sensitive to contextual (typically spatial) configurations and capable of remembering single occurrences. Within the framework of the present theory *an item or place is novel if it does not have a representation in the locale system* and thus excites the mismatch cells in that system.

The implication of this is that novelty is a matter of 'an item in a place'; the location of an object is an integral part of what constitutes its novelty and the uncertainty its occurrence elicits. This aspect of novelty, though rarely commented upon, is supported by several types of research. Peeke and Veno (1973) studied the aggressive responses of fish as a function of both the qualitative properties of the target fish and its location. Responses to a target located in the same place show a steady decrement; this is the process known as *habituation*. A change in either the target or its location reinstated the aggressive response. Thus, habituation, or the decrement in response with increasing familiarity, depended upon the location of the eliciting stimulus. Similar results were reported by Shalter (1975) for the response of birds to calls. This principle applies to neutral, as well as to biologically meaningful, stimuli. Corman, Meyer, and Meyer (1967) and Corman and Shafer (1968) have shown that exploratory responses can be a function of the spatial location of a stimulus.* A more convincing result has been reported by Wilz and Bolton (1971). Gerbils were allowed to explore, in an open field, either a group of objects in a particular spatial arrangement or a single object located in a specific place. The rearrangement of these objects (or a new location for the single object) was as effective in eliciting exploration as a totally novel environment. They conclude that their animals were 'sensitive to change in the spatial orientation of

* In the latter study rats were tested in a black open field with one white square in the centre. After this exploration had waned the white square was replaced by a black one; this 'new' stimulation elicited renewed exploration. Dember (1956) has shown similar effects in a spontaneous alternation situation (p. 260). The nice thing about such tests is that, on the crucial-test trial, they distinguish between the qualitative properties of the stimulus and its location; the field is homogeneous, but certain places are novel. Another example of the effectiveness of familiar stimuli in new places is reported in a study by Karmos et al. (1965), as discussed on p. 167).

familiar objects, even when the position of a single object is involved' (p. 118).

Noticeability, on the other hand, *refers to the degree to which a stimulus excites the nervous system* and elicits a variety of reflexes including the orienting reflex or directed attention. To borrow from part of James's (1890) catalogue of things which attract attention, loud bangs, shiny things, blood, and so on are highly noticeable, though not necessarily novel. The important variables controlling reactions to noticeable stimuli appear to be the recency and frequency of the same or similar experiences, the rate of change, and good or bad associations.* On the present view these context independent reactions are a function of the extra-hippocampal taxon systems. Note, however, that in so far as novelty also involves noticeability, novel items and places will elicit reactions appropriate to both noticeable and novel events.

6.1.2. BEHAVIOUR ELICITED BY NOVELTY/NOTICEABILITY

6.1.2(a). *Exploration*. The hippocampal locale system is assumed to form the substrate for maps of environments an animal has experienced; *these maps are established in the hippocampus during exploration, a species-specific behaviour pattern concerned with the gathering of information*. Animals are assumed to attend only momentarily to those neutral aspects of the environment which are predicted from the map; the appearance of a biologically meaningful event elicits approach (and consummation) or avoidance, and thus allows the taxon system temporarily to control behaviour. However, attention can also be captured, within the locale system, by those aspects of the environment which are unpredicted, or novel. Investigation of this discrepancy ensues, either to fill out the map or to modify it so as to delete features now missing from the environment.** Thus, *exploration is a direct response of the animal to the detection of a mismatch by the locale system; in the absence of the hippocampus all forms of exploratory behaviour should disappear from the animal's repertoire*.

6.1.2(b). *Other reactions to novelty/noticeability*. Traditional theory (e.g. Montgomery 1955) assumed that novelty elicited two states within an animal, *curiosity* and *fear*, and that ensuing behaviour was the result of competition between these two. The dominant response to curiosity was exploration, while the response to fear was either withdrawal or immobility. This distinction is analogous in certain ways to that made by

* Whereas novelty is primarily related to long-term representations, noticeability is basically a short term process, as can be seen in its sensitivity to recency and frequency of stimulation. This separation between long-term and short-term effects is reflected in the kinds of models derived to explain the habituation to novelty and noticeability, as we shall see shortly.

** By delete we do not wish to take the strong position that old maps are destroyed, only that an up-dated map becomes available.

Sokolov (1963b) between the *orienting* and *defensive reflexes* elicited by unexpected stimulation.

Learning theory based on drive reduction models of behaviour has had inordinate difficulty incorporating the existence of exploration. Recently, in one attempt to deal with this problem, Halliday (1968) suggested that novelty elicits only a state of fear, that exploration is motivated by this fear, and that the information obtained during exploration subsequently serves to reduce fear. We prefer to assume that exploration is a specific response to novelty, that it competes with fear, and that it can serve to reduce fear as an indirect by-product (cf. Russell 1973). We do not feel it necessary to account for exploration in terms of hypothetical underlying drives; it is assumed only that exploration is emitted in response to external (unpredicted) stimulation and that its function is the gathering of information about that stimulation, pursuant to the construction of maps.

Most normal animals, however, do display a certain amount of hesitancy when confronted with novelty, and it can be assumed that this reflects fear elicited by novelty. The choice on the part of the animal between approach behaviours, including exploration, and withdrawal behaviours depends upon a number of factors (cf. Bronson 1968) and shows wide individual variation. It is beyond the scope of the present discussion to elaborate on these, though we do consider the nature of reactions to fear-eliciting events later (pp. 294-6). In the remainder of this chapter we concentrate upon those reactions to noticeability and/or novelty which result when generalized fear is not the dominant state elicited by the environment.

Similarly, we do not discuss at length the nature of an animal's reaction to unpredicted stimulation from biologically meaningful stimuli, be they potentially rewarding or punishing. References are occasionally made to such stimuli in order to show that the basic principles applied to neutral stimuli hold for meaningful ones as well, in particular when we discuss the nature of responses to repetitive stimulation. Of course, a number of behavioural situations that we discuss later, such as extinction, discrimination reversal, and reward shifts, all incorporate features of novelty. The animal's ability to adjust rapidly to these changes depends to some extent on the occurrence of exploration. In so far as such exploration is assumed to be lacking in animals without a locale system the discussion of reaction to novelty in the present chapter is germane to our subsequent discussion of these other situations.

6.2. The form of reactions to novelty/noticeability

An animal's immediate reactions to novelty/noticeability should be viewed as preparatory ones which facilitate the reception of information and the subsequent choice among approach, avoidance, or a lack of interest. Intense stimulation, novel or not, tends to elicit a *startle reaction*. In its most developed form this consists in limb extension followed by generalized

flexion leading to a crouching posture, all within 10-20 ms of stimulation (Fleshler 1965, Horlington 1968). The crucial determinants of the startle reaction, which can be classified as a defensive reflex, are the intensity and suddenness of the stimulating event (Landis and Hunt 1939, Fleshler 1965), where intensity is best conceived in terms of signal-to-noise ratios (Davis 1974). Less intense stimulation, which fails to elicit the defensive pattern of the startle reaction, may nevertheless elicit a similar behaviour which can be termed an arrest reaction. This brief reaction consists in a cessation of ongoing activities, a maintenance of the posture exhibited at the onset of stimulation, and various autonomic changes (e.g. Grastyan et al. 1965). The arrest reaction is rapidly followed by a complex of reactions traditionally labelled the orienting response; it includes changes in muscle tonus, respiration and circulation, neuro-endocrine responses, desynchronization of the cortical EEG, and the orienting of the body and sense organs towards the source of stimulation (Sokolov 1963a,b). All these reactions play a role in preparing the animal to register and analyse the stimulation.

Following the orienting response the normal animal will either engage in overt exploration, moving towards and actively investigating the source of stimulation, or it will engage in some form of defensive behaviour. *Only novel stimulation will elicit exploration*; noticeable familiar stimuli will elicit either approach or avoidance in accordance with their biological meaning, or will be ignored if they are insignificant for the animal.

6.2.1. THE RELATIONSHIP BETWEEN EXPLORATION AND RESPONSES TO NOTICEABILITY

The early responses to noticeability just described (with the exception of the startle response) have often been lumped together with exploration under the general rubric of *orienting behaviour*. This characterization, however, overlooks the facts; these early responses neither necessitate exploration, nor are they uniquely elicited by novelty, as is exploration. Further, this does not appear to have been Sokolov's (1963a) intention:

'The orientation reflex in the restricted sense of the word, should be distinguished in the reflex as the non-specific reaction resulting in the tuning of the analyser when exposed to a new stimulus. This elementary reaction is quite distinct from the complex exploratory chain of reflexes, aiming at investigation of the object in detail, and involving a whole series of conditional orientation reflexes' (p. 11).

Thus, there are ample reasons to assume that the early reactions to noticeability form a cluster of responses different from exploration. Particularly important in the present context is the fact that the various components of an organism's reaction to noticeability/novelty develop differently with repeated elicitation. In most, but not all, cases repetitive elicitation causes a decrement in response, termed *habituation*. The habituation of startle, arrest, and orienting, as well as the change in response to repeated presentations

of inherently meaningful stimuli, would appear to follow one set of laws which we shall associate with taxon function. The habituation of behavioural exploration would appear to follow different laws which we shall associate with locale function. We can best document these assertions by briefly considering the general problem of habituation and the theoretical models currently proposed to account for it.

6.2.2. MODELS OF HABITUATION

In general, two types of model have been proposed to account for decrements in response with repeated elicitation. The first class draws its data primarily from the study of short-term response decrements to repetitions of biologically significant stimuli such as those eliciting spinal reflexes, startle reactions, and the species-specific behaviours of the ethologist. Groves and Thompson (1970, 1973; see also Groves and Lynch 1972, Thompson *et al.* 1973) present such a model and suggest that it can account for habituation of the orienting reflex as well as the above behaviours. They postulate two interacting effects of repeated stimulation, one involving sensitization (or an increment in response), the other habituation. These properties are in accordance with the following facts noted by Groves and Thompson concerning short-term sensitization and habituation: (1) during the initial repetitions of a stimulus incremental, rather than decremental, effects are often seen; (2) the extent of the incremental effect is dependent upon the intensity of the stimulus; (3) the incremental effect decays spontaneously upon termination of the stimulus; (4) both incremental and decremental effects are related to the frequency of stimulation in a complex fashion depending in some measure upon intensity; (5) both incremental and decremental effects to an initial repeated stimulus will generalize to another stimulus to the extent that the two stimuli share common elements.*

It should be noted that one can often see quite complex mixtures of incremental and decremental factors operating simultaneously in the response to a repeated stimulus. For example, the changes in the mobbing response of chaffinches repeatedly elicited by a stuffed owl can best be viewed as a decremental process for that exact stimulus combined with an incremental process for similar stimuli (Hinde 1970). Kimble and Ray (1965) have shown that repeated elicitation of the frog scratch reflex leads to decrements if the stimulus is applied in exactly the same spot but increments if the stimulus location is varied, while Ewert and Ingle (1971) have reported similar phenomena for toad's and frog's prey-catching responses. Explanations for these phenomena may reside in the different time courses for incremental and decremental processes within the

* There is a complex, and confusing, relationship between the processes postulated by Groves and Thompson and those postulated by us for the taxon systems. Their processes of sensitization and habituation are both essentially short-term mechanisms and are best seen in the absence of biological rewards or in simplified reflex systems.

hierarchically organized neural systems mediating the reception of the stimulus and the generation of the response (cf. Hinde 1970). Such a proposal is consistent with the local nature of the presumed effects underlying these processes. Thus, this model of habituation, which can be termed the 'self-generated depression' hypothesis (Thompson and Spencer 1966, Horn 1967, Wall 1970, Wickelgren 1967a,b), has been ascribed either to a failure of synapses with use (Thompson and Spencer 1966) or to the parallel activation of an inhibitory pathway (Wickelgren 1967b, Wall 1970). It is important to remember that these models of habituation have been derived from the study of short-term decremental processes and do not necessarily apply to decrements lasting for long periods; Groves and Lynch (1972) explicitly state that their model is meant to account solely for short-term decrements.*

The second model of response decrement with repeated elicitation, associated primarily with Sokolov (1960, 1963a,b), was designed to explain habituation of the orienting reflex to a neutral novel stimulus. According to Sokolov the neo-cortex maintains a model of the stimuli in the environment. Novel stimuli produce a mismatch in this system which signals the reticular formation and thereby produces the orienting reflex. As a model of the stimulus is built up in the neo-cortex the mismatch signal decreases and the orienting reflex habituates. For his part, Sokolov (see Pakula and Sokolov 1973) has indicated that this neuronal model approach is not required when one considers habituation in simplified systems.

Groves and Thompson (1970) argue that habituation of the orienting reflex can be accounted for within their dual-process model, and bearing in mind Sokolov's crucial distinction between orienting and exploring we would agree. It does not appear necessary to postulate the existence of Sokolov-type neuronal models to account for the orienting reflex and its habituation. The self-generated depression mechanism would seem sufficient to handle this. Thus, habituation of orienting reflex components has been reported in unconscious patients whose neo-cortical EEG's were 'very pathological' (Gulbrandsen, Kristiansen, and Ursin 1972).

Exploration of novelty, on the other hand, cannot be analysed in the same manner. There is no obvious relation between frequency and intensity of novelty and exploration. In fact, one could argue that novel environments could not even be described in such terms. Further, habituation of exploration follows a much different time course than does habituation in the other systems; there is no direct analogue to the sensitization often seen in these systems, and the decrement itself usually lasts much longer.

We have suggested that exploration is driven by the occurrence of unpredicted

* Two recent papers by Williams, Hamilton, and Carlton (1974, 1975) document the independence of habituation in the two systems. Anticholinergic drugs influenced the habituation of exploration but not that of the startle response. The latter showed habituation in both 15 and 36 day old rats; exploration habituated only in 36 day olds. The authors concluded that the habituation of reflexes could not be viewed in the same manner as that of exploration.

predicted events and that it ceases when the source of novelty is incorporated into the cognitive map. In a sense, then, a comparator model akin to that postulated by Sokolov, directing exploration rather than reflex orienting, is assumed to exist within the hippocampus.

Thus, two general modes of reaction to noticeability/novelty are postulated for the intact animal: a series of reactions characterized by startle, arrest, and orienting associated with taxon function and of an essentially short-term nature; active investigation of novelty, associated with the locale system and having relatively long-term consequences. On the basis of this distinction we would expect hippocampal animals to show relatively normal startle, arrest, and orienting, including normal short-term habituation of these responses, but not to show behavioural exploration. In their dependence upon taxon systems we would further expect the reactions of these animals to be unusually dependent upon the frequency and intensity of stimulation.

6.3. Effects of hippocampal lesions on reactions to novelty/noticeability

Studies of reactions to novelty/noticeability can be subdivided into those involved with (1) reactions to novel items introduced into basically familiar environments (Table A13), (2) reactions to novel environments (Table A14), and (3) spontaneous alternation (Table A15). By virtue of the procedures used in these studies the first category is primarily concerned with the immediate responses to noticeability, while the remaining two categories are more directly concerned with behavioural exploration. We attempt to show in this review that hippocampal animals react in an essentially normal fashion as regards startle, arrest, and orienting but that they lack exploration. A more detailed discussion of the nature and determinants of exploratory behaviour in normal animals is included prior to the discussion of those studies which attempted to measure it directly. Finally, we briefly discuss several studies investigating *latent learning*, which is typically assumed to involve the acquisition of information during exploration.

6.3.1. A NOVEL ITEM IN A FAMILIAR ENVIRONMENT

An important distinction must be drawn between two related paradigms involving the introduction of a novel item into a familiar situation; this concerns the ongoing behaviour of the animal. In one case the animal is engaged in some directed activity during the introduction of the novel item (the *competitive* case), while in the other the animal is not so engaged (the *non-competitive* case). The relevance of this distinction will be made clear in the ensuing discussion.

In both of these situations one can measure either autonomic or behavioural responses to noticeability/novelty. Unfortunately, experiments using either type of measure have rarely taken into account the differentiations

between the various components of an animal's response to unpredictability. Thus, psychophysiological studies typically confine their measurements to a single response (usually heart rate or galvanic skin response) whose relation to the other components of the overall response is left unspecified, while behavioural studies often ignore the important distinctions between arrest, orienting, and exploration.

6.3.1(a). *Reactions in the absence of directed behaviour.* Psychophysiological measures of an animal's response to a novel item have been taken in a number of studies. Bagshaw, Kimble, and Pribram (1965) presented novel tones to monkeys and measured galvanic skin responses. Hippocampal monkeys showed completely normal reactions to the initial presentations of the tone, to its repetition, and to the introduction of a new, dishabituating tone after response to the initial tone had habituated. Crowne and Riddell (1969) and Sanwald *et al.* (1970) measured cardiac responses to the introduction of novel items, either tone and light combined or tone alone. Work with normal animals indicates that the initial presentations of a moderately intense novel tone produce cardiac deceleration, while later presentations of the same tone may elicit cardiac acceleration (Flynn 1960, Stern and Word 1961, Black 1964, Weisbard and Graham 1971). It has been suggested that the initial deceleration is probably associated with arrest and orienting, while the subsequent acceleration is associated with investigation (Lynn 1966). In both the Crowne and Riddell and Sanwald *et al.* studies the initial deceleration was seen in hippocampal rats; in the latter study the development of the acceleratory response with stimulus repetition was also measured and found to be absent in hippocampal rats. Thus, these studies suggest that the autonomic aspects of orienting, but not exploration, are intact in hippocampal animals.

Behavioural reactions to novel items were measured in several other studies. Startle responses to intense stimulation were reported to be normal (Kemble and Ison 1971) or somewhat exaggerated (Ireland and Isaacson 1968, Coover and Levine 1972) in hippocampal animals; the habituation of startle was normal in all these studies. This exaggerated startle response will be considered shortly when we discuss the general problem of hyperreactivity in hippocampal animals.

Hendrickson, Kimble, and Kimble (1969) measured the orienting response (defined as an arrest reaction and/or somato-motor orienting) to the introduction of novel stimuli. Under conditions where their rats were not engaged in any directed activity hippocampals showed normal orienting behaviour. Kim (1972, and personal communication) reported that in the non-competitive situation hippocampal rats showed significantly less *strong* orienting behaviour (which involved non-transitory reactions) but no deficit in *weak* orienting behaviour (which involved transitory reactions). Hippocampal rats habituated all orienting responses at the same rate

as did control rats. Thus, these studies suggest that the initial stages of orienting are intact in hippocampal animals, and that these reactions habituate normally as well. Later stages, which might involve active exploration, appear to be absent.

In two studies by Rogozea and his colleagues (Rogozea and Ungher 1968, Ungher *et al.* 1971) changes were seen in hippocampal and fornical cats in orienting to repeated neutral stimuli but not in orienting to biologically significant stimuli such as food or tail pinch. Both normal and lesioned cats oriented to the initial presentations of the neutral stimulus. Repetition of the tone, which was presented for 3 s duration at 10 s intervals, led to rapid habituation of orienting in the normal cats. Lesioned cats, however, developed a pattern of compulsive motor activity which took a considerable time to decrement. While the authors felt that this pattern masked defective habituation, this interpretation is not warranted by the data; the motor activity shown by the lesioned cats during the later stages of the study was unlike the orienting behaviour they showed earlier. Similar results for reactions to meaningful stimuli were seen in a study by Nonneman and Kolb (1974). Hippocampal cats oriented normally to model cats or the smell of urine introduced into a novel environment. Habituation to these stimuli was virtually normal, though there were some changes. This situation, of course, shades into a study of fear responses which we shall consider in greater detail later (pp. 294-315).

Some informal observations of our own could be mentioned here. We placed normal and hippocampal rats in a relatively small open box with low sides and tested their responses to various weak auditory stimuli. Their responses to scratching the side of the box with a pen top every minute or so were especially interesting. Normal rats ceased responding after a few such stimulations, showing dishabituation when the location of the stimulus was shifted or the sound markedly changed. Hippocampals, on the other hand, became quite agitated with each stimulation; regardless of what they were doing at the time they almost invariably began to run in response to the scratching sound. At times they ran in the general direction of the stimulus as long as it was maintained, while at other times they simply ran forward. The running usually ceased with stimulus offset. When the frequency of stimulation was increased to once every 5-10 s the running pattern decremented with a few minutes. Neither the running we observed, nor the compulsive motor activity reported by Ungher *et al.* can be considered orienting behaviour. Rather, these data suggest again that hippocampal animals can be hyper-reactive to certain stimuli. Further, they indicate that *the interval between repetitions of the eliciting stimulus is an important variable determining the occurrence of response decrement in hippocampal animals.**

* In general, these results agree with the Groves and Thompson model concerning the correlation between habituation and repetition rates.

There is some direct evidence that behavioural exploration of a novel item in a familiar environment is deficient in hippocampal animals. Glickman, Higgins, and Isaacson (1970) have shown that hippocampal gerbils react to, and explore, novel objects placed into their home cages significantly less than do normal gerbils. Similarly, Ungher *et al.* (1971) note that while their feral cats orient normally to meaningful stimuli they are deficient in their investigatory reactions towards these stimuli. Finally, Dalland (1976b) has shown that hippocampal rats do not react to novel objects introduced into their living situation.

Thus, available evidence suggests that hippocampal animals show normal startle, arrest, and orienting, and that their habituation of these reactions upon stimulus repetition proceeds normally as well. However, little behavioural exploration of novel items is seen in these animals. Lastly, there are several indications that hippocampals over-react to some stimuli in a compulsive manner, though these aberrant responses can be made to decrement with appropriate inter-stimulus intervals.

6.3.1(b) Reactions in the presence of directed behaviour. A more powerful test of the attractive force of a novel item is to introduce it while the animal is engaged in some directed activity, such as a motivated task. The normal animal is usually distracted from its task and explores the novel item. If, for instance, a rat is running for food in an alley and white walls are suddenly introduced on a particular trial, the rat will stop and explore the new walls.

Hendrickson, Kimble, and Kimble (1969) measured orienting responses to novel items while rats were either drinking or attending to the source of a massed barrage of tones. There was a strong suggestion in this experiment that the hippocampal rats totally failed to orient while they were engaged in these other tasks. Similarly, Wickelgren and Isaacson (1963) report that hippocampal rats fail completely to orient to a distracting stimulus (white walls) introduced while the rats were running in an alley for reward. There seems little doubt that in these competitive situations hippocampal animals are less distractible than are normal animals (see Table A13); the question is whether this signifies a total lack of response, or merely an absence of exploration. In a recent paper Harley (1972) discusses an interesting aspect of the Hendrickson *et al.* paper that was not pursued in the original report. She states that

'In one condition the same hippocampally lesioned animals were tested for orienting to an auditory stimulus first in a competitive and then in a noncompetitive situation. They showed no orienting in the first situation as expected but oriented in the second situation at the same level as control rats which had habituated to the stimuli during the first presentation. This implies that the first experience had affected the hippocampally lesioned animals despite their behavioural unresponsiveness.

Naive animals both lesioned and normal, oriented at clearly higher levels when tested in the noncompetitive situation without prior exposure to the competitive one' (p. 347)

Thus, the 'failure of orienting' in the competitive situation, as reflected in the behavioural measures used in the Hendrickson *et al.* (1969) study, may have resulted from the lack of exploration, rather than orienting. In the original report the authors attributed what they conceived as a total lack of distraction to an inability to 'shift attention during the presentation of novel stimuli or in mismatch situations' (p. 226). The comments of Harley (1972) indicate that this cannot have been the case. The hippocampal animals clearly attended to the novel stimuli (in the sense that they perceived and habituated to them), though they did not investigate them directly.

Kim (1972, and personal communication) has also tested the orienting reactions of hippocampal rats in a competitive situation similar to that used by Hendrickson *et al.* As before, Kim separated orienting responses into those which were weak or strong, with the defining difference between the two being the persistence of the response. Kim found that hippocampal rats in the competitive situation showed significantly less strong orienting, significantly more weak orienting, and significantly shorter durations of orienting when both categories of responses were combined. Thus, Kim's data suggest that the primary defect in orienting behaviour in hippocampal rats in competitive situations is that they orient for a shorter period of time and in a weaker fashion. This is consistent with the view that they do not fail to shift attention, but rather fail to react beyond an initial, transitory, orienting response.

Other workers have similarly stressed the fact that the deficit in distractibility is rarely complete. Thus, Raphelson, Isaacson, and Douglas (1965) and Riddell, Rothblat, and Wilson (1969) report that the latency of hippocampal rats in a runway is affected by the introduction of novel stimuli, though this effect is considerably less than that seen in normal animals. Similarly, Crowne and Ridden (1969) report that an increase in latency to respond on a discrimination problem in hippocampal rats upon introduction of novel stimuli indicates the partial nature of the defect. A study by Kaplan (1968) provides an important clue to the nature of the hippocampal impairment in these situations. Rats were trained to press a lever for food and were then tested for their reactions to the introduction of a flashing light. Kaplan noted that control rats 'typically froze when the flashing light was initially introduced, then explored the area surrounding the light before starting to bar press again'. As to the hippocampal rats: 'when the light was first introduced, there was a brief startle reaction, followed by orientation toward the light' (p. 277-278). The hippocampal rats returned to their lever-pressing behaviour quite rapidly. These observations

suggest that hippocampal animals, even while engaged in some directed activity, show normal arrest and orienting responses to a novel stimulus. However, they fail to explore the stimulus, returning instead to their motivated task. Thus, Cohen (1970) and Cohen and Swenson (1970) report that hippocampal rats explore distracting stimuli significantly less than do normal rats. Their animals were trained a runway response and then subjected to the introduction of a novel side alley. The hippocampal rats almost never entered this new alley.

The most startling example of distractibility in hippocampal animals engaged in directed activity was provided by Douglas (1972). Monkeys were engaged in a sequential response task; on certain trials the first response in the sequence initiated a loud buzzer. Both control and hippocampal monkeys were visibly startled by this buzzer; some literally hit the roof of the apparatus. Normal monkeys 'failed completely to complete the sequence and instead turned away from the stimulus and investigated the source of the buzzer' (p. 536). They returned to the task a minute or two later. The hippocampal monkeys 'though startled, completed the sequential response while on the way up' (p. 536). After settling down they secured the reward before attending to the source of the buzzer.

We can see from these observations that a strong distracting stimulus will affect hippocampal as well as normal animals, though the former seem to lack the normal tendency to explore the distracter and have a strong tendency to complete any behavioural sequence that they have begun. These findings suggest that the reactions of the hippocampal animal are dependent not upon novelty *per se*, but rather on the relative intensity (or noticeability) of the various stimuli in the environment. In any case the hippocampal animal fails to react to stimuli, novel or otherwise, with exploration, though startle, arrest, and orienting can be intact. This has been directly confirmed in a recent study by Gustafson (1975), who found that distraction durations were lower in hippocampal rats and that this was due to reduced exploration coupled with normal orienting. This dissociation between the effects of any stimulation and the exploration-eliciting effects of specifically novel stimulation is an important one, to which we shall return shortly.

As a final point we should mention an apparent exception to the general finding of decreased distraction in hippocampal animals reported in a study by Douglas and Pribram (1966). Their lesioned monkeys displayed greater than normal distraction under certain circumstances when the distracter was introduced into a discrimination procedure. The most plausible explanation for this finding is that the distracter was so similar to the stimulus controlling the animal's ongoing behaviour as to be confused with it; we shall consider this study in greater detail later (pp. 275-6). However, it is worth noting that this increased distraction was only seen when a new stimulus was used; it was not seen when a familiar stimulus (to

which the animals had already stopped responding) was introduced in a new place. This clearly indicates that 'a familiar stimulus in a new place' is not treated as a noticeable event by hippocampal animals.

6.3.2. GENERAL ACTIVITY AND EXPLORATION IN NOVEL ENVIRONMENTS

Responses to novelty have also been tested by placing animals in novel environments and measuring their reactions, usually in terms of rather gross activity scores. Before we consider the behaviour of hippocampal animals in such situations we need to discuss the way in which measures of general activity are related to the occurrence of exploration.

6.3.2(a). *General activity and exploration.* Behaviours that are active, but without any obvious goal such as food or water, have commonly been referred to as exploratory. However, it was recognized almost 20 years ago that not all of such activity could be classified as exploration (e.g. Montgomery 1953b). As Bindra (1959) pointed out, *general activity* is concerned not with the 'incidence of a given class of response' but with the 'extent to which an animal makes *any* type of response' (p. 31). *Exploration*, on the other hand, according to Bindra, 'refers to the incidence of only certain classes of acts . . . associated with . . . novel environmental stimuli' (p. 33). Novelty, of course, can only be specified in relation to an animal's past experience. Halliday (1968) suggested that

'an animal explores a stimulus situation if it cannot match it on the basis of its past experience . . . An animal would therefore explore a situation with which it was unfamiliar until its "internal representation" of the situation matched the external environment' (p. 113).

Exploration, in that it is aimed at learning about novelty, decrements with continued exposure to an initially novel environment (e.g. Glanzer 1961). However, an animal no longer exploring one environment will immediately begin to explore another, new environment (Halliday 1966). As we have seen, this re-activation of exploration also follows from a spatial rearrangement of familiar objects in the same 'environment'.

The above indicates that general activity, as a behaviour separable from exploration, can only be appropriately measured under *constant* and *familiar* environmental conditions, with no confounding element of environmental change. Such activity shows a regular circadian rhythm; that is, it varies over time in a cyclical fashion (Richter 1922). It is increased by hunger (or thirst) in a variety of situations, including open fields (Fehrer 1956) and complex mazes (Dashiell 1925). Moreover, *general activity is greater in the presence of increased environmental stimulation, though this need not be novel stimulation* (Hall 1956). By comparison, exploration is either decreased by food deprivation (Montgomery 1953a, Zimbardo

and Montgomery 1957) or is marginally increased (Bones and de Lorge 1962). *It is substantially increased only in the presence of specifically novel stimulation*, and this has led Bolles (1967) to conclude that its 'main determinants ... are associative' (p. 290). This differentiation between general activity and exploration was seen in a study by Halliday (1967); no correlation between the amount of activity and the extent of exploration in a Y-maze was found, though they both tended to drop out at about the same time.*

Berlyne (1966) has discussed two types of 'exploratory' behaviour under the terms 'specific' and 'diversive' exploration. Within a somewhat different framework he referred to some of the properties of exploration and general activity that we have just pointed out. Specific exploration, in Berlyne's terminology, is nearly identical to what we have called exploration. It occurs when an 'animal is disturbed by a lack of information' and it supplies the 'precise information that the animal misses' (p. 26). Berlyne's diversive exploration, which resembles (with certain qualifications) what we have called general activity, 'is not preceded by receipt of partial information about the stimulus patterns at which it is aimed, and thus seems to be motivated by factors quite different from curiosity' (p. 27). This distinction between exploration and diversive, or general, activity is being pursued at great length here partly because it has not often been made within the literature concerned with lesion effects on reactions to novelty. More important, exploration, as a response to specifically novel stimulation, is assumed to be a function of the cognitive-mapping system, while general activity, as a set of responses to any form of stimulation, is not.

Berlyne compares exploration, in humans, to epistemic behaviour, stating that it is 'aimed not only at obtaining access to information-bearing stimulation, capable of dispelling the uncertainties of the moment, but also at acquiring knowledge, that is, information stored in the form of ideational structures and giving rise to internal symbolic responses that can guide behaviour on future occasions' (p. 31).

This description, without the reference to symbolic responses, is close to what we mean by cognitive maps. With the distinction between exploration and general activity in mind and the prediction that only exploration is a function of the locale system, we can now turn to a discussion of the behaviour of normal and hippocampal animals in novel environments.

6.3.2(b). *Responses to novel environments.* In a novel environment the normal animal's behaviour reflects a mixture of curiosity and fear, as we

* The distinction between exploration and general activity comes out clearly in studies concerned with the effects of early sensory deprivation, which increases general activity, but not exploration (Montgomery 1953b, Nielsen 1971), as well as in studies of the effects of amphetamine treatments (e.g. Kumar 1969, Ibuka 1971).

have already noted. Typically,* the animal will remain quiet for a while, perhaps sniffing about its perimeter. Slowly, it will move out and explore its surrounding, often withdrawing back into areas already explored (and hence known to be safe). Once explored, an area is less likely to be visited again on a subsequent foray. In time, the animal will thoroughly explore the entire situation and will become relatively quiescent, or eat if it is hungry and there is food available. At this point we can say that the animal has completed its exploration of the novel situation. On subsequent exposures to the situation the animal might make a cursory check to ensure that nothing has changed, but its activity will be much less than it was on the first occasion. The tendency to explore is quite strong in normal animals; for instance, in a maze with several routes to the goal hungry animals will vary their paths, often taking some that involve more work rather than sticking to the same familiar path (Dashiell 1925).

This normal preference for novel situations over familiar ones reflects the predominance of curiosity over fear; this predominance is not inevitable. Thus, if a buzzer is sounded just prior to allowing an animal to choose between novel and familiar places (thus inducing a certain amount of fear) the animal will tend to prefer the familiar place (Montgomery and Monkman 1955), indicating that fear has become predominant. All this provides a picture of a curious, active animal, seeking out and exploring new situations but constantly pulling back from such novelty when afraid.

Compare this with the behaviour of hippocampal rats. Some move off immediately they are placed in a novel situation; others sit quietly for a while before becoming active. Once active, all hippocampals adopt a stereotyped pattern of behaviour; this typically involves moving about more than normals would do, with a noticeable tendency to go back to the same areas over and over again. In a large box this repetitive behaviour takes the form of running (Kimble 1963, Eichelman 1971), usually around the perimeter (Jackson 1967), and there can be surprisingly little decrement in this behaviour with time. Table A 14 lists those studies which have measured activity levels in a variety of situations. Except for a few cases the consensus is that hippocampals are more active than normals.

This difference could be due to one or more of the following causes: (a) increased exploration; (b) decreased habituation of exploration; (c) decreased fear of novelty; (d) increased drive; (e) increased general motor activity; (f) increased reactivity to stimuli. We shall consider each of these in turn.

* The typical rat, like the average man, is a statistical fiction. Our purpose here is to describe the behaviour of a well-handled rat whose personality falls in the middle of a continuum. We have seen introverted, scared rats which remain immobile for tens of minutes in novel situations, as well as exuberant extroverts which race off within seconds of entering a new situation. One cannot generalize to feral animals or other species, of course. Thus, wild rats are a good deal less curious about novelty (Barnett 1958).

(a) *Increased exploration.* There is no suggestion, either in the literature or in our own observations, that hippocampals engage in what is clearly exploratory behaviour. In line with the distinction between general activity and exploration, hippocampals would appear to be *hyperactive*, but at the same time *hypoexploratory*. Thus, they do not selectively investigate novel, as opposed to familiar, objects, even when such objects are placed into their home cages (Dalland 1970, Glickman, Higgins, and Isaacson 1976b). Their responses to neutral objects often do not decrement from test session to test session. On the contrary, there is the possibility that responses to an object increase with the passage of time, at least with certain inter-response intervals; that is, that sensitization effects are seen. We describe an example of this shortly.

(b) *Decreased habituation of exploration.* Since there is no reason to believe that hippocampal animals explore, it follows that their hyperactivity is not due to a failure to habituate exploration. We would add, moreover, that given any meaningful definition of exploration the notion of exploratory behaviour which does not decrement with repeated exposure to the explored situation is a logical contradiction.

(c) *Decreased fear of novelty.* The observation that some hippocampals, like normals, do not begin to move for a few minutes when first introduced into a novel situation might be interpreted as fear of that situation. The fact that most do not hesitate in this way strongly suggests that there is a reduction in such fear in hippocampal animals. The failure of all hippocampal animals to respond immediately in novel situations means that activity measures must not be too brief if they are to reveal differences between normals and hippocampals. The consistent failure to find such differences in one laboratory (Bender, Hostetter, and Thomas 1968, Hostetter and Thomas 1967, Spiegel, Hostetter and Thomas 1966) might be due to the fact that they observed their animals for only four minutes in an open field.

Evidence consistent with the hypothesis of decreased fear of novel situations comes from the study of Glickman *et al.* (1970). They found that hippocampal gerbils defecate less in the open field than do normal gerbils; Kimble (1963), however, found no differences between normal and hippocampal rats on this measure. Nonneman, Voigt, and Kolb (1974) also reported no differences on this measure, but they felt that both defecation and urination were poor indicators of emotional reactivity. Perhaps better evidence concerns the finding that hippocampal rats, unlike normal rats, do not attempt to jump out of the open field box (Jackson 1967, Eichelman 1971). Jarrard and Korn (1969) have shown that hippocampal rats have somewhat lower heart rates than do normal rats in the open field, in spite of their increased activity. Finally, Jarrard (1968) has shown that hippocampal rats will begin to eat in an open field much more readily than

will normal rats. This could reflect both decreased exploration and decreased fear.*

(d) *Increased drive.* The repetitive running behaviour of hippocampal rats in the open field and their raised baseline of general activity might suggest an increased drive state. Evidence against this view is the finding that the amount of running in an activity wheel, typically assumed to reflect drive (Strong 1957), is virtually unchanged or actually decreased in hippocampal rats (Douglas and Isaacson 1964, Strong and Jackson 1970, Campbell *et al.* 1971, but see Peters and Brunner 1976). Further, food or water deprivation usually affect the activity of hippocampal animals in a completely normal way (Gotsick 1969, Sengstake 1968).

(e) *Increased general motor activity.* It might be argued that the increased activity of hippocampal animals reflects a general motor system excitation which enhances the normal pattern of activity. The main argument against this view is the selective increase in certain behaviours as opposed to others that has been observed in most studies. Time sampling of the behaviour of animals in their home cages shows that hippocampals sleep less and sniff more during the night (Jarrard 1968, Kim *et al.* 1970, 1971a). In the Jarrard study this result was obtained 45 days after the animals were placed in the observation cages, indicating that the increased sniffing was unrelated to novelty.

As noted above, hippocampal rats spend much of their time in the open field running around the perimeter in a stereotyped fashion. On the other hand, they have been reported to rear significantly less than do normals in this situation (Jackson 1967), as well as in an enclosed box (Clark 1970). Similarly, as we have seen, they rarely attempt to jump out of open fields.

The evidence, then, suggests that the hyperactivity of hippocampal animals does not reflect a general increase in all activities, but rather a shift in the probability of occurrence of certain behaviours. Many of those behaviours which are diminished reflect exploration or the operation of the cognitive-mapping system. These shifts appear related in some way to the specific environment to which the animal is exposed; this brings us to the last postulated cause of hyperactivity in hippocampal animals, one noted already in discussing reactions to intense stimulation, the exaggerated reaction to external stimulation.

(f) *Increased reactivity to stimuli.* Kaplan (1968) thought that the hyperactivity of hippocampals might be due to a hyper-reactivity to stimuli, since there were indications in the literature that the difference in activity between normals and hippocampals increases with the size and complexity of the environment.

* We discuss later several studies of hoarding behaviour in rats which suggest that hippocampal animals are not affected by the insecurity inherent in a novel environment (pp. 353-4). These studies, in conjunction with that of Jarrard (1968), indicate that hippocampal animals lack the normal fear of unknown places. See our discussion of fear (pp. 304-6).

He showed that the same group of hippocampals were hyperactive in a large, well-lit box with holes, but not in a small, dark jiggle-box (a box with a sprung floor which can be used to register movement). This suggests that activity in hippocampal animals is related to the extent of external stimulation of any sort, and is thus general activity rather than exploration.

We have come to the same conclusion on the basis of our own observations of fornical and hippocampal rats in various novel environments. Two of our observations are worth mentioning in this context as they shed some light on the mechanisms controlling the behaviour of hippocampal animals. The first, of one of our hippocampals on a novel elevated plus maze, underlines the sensitization to stimuli that can sometimes occur with repeated responses and calls to mind our discussion of the self-generated depression model of habituation and its postulation of incremental, rather than decremental, effects under certain conditions. The plus-maze was in constant use and had a number of fecal boli strewn about it. When first placed on the maze the rat sat for about a minute and then began to move off. As it did so it sniffed at a fresh bolus left by the preceding animal. Subsequently, its activity steadily increased as it ran back and forth from arm to arm, often visiting only two of the four arms for several minutes. During this period it never passed that bolus without pausing to sniff at it. Yet at the same time it ignored all the other boli on the maze. After 10 minutes or so the rat began to sniff at another bolus in the same arm. After that, with each passing minute, more and more boli were sniffed until the animal was spending most of its time running from bolus to bolus, devoting one or two sniffs to each. Thirty minutes after the rat had first been placed on the maze this behaviour continued unabated.

This observation demonstrates the complete absence of anything remotely comparable to exploration in hippocampal animals, their high-activity level consisting almost entirely in repetitively stereotyped behaviours; these are best described as microstereotypies, for the form of the behaviour can be remarkably constant. We have noted that behaviours related exclusively to the taxon systems, such as these stereotypies, should depend exclusively on such variables as frequency and constancy of stimulation for their habituation. High stimulation rates and constant stimuli favour decrements in response, while low rates and variation in the eliciting stimulus could yield incremental effects instead. If the behaviour of the hippocampal animal is due to processes such as these we would expect the incremental effects just described. Further, we would expect a rapid decrease in responsiveness with increased consistency and frequency of stimulation. Our second observation, that of hippocampals in a small glass jar, is pertinent here. One animal in this situation remained motionless for 2 min and then developed a stereotyped sniff-rear pattern which was repeated at the rate of once every 10 s or so. However, this pattern

was almost never repeated twice in the same part of the jar. Typically, the animal sniffed-reared-sniffed in one place and then moved a certain minimal distance before repeating the sequence; sometimes the second sniff was followed by a partial rear in the same place. This pattern suggests that each sniff and rear cycle has two effects: it increased the likelihood of further sniffs and rears, but decreased the probability that the particular stimuli immediately available would trigger such behaviour.

These observations, and the mechanisms we have postulated to explain them, help to account for many of the behaviours of the hippocampal animal. In large open boxes more stimuli are available and consequently activity levels will be higher than in small boxes. Further, and most important for the hippocampal animal, the time between successive exposures to the same stimuli increases in large boxes. In smaller boxes the rate of repetition of the same stimuli could 'allow' the hippocampal animal to habituate as rapidly as the normal animal, though these two types of animal appear to be habituating in markedly different ways. This analysis also explains why there should be no difference in activity wheel behaviour between normals and hippocampals; animals in this situation are repeatedly and rapidly exposed to the same stimuli. Thus, the peculiar features of the behaviour of hippocampal animals in novel situations can be ascribed to two main factors: first, the absence of exploration is due to the lack of a cognitive-mapping system; second, the stereotyped behaviour patterns that are seen, and the importance of such variables as frequency and consistency of stimulation, are due to the remaining influence of the taxon systems. We see later, in our discussion of extinction, another example of how important these characteristics of the taxon system are in determining the behaviour of the hippocampal animal.

Before moving on to discuss spontaneous alternation behaviour there remains the problem of explaining the curious fact that studies employing an ultrasonic activity-measuring device (Boitano and Isaacson 1967, Boitano et al. 1968, Jarrard and Korn 1969) have failed to report hyperactivity in hippocampal rats. It is known that the rat's hearing extends at least as high as the frequency used in these devices (40 KHz, Gould and Morgan 1942), and, in fact, is probably maximally sensitive in that very range (Gourevitch and Hack 1966). We therefore decided to see if there were any differences in the responses of normal and hippocampal rats to this sound. Three normals and three hippocampals were tested in an elevated box with the transmitting and receiving heads of the ultrasonic device located about a metre away. None of the normals paid much attention to the onset of the sound beyond a slight ear flick. Two of the three hippocampals immediately ran to the side of the box closest to the source of the sound and spent a considerable portion of their time leaning out over the edge towards the source. The third did not orient towards the sound in such an obvious way but instead became extremely agitated. He, and one of

the other hippocampals, developed audiogenic seizures at 8 and 6 min after the sound onset, respectively, and remained for the rest of the observation period huddled in post-ictal depression. It appears, then, that the sound emitted by these devices is both audible and strong for the rat, that the normal rat rapidly habituates to it, but that the hippocampal rat, as is the case with other strong stimuli, suffers incremental effects, leading in some cases to increased running and possibly seizures. Although it is not possible to demonstrate that similar effects were produced in the three studies under discussion we would caution against the use of these devices, particularly in the study of brain-damaged animals.

6.3.3. SPONTANEOUS ALTERNATION

When a sated rat is given two consecutive trials in a two-choice apparatus, such as a T-maze, it is highly likely that its second choice will differ from the first. This phenomenon, termed spontaneous alternation, tells us basically two things about an animal. First, some trace of the first choice and its consequences is available to the animal later, and, second, the animal is motivated to change its behaviour on the second trial, relative to some dimension of the situation. It is clear that normal animals rarely alternate responses (in the sense of left or right turns) *per se*, but rather alternate the place to which they go, or the particular stimuli they approach (e.g. Walker *et al.* 1955). Alternation tends to increase as the animals are confined for longer periods in the initially chosen goal area, and it has been suggested that something akin to stimulus satiation accounts for this effect (Glanzer 1953b). Placing the animal in one of the goal boxes for a period of time causes the animal to choose the arm leading to the other goal box on a subsequent trial (Glanzer 1953a). The strength of this alternation tendency is demonstrated by the fact that after 10 forced trials to one choice arm rewarded by food the hungry animal will alternate to the nonfood side when given a free choice (Sutherland 1957).

Alternation behaviour can be viewed most simply as reflecting a tendency on the part of the animal to acquire information about unknown parts of its environment, and thus as exploratory behaviour; the longer the animal is allowed to explore one part of the environment the less attraction this part holds relative to other, unknown, areas. Strong support for this information-acquisition view of spontaneous alternation was provided by Sutherland (1957). He showed that alternation will occur when the two arms of a T-maze lead to different goal boxes, but will be decreased when the arms are extended to lead to a common goal box. This shows that stimuli which are not available at the choice point can determine alternation behaviour; the rat will vary its choices in so far as such variation brings it into contact with new places or stimuli.

The hippocampal animal approaches the alternation situation on somewhat different terms. According to the present model, it is bereft of

cognitive maps and any tendency to explore novelty. It would thus be predicted that these animals would not alternate. Table A 15 lists the results of those studies concerned with the behaviour of hippocampal animals in spontaneous alternation situations. The general picture is that these animals do not alternate.

6.3.3(a). The hippocampus and spontaneous alternation. The first time an animal is confronted with a choice its particular response is assumed to be random. This is yet another statistical fiction. The first choice of an animal reflects a number of factors, motivational, emotional, and other, and can be taken as a reliable indicator of the hierarchy of response alternatives in that animal's repertoire at that particular moment. When confronted with the same situation shortly thereafter, assuming no change whatever (including no effect of the first choice), one must predict that the choice would be the same, reflecting the action of the same factors that led to the initial choice. Of course, as we have just seen, the first choice biases the second in determinable ways. In the normal animal the action of the locale system is assumed to produce a strong tendency to alternate place. In the hippocampal animal, on the other hand, response factors seem to be the main ones that bias second choices, and they bias these animals towards repeating their first choice.

The studies listed in Table A15 provide some support for this response-repetition view of the behaviour of hippocampal animals in spontaneous alternation situations. Nevertheless, we should point out that there is a serious methodological flaw in all but four of these studies (Dalland 1970, 1976, Stevens 1973a, Stevens and Cowey 1973). Alternation tests in the remainder of the studies were applied successively to the same animal, varying from one test per day to five tests per day (that is, six trials in all): Underlying this methodology is the assumption that, in the normal rat, all traces of previous experience in the maze are gone within some short period of time. This, however, is strongly contradicted by the study of Blanchard, Shelton, and Blanchard (1970b), which showed that the memory for a single experience with non-reward objects can last up to nine days. Optimally, animals should be tested for alternation only once, as in the studies noted above.

While many of the studies support the view that hippocampal animals fail to alternate in the spontaneous alternation situation, there are some exceptions. Two factors seem to be important: (1) intertrial interval; (2) confinement in the goal arm chosen on the first trial. According to Roberts, Dember, and Brodwick (1962) and Kirkby *et al.* (1967) hippocampal rats repeat responses after 8-10 min inter-trial interval. However, 50 min inter-trial interval can lead to other behaviour. If this time is spent in the goalbox then alternation is seen on the next trial (Kirkby *et al.* 1967, Stevens 1973, Stevens and Cowey 1973). If the time is spent in a

waiting cage outside the apparatus, random choices ensue (Stevens 1973a). These data suggest that satiation to the goal-arm stimuli can lead to alternation in lesioned rats. However, the Stevens and Cowey data confuse the issue somewhat. Rats with dorsal hippocampal lesions respond randomly with 50s inter-trial interval and repeat responses with a 50 min interval spent in a waiting box. On the other hand, rats with ventral hippocampal lesions repeat responses after 50s, but alternate after 50 min in the waiting box. These data stand in opposition to the results of the Dalland (1970) and Stevens 1973a) studies, though there were lesion site differences, of course. We have no explanation for these discrepancies.

In addition to these conflicting data there are two studies using multiple tests which produced alternation (Gross, Black, and Chorover 1968, Ellen and DeLoache 1968). The first study produced alternation with short inter-trial intervals but not long ones; it is possible that very short inter-trial intervals will produce response alternation due to a short lived inhibition in the response system. The second study produced alternation in the lesioned animals to the brightness of the goal arm but not to spatial direction. These exceptions to the general picture of absent alternation in hippocampals suggest that there are taxon mechanisms available for shifting an animal's responses and that they are sensitive to such things as stimulus satiation and repetition rate. This agrees, of course, with what we have already seen in discussing habituation, and we shall see that it is important in understanding the behaviour of hippocampals in a wide variety of situations. We shall consider the mechanisms underlying such shifts in behaviour in hippocampal animals in detail later (pp. 337-48). The bulk of the data under discussion here indicate that spontaneous alternation is driven primarily by the locale system and that it is absent in hippocampal animals, except with very short inter-trial intervals or very long confinement in the goal box.

Dalland's study provides the clearest picture. She showed that her lesioned rats were specifically repeating responses, and not approaches to specific stimuli, by rotating the start arm 180° on the second trial. In a recent report (Dalland 1976a) this response repetition finding was replicated and extended to show that it occurred regardless of the place or stimuli to which the response led. However, in a separate experiment she found that preventing lesioned rats from entering one goal arm (by a nylon mesh door) led to the choice of that arm on a subsequent free-choice trial. A control study showed that this result was not due to the novelty of a door being removed on the second trial; the mere removal of a hurdle from a normal two-choice T-maze had no effect on the responses of hippocampal rats. These data, for which we have no simple explanation, were interpreted by Dalland to suggest that one of the variables controlling the repetition of responses is the voluntary nature of the first choice.

Gaffan (1972) has shown the hippocampal deficit in spontaneous

alternation using a design which rules out response factors. On the first exposure to a T-maze rats were allowed to move about only in the start arm, though they could see both goal arms through clear plastic doors. One of these arms was white, the other black, on this trial. On the second trial the plastic doors were removed and the colour of one of the arms changed so that both arms were the same. This second trial was given under one of two conditions: either the same as the first trial or with the rats made fearful by the sounding of a buzzer just prior to the trial. Normal animals chose the arm which had been changed when tested under nonfear conditions and the arm which had not been changed when tested under fear conditions. Hippocampal animals chose randomly on both conditions. This study clearly shows that the normals, but not the hippocampals, are choosing on the basis of information about stimuli in particular locations and not on the basis of previous responses or the amount of exposure to the stimuli in the situation.

It appears then, that the normal animal tends not to repeat its responses over two choices when such repetition involves the simultaneous repetition of location and/or stimuli. On the other hand, the hippocampal animal tends to repeat its responses whether or not this entails going to the same place, or to go randomly. Only very short inter-trial intervals or confinement to the initially chosen goal area can alter this picture. These data support the view that hippocampal animals lack those mechanisms driving exploratory behaviour in normal animals.*

6.3.4. LATENT LEARNING

In the typical latent-learning situation an animal is put in a novel environment and allowed to explore. The animal is neither hungry nor thirsty, and the location of food or water within this environment is not the source of motivation for the animal's exploration. Nevertheless, if subsequently made hungry or thirsty, the animal will quickly learn to go to the proper location to find its reward. This type of learning, which depends upon exploration, has been termed *incidental*, in that it does not appear to be a direct result of the animal's interests or motivations. Within the framework of the present model latent learning is neither incidental nor unmotivated. It results from the action of the cognitive-mapping system and leads to the development of maps of experienced environments. Thus, we would predict that hippocampal animals would not show latent learning. Two studies of latent learning in hippocampal rats have been reported, neither of which found dramatic effects in their normal subjects. Means (1969b) reported some latent learning in his hippocampal rats but the data are unconvincing.

* The data on spontaneous alternation provide a good example of the problems associated with the use of combined cortical-hippocampal lesions. In a few of these studies the cortically lesioned controls failed to alternate properly (Means, Woodruff, and Isaacson 1972, Stevens 1973a). The interpretation of a deficit in the experimental lesion group is impossible with such control data.

Kimble and Greene (1968) report no latent learning in their hippocampal rats and conclude that these animals may have 'built a poorer "cognitive map"' (p. 100), but these data are also not very convincing. A definite conclusion concerning latent learning in hippocampal animals awaits a proper experiment, one in which normal animals show a clear-cut effect.

6.3.5. CONCLUDING COMMENTS ON EXPLORATION

We have observed that the behaviour of hippocampal animals in response to novelty differs from that of normal animals in several ways. First, hippocampal animals betray no knowledge of the unfamiliarity of a new place, either in terms of curiosity or fear. Second, they explore novel items less than do normals. Third, their hyperactivity in novel, or other, environments results from their lack of fear, their tendency to engage in repetitive, stereotyped behaviours, and their hyper-reactivity to stimuli. Fourth, they fail to alternate choices in most spontaneous alternation situations.

The distinction between exploration and general activity is a particularly important one in the context of hippocampal lesion effects. Activity seen in hippocampal animals would not appear to be exploration. It does not decrement with continued exposure to a novel situation in any way specific to that situation, at least when the situation provides adequate variation. The absence of this important defining characteristic of exploration is seen clearly in a study by Kamback (1967). Rats were given the opportunity to press either of two levers in an operant chamber, one providing light, the other nothing. Both normal and hippocampal rats preferred to press the light-on lever. In the normal animals this preference declined over time, suggesting that it was based to some extent on curiosity and exploration. In the hippocampal animals the preference did not decline over time. As Halliday (1968) pointed out, light-contingent lever pressing can only be considered as exploratory when it declines over time. The absence of such a decline in hippocampals is consistent with the view that in these animals the preference was based on the greater stimulation the response provided, and was not based on an exploratory tendency.

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