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Spatial behaviour

IN the first chapter we concluded that the ability to represent objectively the world in three-dimensional space, that is, to build cognitive maps, must be innate. In this chapter we shall concentrate on specifying those behaviours dependent on cognitive maps. It is quite a recent development that one could argue whether or not cognitive maps were innate; for much of this century the concept in its entirety was rejected by mainstream psychology. Mental maps, mentioned at the start of the century by Gulliver (1908), were banished, along with introspective data, during the dark night of the ascendancy of behaviourist theory in America.

Notwithstanding this ostracism, we can call upon a varied literature in specifying behaviours that would seem to require cognitive mapping. Much of this has been generated in the past 10 years in the course of a dramatic upsurge of interest in *environmental psychology*, which concerns itself with the perception and utilization of large-scale, or macro-, environments (e.g. Wohlwill 1970). Before turning to this new evidence, however, we can briefly look at two other areas of research which have contributed to the current popularity of the idea of cognitive mapping: (1) studies of navigation in various species, but mostly birds; (2) the work of Tolman and others on place learning in simple and complex mazes.

Though these data provide a justification for thinking about cognitive maps in our theories of behaviour, they fail to provide an appropriate formalization of the concept, and certainly not one that would be useful for translation into neural terms (see Olds (1954) for an early attempt at such a translation). Consequently, we devote the second section of this chapter to a more formal treatment of maps. Here, we contrast *maps* to *routes*, as we shall suggest that spatial behaviours based on the taxon systems can be viewed as connected series of specific behaviours. The term route, with its implication of landmarks and specific responses guided by these, serves as a useful metaphor in describing taxon behaviours. Similarly, the use of the term map implies the availability of an aggregate of interrelated information with no necessary specification of guides. We intend in this section to determine those features of maps which must be incorporated in any theory of cognitive mapping.

In the final section of this chapter we translate these ideas about maps and routes into more familiar psychological terminology, providing a

means for evaluating behaviours based on the two. Here, we outline the properties of the locale (map) and taxon (route) systems.

2.1. Some examples of mapping

2.1.1. STUDIES OF NAVIGATION

The ability of many animals to find their way back to their nests over large distances would appear to be based on some type of mapping system. We shall discuss two examples from the vast literature on this subject: *homing* and *migration* in birds, and open-sea navigation in humans. In the introduction to their well-known classic study of homing in the noddy and sooty tern Watson and Lashley (1915) summarized previous studies of migration and homing and the hypotheses generated to account for them. It was already known that many species of birds migrated hundreds and even thousands of miles every year to reach their breeding grounds. The most extreme example of this was the arctic tern, which appeared to spend 14 weeks of the year in its arctic home, slightly longer in its antarctic home, and the rest of the year making the 22,000 mile round-trip flight between the two. Similarly, homing pigeons could be released from new locations hundreds of miles from their nest and find their way home in remarkably short times.

In their own experiments, Watson and Lashley studied both the long-distance homing of the tern and its short-distance ability to locate its nest on the island. Although they were able to demonstrate that the birds could return to Key Island, Florida when released at distances of up to 1000 miles away, they were unable to provide evidence in support of any particular hypothesis as to how the birds accomplished this feat. Hypotheses current at that time included suggestions as to what stimuli were directing the animals and which sense organs were sensitive to these (magnetism, wind currents, direction of the sun or light, direct visual perception of the goal, special nasal senses), in addition to vaguer suggestions about hereditary topographical memory. They found no effect of occluding the nares and calculated that the island could not be visible from release points greater than 100 miles.

In contrast to these essentially negative conclusions on long-distance homing, their studies on the proximal nest-finding ability of the birds were more successful and led them to conclude that

'coming in from the sea, they direct their flight by the more conspicuous features of the island, the buildings, prominent bushes, etc. From these the direction is taken along the shore-line, or the edge of the cleared nesting area to the alighting place, which also offers prominent visual stimuli. From this the path to the nest is followed, either by a series of visual-motor habits built up around other nests, debris, etc., or by a series of kinaesthetic-motor habits irrespective of external stimuli' (p. 75).*

* As we shall see, this is a good description of what we call a route (pp. 83-6).

Furthermore, they were impressed by the relative autonomy of the individual components of the route:

'the same lack of coordination in reactions to complex situations is seen in the choice between two nests, in the re-orientation in the path to the nest, and in the reaction to changes in the appearance of the path. The reactions are to separate groups of stimuli and there is clearly no analysis of the situation as a whole. The birds do what a man would only consider doing under like circumstances; that is, they carry out in overt activity many of the same processes which in man are restricted to the language mechanism. In subjective terms, they show little or no evidence of "ideational processes" in their activities' (p. 83).

Although they recognized that this analysis could not be extended to include long-range homing abilities, they failed to consider whether these latter might be connected with the 'ideational processes' seemingly absent in the more proximal orientation abilities. Instead, they both abandoned field studies for the laboratory with Watson in particular, concentrating on experiments more similar to the habit-based proximal orientations, to the neglect of the more cognitive map-based distant homing.

Until recently, studies of homing and migration have concentrated on testing hypotheses directed towards the identification of the sensory information which the bird used to locate itself and guide it towards the goal (see, e.g., reviews by Matthews 1955, 1968). In spite of much research no single stimulus has been isolated, and work has turned towards the testing of more complicated 'cognitive' models. The most successful of these is the map-and-compass hypothesis of Kramer (1953). Griffin (1955) has pointed out that animals could find their way to a goal in several different ways: (1) piloting, which is steering by familiar landmarks; (2) compass steering, which is heading in a constant compass direction; (3) true navigation, which is heading towards a specific goal regardless of the original starting place and the direction necessary to achieve the goal. These are roughly equivalent to what we shall call *guidances*, *orientations*, and *map following* in the next section. It now seems clear that birds can use both compass steering and navigation in addition to piloting, as Watson and Lashley had shown. For example, if migratory birds are captured and transported in a direction perpendicular to that in which they were flying, naïve birds on their maiden flight will continue to fly in the same direction in which they had been headed and will thus miss the goal by the amount transported, while experienced birds which have made the trip before will correct for the distance they have been displaced and eventually attain their destination. The naïve birds are following a compass direction while the experienced birds are flying towards a goal.

The most adequate hypothesis to explain true homing behaviour is, as noted already, the map-and-compass hypothesis. This postulates that the bird has a map by which it can locate its present position, that of the goal, and the direction between the two, and a compass which will enable

it to calculate that direction. Recent work has concentrated on the features of the compass (e.g. Keeton 1974). Thus far there are three different mechanisms by which birds have been shown to calculate compass direction; these involve the use of the sun, the stars, and magnetic fields.

Birds use the sun to calculate compass direction by measuring its azimuth* and calculating where the sun is located at that time of day according to their internal biological clock. Thus, for example, if their internal clock tells them it is noon and that the sun is in the south at noon, the bird will fly 90° counter-clockwise to the sun if its map requires it to go east to get home. The best evidence for this mechanism comes from studies in which the animal's internal diurnal clock has been artificially shifted by altering its day-night cycle. In such studies the birds do not fly in the homeward direction when released at a distant site, but head off in a direction consistent with the notion that they are calculating the compass direction of the sun on the basis of their internal clock.

A second source of compass information is geomagnetism. Again, Keeton (1974) is our source. Earlier attempts to demonstrate the use of magnetism for orientation by birds failed because the birds seemed lost when required to fly when the sky was overcast. The conclusion seems unwarranted since Keeton and his colleagues have now shown that the difficulty was an unwillingness on the part of the birds (pigeons in this case) to fly in bad weather and not an inability to orient towards home. Pigeons trained to fly in bad weather orient very well. Furthermore, this orientation appears to be independent of the bird's biological clock, since clock-shift studies do not alter the direction in which the animals fly when released. Birds flying under overcast skies are severely disrupted if magnets are fixed to their heads, and can even be made to fly in the wrong direction by the appropriate applied magnetic field. Neither of the latter two conditions has any effect on pigeons flying in unclouded skies, which might explain why the use of geomagnetism went undetected until recently.

Thus, in the adult pigeon the orientational ability is an over-determined one, and the animal can use either the sun or magnetic fields. Interestingly, in the young inexperienced bird both sources of information are required. Thus, young pigeons cannot home with magnets on their heads even in clear skies.

The third source of compass information arises from the stars. This does not appear to be used by pigeons, who are reluctant to fly at night, but is used by migratory birds. Emlen (1975) has studied the ability of indigo buntings to use this information. These birds are not born with an innately wired star map, but are born with the ability to construct map-like representations on the basis of their observations of the heavens. They need a view of the stars before they set off on their migration. During this

* The azimuth is the arc which the sun makes with the horizon.

exposure period they 'learn' how to orient themselves by establishing a fixed reference framework consisting of the pole-star (the North star, whose position in the sky remains constant through the night) and the set of rotational movements of the surrounding stars. Thus, in addition to acquiring the ability to use the immobile pole-star, the birds can also use any of the surrounding clusters of stars which move during the night. Clock-shift experiments show that this ability, like the sun compass system, relies on the animal's use of its internal diurnal cycle to calculate the direction of the star pattern at any given time of night. Planetarium experiments, in which the 'sky' can be rotated around any star, show that the immobility of the pole-star is the crucial feature determining its choice by birds.

There would appear, then, to be considerable information about the mechanisms by which birds determine compass direction once they have located themselves and their goal on the map. However, what about the map itself? Unfortunately, little is known here, aside from some preliminary findings that pigeons systematically head off in the wrong direction at certain release sites and that these errors are probably related to local distortions in the map; the animals act as though they were some place else in the world (Keeton 1974). One thing seems clear: the birds are not using landmarks of any sort, nor are they following routes. Airplane tracking of individual birds shows that they seldom, if ever, return home by the same route from the same release site and that even when, on the later returns of a series, they come across landmarks associated with previous return flights they do not change flight plans and follow the previously used route.

Gladwin (1970) has described how South Sea islanders (Puluwatans) navigate across large stretches of open sea without the use of technical aids in his fascinating book *East is a big bird*. Very much in the same way as we have just described for birds, they seem to employ all three of the theoretical navigational devices listed by Griffin: piloting by landmarks near the end of the journey, orienting relative to the stars and sun to remain on course, and, most importantly, cognitive mapping. The major device is a spatial map of the region which locates all of the islands relative to each other, together with a large panoply of natural seamarks such as reefs and whirlpools, and mythical ones such as identifiable sea birds, fish, etc.; these latter are never observed in the places where they are supposed to be located but serve mainly to fill up the large gaps in the map which would otherwise remain undifferentiated and might suffer compression. The map also contains a superimposed star map which consists of 32 of the most prominent stars in the sky situated around the periphery of the map according to the points on the horizon at which they rise or set. The stars are chosen to cover roughly the 360° of the compass. It should be noted that in this area of the world, near to the equator, stars rise and set

horizontally, so that a knowledge of the time of night and the azimuth of the star will locate it on the star map. It is clear, however, that the location of individual stars is not important but that, in a fashion similar to birds, it is the pattern of stars which provides the necessary information:

'it is not necessary to have a discrete point on which to set a course. Instead, to borrow an expressive image from the Mississippi River pilots of Mark Twain's day, you steer by the shape of the sky. You are sailing into a part of the heavens, not towards a dot of light' (p. 152).

In addition to memorizing the position of the islands and the stars, the Puluwatans remember all of the star courses which must be followed while navigating between any two islands.

Thus, when a boat wishes to go from one island to another, it sets off in the direction designated by the appropriate star or star pattern and maintains that direction. In addition to the stars at night and the sun in the day, the human navigator, like the bird, uses all available cues to maintain the appropriate orientation. These include a back-sight along two landmarks on the island which is being left behind to get a precise initial orientation and the use of characteristic wave patterns to maintain orientation. In addition to direction, a navigation system needs some information about distance travelled. We shall suggest in a later chapter that in animals locomoting over land this is provided in part by a collateral output from the movement-generating circuits to the map. For birds a similar output would provide less reliable information because of the large effect of wind currents. For humans incarcerated in a self-propelled vehicle no such information about speed is available. The Puluwatans have solved this problem in an ingenious way. Instead of picturing the boat moving through a stationary map they view the boat as stationary and the world as moving past them. Within this scheme each course between a pair of islands has a reference (or *Etak*) island associated with it, usually one 50 miles or so off to one side. During the voyage the navigator mentally calculates the movement of this (unseen) island relative to the star map and divides the journey into segments of time corresponding to the movement of the *Etak* island from one star to the next. This device, together with a rough knowledge of speed under different ocean currents, seems to predict accurately the distance and time of travel.

This brief summary of the navigational abilities of birds and humans points to the existence in both of a sophisticated mapping device together with a host of associated devices for operating on that system, providing information by which the organism can locate itself and other places within the map and determining the appropriate direction between these places. In the human system all of the information in the map has to be painstakingly learned and even to some degree the mode of using the map must be acquired. In the migratory bunting the star map which the animal uses

to orient itself would appear to be pre-programmed to accept only information about star configurations and their patterns of movement during the night. Notice that a genetically pre-wired map of the stars would be disadvantageous, since the pattern of the stars slowly shifts in the sky over several thousands of years. Little is known of the map in the homing pigeon, but it would seem reasonable to assume that, by analogy with the compass in these birds, it is over-determined and receives information from several different types of stimuli distributed across the surface of the earth, such as magnetic fields and other types of radiation. In that case, it is likely to be completely innate.

Before leaving the topic of navigation there are several other studies we should consider for they all agree in concluding that something like a cognitive map must underlie complex behaviour in space. Zanforlin and Poli (1970) studied the digging activity of rats, focusing on their ability to move accurately through space while burrowing. Rats were allowed to run through an opaque tube placed in a sand-box, leading from start (A) to goal (B). Following this, they were required to burrow from A to B under either of two conditions: with or without sight of the visual landmarks associated with start and goal at the initiation of a trial. Under both conditions rats succeeded in getting to the goal through the sand, though visual cues facilitated performance noticeably. The authors excluded the possibility that magnetic, olfactory, or visual cues were used during the actual burrowing. Further, the routes taken by the rats did not match the shape of the routes used in the training tubes, eliminating the possibility that fixed sequences of responses were involved. Thus, they concluded that

'the burrowing rats use a complex system of kinesthetic-vestibular cues for orientation coupled with a previously acquired mental map' (p. 667).

The fact that accurate burrowing could be accomplished without visual cues indicates that localization 'in the map' can be achieved by other means, but these remain unspecified and are clearly less accurate than is vision.

Peters (1973) has described hunting behaviour in wolf-packs which, he feels, necessitates the use of the cognitive mapping concept. He cites three pieces of evidence: (1) wolves can take intentional short cuts, or detours; (2) packs can split up and re-group at some distant point, beyond the effective range of howling, such that some idea of distance and direction is required; (3) wolves can return to a rendezvous point where pups have been left *from any direction*. All this strongly implies a map-like organization of their psychological space. Peters stresses that these maps are likely to be heavily dependent upon smells, an important point as it extends the notion of mapping to other modalities. We assume, in fact, that all cognitive maps are at least potentially multi-modal.*

* Peters also discusses why maps would provide a firmer basis for behaviour than routes. We shall be discussing this in the next section.

Menzel (1973) has described the way in which chimpanzees move about space in similar terms. A young chimp was carried (in a cage) around a field and allowed to see an experimenter hide a piece of fruit in 18 designated locations about the field. The chimps could do nothing but watch. After all the food was hidden the chimp was returned to the start and, some minutes later, set free. Five control chimps who had not been able to observe the placements of the food were also set free at the same time. The results were clear cut; the chimp who had observed the food being hidden got virtually all of it, and the others almost nothing. The detailed behaviour of these animals was noteworthy; the successful observer chimp typically ran directly to the food, ate it, then ran directly to another food site, and so on. Menzel provided routes of the animals' performances which indicate that they were using something like a least distance principle; they never behaved as though engaged in a general search strategy. Further, they rarely returned to a place from which the food had already been obtained.

In a further set of tests Menzel showed (1) that the chimps were not simply retracing routes taken while the food was being hidden, (2) that the task could be solved even when the chimp was not carried along, but instead could observe where the experimenter placed the food (it was not hidden in this study, merely placed on the grass), and (3) that the choice of where to go first was dependent upon the overall clustering of food in a given area. Note that the information used by the chimp did not depend on their own movements.

In an important set of experiments Olton and his collaborators have studied the ability of rats to collect food efficiently from several locations (Olton and Samuelson 1976, Olton 1977, Olton, Collison, and Werz 1977). They used a more formal testing situation than Menzel, a maze with eight or seventeen arms radiating from a central platform. Each arm was baited with food once at the beginning of a trial and the problem for the rat was to visit all of the baited arms without returning to a previously visited (and therefore empty) arm. Rats quickly learned to visit seven or eight arms before making a 'mistake' in the eight-arm maze and fourteen or more arms in the seventeen-arm maze. They did not use obvious strategies such as entering the arm next to the one from which they had just emerged, nor did they avoid the smells or other proximal properties of the arms they had previously entered. They appeared to be visiting spatial locations as defined by extra-maze cues. In other experiments it was shown that the memory for locations visited was not a short-lasting one since confining rats to the centre platform for several minutes after the third choice or increasing the overall time to make all choices had no effect on accuracy.

Experiments such as those of Menzel and Olton suggest that animals have a memory system for spatial locations and what occupies them, and

that this memory has a high information capacity, can be permanently modified by a single experience, and can be used in a flexible and efficient manner so that, for example, the order in which information is retrieved from the system is not necessarily the order in which it was stored. In reference to the various facts about place learning which his experiments on chimpanzees had shown, Menzel concluded that

'Mentalistic terms such as "cognitive mapping" do not necessarily explain the above facts, but they predict them accurately and describe them successfully' (p. 945).

It is in the hope of providing a neural explanation for such facts that the present theory has been constructed.

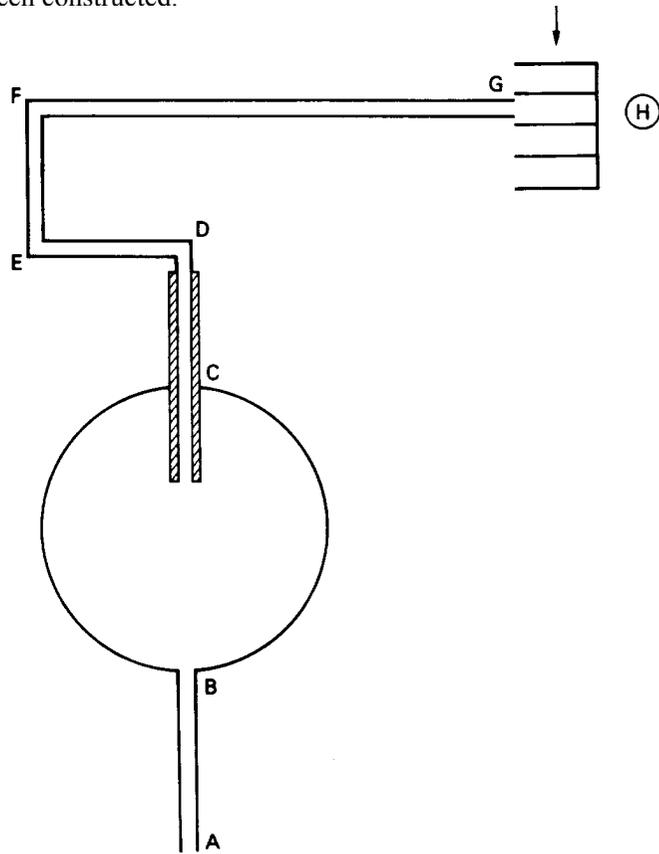


FIG. 1(a). Apparatus used in the preliminary training in the Tolman *et al.* (1946) study. A-B and D-G were elevated pathways while C had 18-in. high walls which obstructed the rat's vision. H was a 5-W lamp oriented to project along the alley F-G. The goal at G consisted of a series of enclosed feeding stalls so that a new rat could be tested the minute the previous rat entered the goal.

2.1.2. PLACE LEARNING

In his paper *Cognitive maps in rats and men* Tolman (1948) outlined the evidence upon which he based his theory that rats use field maps of their environment in getting from one place to another. It is worth describing one of the most well known of these findings, as we shall have cause to refer to the task again. The relevant study (Tolman, Ritchie, and Kalish 1946) used the so-called sun-burst maze (see Fig. 1(a)). Rats were trained to run from A along the path BCDEF to the goal G.* Following training, the sunburst (Fig. 1(b)) was introduced and the rats allowed to choose. The greatest number chose the arm pointing directly towards the goal; this is classic detour behaviour, the animal going to a place rather than making a particular response.

Hebb (1949) has described similar place-learning tendencies. For instance

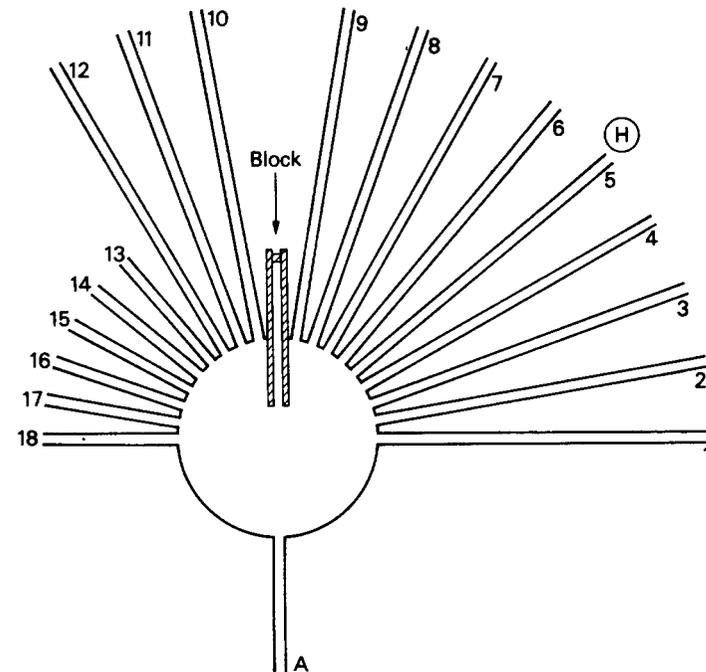


FIG. 1(b) Apparatus used to test the directional sense of the rats after the preliminary training was completed. The exit from the walled alley C was blocked and pathway D-G removed. Radial arms gave the animal a choice of direction over the full 180° including one (6) which pointed directly to the mouth of the goal box. In the Tolman *et al.* study 36 per cent of the rats chose this arm, while 17 per cent chose arm (c) which pointed in the correct direction. (Copyright 1948 by the American Psychological Association. Reprinted by permission.)

*Unfortunately, a light H was located at the goal, making a strong place-learning interpretation of these data impossible.

rats were taught to run to a food dish located at the edge of an open table. Following this the table (and dish) were rotated 90°. The rats ran at least once to where the dish was previously located relative to the room. Similarly, rats will choose to approach goals which are located in the correct place, but contain the wrong cues, rather than the reverse (Hebb 1938a,b). Hebb also quotes an observation of Lashley's where rats literally jumped off into space towards the place they had previously jumped after the platform that had been there was moved.

We have recently observed the same phenomenon in an avoidance situation (Nadel, O'Keefe, and Somerville, unpublished observations, Black, Nadel, and O'Keefe 1976). Rats were trained to avoid shock in a 5 x 5 ft gridded, topless box (the walls were 4 ft high) by climbing onto a platform (8 in. square, 3 in. high) located near one corner of the box. After the rats learned to avoid, the entire apparatus was rotated 180° relative to the room and the rats placed in a corner midway between the old and new positions of the platform. Most (11 / 12) of the rats went to the *place* where the platform had been, rather than where it currently was.

All of these results attest to the importance of what is usually called place learning. This conclusion had already been reached by Woodworth (1938) in his review article, though an explanation for it was lacking. Tryon (1939) described the ability involved in terms strikingly similar to those employed in our discussion of navigation, suggesting it incorporated

'the *native* capacity of the animal to evolve directional abstractions regarding the plan of the maze. These abstractions are developed out of sensations *derived from stimuli received from the maze during learning* . . . when a rat has developed these directional sets, they guide his movements in the maze, even in the presence of radical stimulus changes—he becomes free of the specific stimulus features of the maze' (p. 414).

While most authors agreed with Tryon as to the nature of the behaviour shown, most disagreed as to the source of the information providing orientations. Hebb (1938a), for instance, felt that information from the distal environment, rather than the test apparatus itself, was crucially important in defining places and allowing for general orientation.*

This emphasis upon the information provided by the remote environment eventually led to a 'resolution' of the extensive battle between the proponents of cognitive map theory and S-R learning theory concerning the validity of place- and response-learning explanations of maze behaviour. This issue was fought out primarily on the miniature battlefield of the T-maze and involved dozens of studies in the late 1940s and early 1950s. Hull's supporters attempted to show that animals always make turns, while Tolman's supporters attempted to define conditions under

* He concluded that 'lower mammals may have a type of visual organization . . . dominated by a perception of spatial relations between objects rather than of their intrinsic properties' (p. 350).

which animals went to a place, regardless of the response involved.* Munn (1950) summarized much of this work by noting that

'experiments on place-*versus*-response learning have, in general confirmed Tolman's prediction that *in a heterogeneous environment* . . . rats will learn to run to one place from two different directions more readily than they will learn to make the same turn (right or left) to different places' (p. 413).

In such a situation the place-learning group reaches criterion faster than the response-learning group if a relatively constant heterogeneous environment is available. When a homogeneous environment is used (e.g. Blodgett and McCutchan 1947) this superiority disappears.

In his paper *A resolution of the place-vs-response question* Restle (1957) concluded that

'there is nothing in the nature of a rat which makes it a "place" learner or a "response" learner. A rat in a maze will use all relevant cues, and the importance of any class of cues depends on the amount of relevant stimulation provided as well as the sensory capacities of the animal. In place-response experiments, the importance of place cues depends on the amount of differential extra-maze stimulation' (p. 226).

Thus, according to Restle place learning was no different than response learning; it merely utilized a different class of cues. This, of course, left unresolved the issue of why place learning seemed to have different properties than response learning, e.g. flexibility.

It was still necessary to explain why, within this view, distal cues should be so effective in specifying places. Hebb (1949) suggested that it had something to do with the fact that distant objects remain more constant (in perception) as animals moved compared with nearby objects. Though Hebb mentioned the *order* between stimuli he did not stress this point, rather he stressed the single object. By so doing, he missed not only the theory of invariance later proposed by Gibson (1950) but also the central point of the role of distant objects. In our view distal cues are important in specifying *directions*, since they do not change relative positions as the organism moves in its local environment; on the other hand, this very property means that distal cues, by themselves, cannot distinguish amongst *places* in that environment. Places would seem to be defined by extra-maze cues which are close enough to the animal for its movement to change the angles between them but not so close that movement causes changes in their spatial ordering. There is another reason for assuming that the distal cue hypothesis of place learning cannot be correct. It is well known that when a cue is spatially distant from the site of the response to be made to it,

* Tulving and Madigan (1970) summarized this particularly lively period in rat psychology as follows: 'place-learning organisms, guided by cognitive maps in their head, successfully negotiated obstacle courses to food at Berkeley, while their response-learning counterparts, propelled by habits and drives, performed similar feats at Yale' (p. 440).

organisms have great difficulty in learning (cf. Cowey 1968). If place learning involved nothing more than the use of a distal cue it should fall prey to this difficulty; on the contrary, place learning often occurs much more rapidly than does cue learning, as the Menzel (1973) and other studies show.

In summary, Restle denied that there is anything distinctive about the way in which places are defined. By so doing, place learning could be incorporated within the broad S-R framework, and there was no need to talk about cognitive maps or qualitatively different forms of learning. In contrast, Tolman and his colleagues saw place learning as quite a different kind of learning. Within a cognitive map the *relations* between objects were crucial, not the relations between specific objects and the organism. The overall conclusion from the early work with animals, then, was that something like place learning existed, but that it was not anything unique. The concept of cognitive mapping as an explanation for place learning lost favour. We have just discussed several areas of research indicating that Tolman was probably on the right track. The continuation of the story about cognitive mapping requires that we turn to the burgeoning field of environmental perception, where geographers, architects, and psychologists join hands (reluctantly) to explore ways of conceptualizing spaces too vast to be experienced in a single take.

2.1.3. COGNITIVE MAPPING IN HUMANS

Environmental psychology, or behavioural geography, grew out of the need to explain man's perception of large-scale environments, those which extended beyond the range of immediate perception. In other words, it is directly concerned with what we have been calling unitary space. For most of the 20th century this problem was either ignored or treated as a mere extension of other perceptual problems. The failure of this approach to account for environment perception, which we have documented, has led to a radically different approach within which the notion of cognitive mapping is central. In a recent article Ittelson (1973) both summarizes the failure of the old methods and the reasons why environments must be considered in themselves:

'in the history of experimental psychology the overwhelming bulk of perception research has been carried out in the context of object perception, rather than environment perception, with the findings of the former providing the basis for understanding the latter. Virtually every major school of psychology in the past 100 years has investigated its perception problems in the context of object perception; has developed its theory of perception from the results of these studies; and has then transferred the explanatory system thus derived into the context of environmental perception. As a result, the investigation of perception has lost the essential esthetic unity without which any pursuit leads to chaos, rather than resolution' (p. 3).

and

'the distinction between object and environment is crucial. Objects require subjects—a truism whether one is concerned with the philosophical unity of the subject-object duo, or is thinking more naively of the object as a 'thing' which becomes a matter for psychological study only when observed by a subject. In contrast, one cannot be a subject of an environment, one can only be a participant. The very distinction between self and nonself breaks down: the environment surrounds, enfolds, engulfs, and no thing and no one can be isolated and identified as standing outside of, and apart from, it' (p. 12-13).

Ittelson goes on to describe those features of environments which demand that they be treated separately in theories of perception. The fact that they surround means that one cannot observe an environment; rather, the organism *explores* it. Ittelson states that 'the problem of exploratory behavior . . . becomes central to the study of environment perception' (p. 13). Further, he stresses the fact that environments are multi-modal and unitary. Added to these characteristics which separate environments from objects, and with which we would agree, Ittelson discusses features of environments which must be included in any assessment of perception. Thus, environments involve actions which are purposeful because they possess meaning and ambience. This emphasis upon action relative to a meaningful environment has been incorporated within most work in this area, and it has led to the assumption that cognitive maps must code both meaning and response. We shall argue, on the contrary, that such information, though certainly applied to environments as well as to objects, does not necessarily form part of what is encoded within cognitive maps.

2.1.3(a). Evidence for mapping. Three papers at the start of this century introduced the concept of 'mental maps' to the geographical and psychological literature. Gulliver's (1908) brief note mentioned such maps in the context of teaching children orientation. A much more interesting paper was published by Hutorowicz (1911), comprising an abridged translation of a monograph written by B. F. Adler on the *Maps of primitive peoples*. In this survey of the folklore of map making Adler collected maps and anecdotes concerned with the various forms of geographical representations used by different cultures. He commented on the island navigators and their use of navigation by the stars, and also noted that nomadic tribes in Siberia, as well as Eskimos, had devised a similar form of navigation using the North star. Adler quoted a number of interesting examples of the way in which so-called primitive people prefer to draw a map when asked for directions, and comments that

'they seem to think that this graphic delineation will be more helpful than mere verbal guidance' (p. 670).

This description of the widespread existence of maps was followed shortly after by Trowbridge's (1913) article on 'imaginary maps', which provided the first clues to the structure of cognitive maps. Trowbridge distinguished

between two sorts of maps, varying in the focus of orientation: *egocentric maps* use the four points of the compass and are found in 'civilized' man; *domicentric maps* orient one according to some fixed reference point, usually the home, and are found in birds, beasts, young children, and 'primitive' man.

Trowbridge noted, but did not comment upon, the fact that the 'advanced' egocentric maps could not direct an organism accurately unless 'the path which he passed over is known' (p. 889), while the 'less-advanced' domicentric maps could provide accurate localization. The latter are more likely to keep one oriented, while the former can cause confusion and the loss of bearings. Much of this seminal article is concerned with the kinds of systematic errors introduced by the use of egocentric maps, including the way in which reliance upon compass bearings can induce massive errors in distance judgments. All of these distortions could be described as subjective rotations of egocentric space within the arbitrary reference framework of the compass. Such things as rivers and city-street orientations were often responsible for the distortions. At the same time, Trowbridge indicated that the people with these distorted imaginary maps *were* aware of proper directions, but that these were somehow overridden by the egocentric maps.

Given that the use of these imaginary maps often led to disorientation, it is surprising that Trowbridge did not comment further on the superiority of the domicentric maps. None the less, it seems clear from his report that an abstract orientation system, capable of introducing vast distortions in environment perception, is often superimposed upon a more primitive system capable of roughly veridical representation. These data suggest that the insistence upon subjective loadings of map information might refer primarily to imaginary maps, and not necessarily to the primitive maps that seem to provide an objective view of the environment and its dimensions.*

For some 40 years, excluding studies on the orientation of the blind,** the concept of mental mapping virtually disappeared from the literature,***

* In a recent book on *Mental maps*, Gould and White (1974) seem to have misunderstood the point of Trowbridge's work.

** A monograph on this topic was published by Worchel (1951). He described the use of a test of triangulation; subjects were walked two legs of a triangle and required to return to the start. Blind subjects were worse than sighted subjects, but their performance was reasonably good none the less. More important, age of blinding, as well as chronological age, did not correlate with performance. Considerable other work on spatial orientation in the blind has appeared (cf. Jones 1975 for a review). As this work is primarily concerned with the primacy of vision, or touch, in spatial knowledge, we shall not treat it here.

*** A few papers did appear (e.g. Ryan and Ryan 1940, Lord 1941, Gregg 1939). Of course, we are omitting mention of Tolman and Lewin in this context, though they certainly carried forth the tradition of environmental perception during this time. One last pioneer in the wilderness worth noting was Bartlett (1932). His notions of mental schemas were close to the idea of mental mapping, though his interests were more related to the cognitive aspect of these representations than to any spatial component they might have. His work clearly prefigured the current popularity of research on imagery, about which we will have more to say later (pp. 389-91).

to reappear only in the past decade. These recent studies (cf. Downs and Stea (1973) for a sample of recent work and references to most of what is available in this field) basically confirm the picture presented by Trowbridge, though few of them are directed towards an understanding of the primitive, but more accurate, maps. The reasons for this can be seen in the basic definitions given to mental maps by most authors, which follow Ittelson's ideas. Kaplan (1973) defined cognitive maps in a representative way:

'The cognitive map is a construct that has been proposed to explain how individuals know their environment. It assumes that people store information about their environment in a simplified form and in relation to other information they already have. It further assumes that this information is coded in a structure which people carry around in their heads, and that this structure corresponds, at least to a reasonable degree, to the environment it represents. It is as if an individual carried a map or model of the environment in his head' (pp. 275-6).

Kaplan assumed that there were four types of information that would *necessarily* be contained in a cognitive map, pertaining to four psychological processes: (1) recognition of location and objects; (2) prediction of what leads to what; (3) evaluation of what is good or bad; (4) action relative to the environment. This set of assumptions parallels those of Ittelson and has formed the basis for research in this area. It has proven much easier to study motivation and action than localization and prediction, for the former often distort the latter. Many studies have shown that the value one attaches to a place affects one's perceptions of its distance from other places (e.g. Briggs 1973).

There are various ways in which these data stressing the distortions and non-objectivity of cognitive maps can be interpreted. First, one could assume that cognitive maps must be value oriented. Lewin's field theory then becomes the progenitor of present-day research, and the notion of objective spatial mapping is discarded; this approach has dominated environmental psychology to date. On the other hand, one could assume that information pertaining to values is not part of the map itself, but rather is attached to an output from a veridical map. We feel this latter approach is the better one.

Trowbridge's data favour our view. The distortions seen in his egocentric imaginary maps were imposed by various environmental features and the cardinal system of orientation *upon a more primitive veridical map*. Assuming the subjectivity of the cognitive map raises logical difficulties, it is hard to imagine how the non-commutativity of distances (e.g. Lee 1970) could be encoded in the same structure which provides for the easy use of alternative paths to the same goal and for the rapid reversal of paths. Non-commutativity almost demands that the map represent paths in terms of the individual responses, or landmarks, involved in traversing them, and this might be why Kaplan and others insist that action patterns

are also encoded in the map. We feel that this seriously overloads the system, as well as raising considerable difficulties in converting the concept to some neural reality. Some recent research supports our approach; Moore (1973) has shown that reversibility of spatial operations (going from A to B and B to A) correlates with the presence of map-like representations, particularly in basically unfamiliar areas. In the absence of such representations reversibility seems to involve the learning of two separate routes.* Similarly, the logic of how cognitive maps are built up through action, and the ability they impart to get from any place to any other place, argue against the assumption that actual behaviours are coded into the map. This would greatly limit the flexibility associated with behaviours based on cognitive maps.

Thus, there seems little doubt that map-like representations of the environment are constructed by humans, as well as by other species, but there remains some doubt as to the nature of the information included in these maps. It must be stressed that cognitive maps are *not* models, in the organism's head, of the environment. Kaplan (1973) seems to imply this, as the quote above indicates, while others argue against this view. Thus, Blaut, McCleary, and Blaut (1970) note that the cognitive structure 'has the functions of a map but not necessarily the properties of a pictorial mental image' (p. 337). This distinction is important, both in considering mental maps in particular and any form of abstract imagery in general, as we shall see later (pp. 389-91). The cognitive map is *not* a picture or image which 'looks like' what it represents; rather, it is an information structure from which map-like images can be reconstructed and from which behaviour dependent upon place information can be generated. While we shall argue that this information base pertains solely to processes of recognition and prediction, in Kaplan's terms, we are aware that other forms of information might be included as well.

2.1.3(b). Ontogeny of cognitive mapping in humans. It is obviously of great interest to ask when these cognitive maps first appear in children. The study of the ontogeny of mapping, however, is hindered by the difficulty in getting relevant data from infants; it is virtually impossible to get an answer to the question of whether or not the mapping system is innate. However, it remains possible to assess Piaget's model in this light, for he postulates that the ability to generate representations of the environment involving unitary space becomes available only after extensive learning, certainly not before 10-12 years. Studies such as those by Olson and Baker (1969) and Shantz and Watson (1971) suggest that complex spatial abilities

* Stea (1969) has provided some data on the relationship between familiarity, subjectivity, and non-commutativity, which suggest that 'the more familiar a subject is with a given trip, the more accurate is his estimate (of distance), but the more discrepant are his estimates in the two directions of travel' (p. 240). He assumes this discrepancy arises as a function of the diverging attractiveness of the two end points with increasing familiarity.

arise much sooner than Piaget would predict, but they do not directly test mapping.

More recently, Blaut and his co-workers (Blaut *et al.* 1970, Muir and Blaut 1969-70) have tested young children from various cultures on map reading. They found that this ability exists prior to training in children as young as four years old. They state that their evidence

'seems to require a developmental model of environmental behavior in which the early emergence of mapping behavior is explicitly predicted' (Blaut *et al.* 1970, p. 347).

Kosslyn, Pick, and Fariello (1974) have shown that while adults are better at estimating veridical distances, children (4-11 years) are none the less remarkably good at it. Further, the data provided by their subjects were scaled to determine whether they were best represented as using a Euclidean metric or a city-block reference frame. The data suggest that

'the Euclidean solutions more effectively capture the *S*'s spatial representations' (p. 713).

In fact, the city-block method provided a poor fit to the data.* This is reminiscent of Trowbridge's work. All these data, then, indicate that young children can use a mapping system and that it seems to work according to Euclidean principles. Taken in conjunction with the data reviewed earlier, it would seem as though Piaget's assumptions about the ages at which various concepts of space arise are incorrect. We cannot say, for humans, whether or not mapping is available at birth, though the perceptual capacities for it seem present shortly thereafter. As we have seen, the data from infra-humans point in the same direction.

2.1.3(c). Conclusions. The fact that most investigators have stressed the subjective aspect of mental maps means that the models derived from their studies are not really suitable for our purposes. These studies support the notion that such maps exist in adults and young children equally, but they do not tell us much about how these maps function. Before we can translate these ideas into a neural theory we must formalize them. The best way to do this is to go back to the beginning and look directly at the properties of maps and the major alternative means of representation, routes. This connection between mapping, the concern of the geographer, and cognition, the concern of the psychologist, has been central to the efforts of both environmental psychology and behavioural geography. The circle leading from Kant to cognitive maps comes full turn, as epitomized in a recent paper by Richards (1974), *Kant's geography and mental maps*:

* The authors concluded that this 'mapping' did not include information about the movements involved in going from location to location.

'How then- if at all- do we manage to pass beyond the field of our immediate sensations and connect up the diverse experiences which we have of our environment? . . . The answer proposed by the contemporary behavioural geographer is that we impose a synthetic unity on the manifold of our spatial perceptions (to borrow Kantian terminology) through the construction of mental maps' (p. 10).

2.2. Maps and routes

One of the deficiencies in Tolman's notion of a cognitive map is that neither he nor any of his students tried to specify in detail the properties of maps and to contrast these with other potential means for getting around in the world. We hope to remedy this situation here by giving a detailed account of the properties of maps and routes. We hope the reader will bear with us here in what may appear at first glance an unnecessary digression into theoretical geography. We shall draw heavily on the properties of maps in subsequent chapters in our attempt to spell out the workings of a neural cognitive map.

2.2.1. TO GET SOMEWHERE

'How do I get to Upshire?' enquires the lost rambler.* Several different answers are possible. In the relatively rare case in which Upshire is visible from the start it can be pointed out, or its direction indicated. Usually this is not possible, and it is necessary either to provide the rambler with a more elaborate set of instructions as a *route* or to locate the rambler and destination on an Ordnance Survey map, leaving the choice of a path to the walker. Such routes and maps have quite a different form, though they can serve the same purpose at times. In the discussion which follows we shall set out the properties of routes and their components, *guides*, and *orientations*, on the one hand, and maps on the other. Then we shall compare and contrast them, pointing out the advantages and disadvantages of each. Some of our ideas on this subject owe their origin to the philosopher Toulmin (1953) and the geographer Board (1967). As illustrations we have chosen part of a route from a popular book on country walks in and around London (*Country Walks* 1971). A map of the area through which the route goes is shown as Fig. 2. The excerpt from the route, which starts at High Beach, is as follows:

'Keep forward for 500 yards beyond the little tea hut to a point where the road divides after bearing leftwards. Go along the right fork for 30 yards, then strike obliquely left into the forest, passing between two massive beeches. The old track, the Verderer's Ride, is now elusive, but there is no need to fear going too far astray. If you continue ahead, leaving the road gradually on the right, you soon find that the ground falls away sharply on the left. Bear slightly right, and pick your own way through the trees; all you have to remember is to keep near the upper slopes of the wood, keeping the lower ground on your left. Keep on for

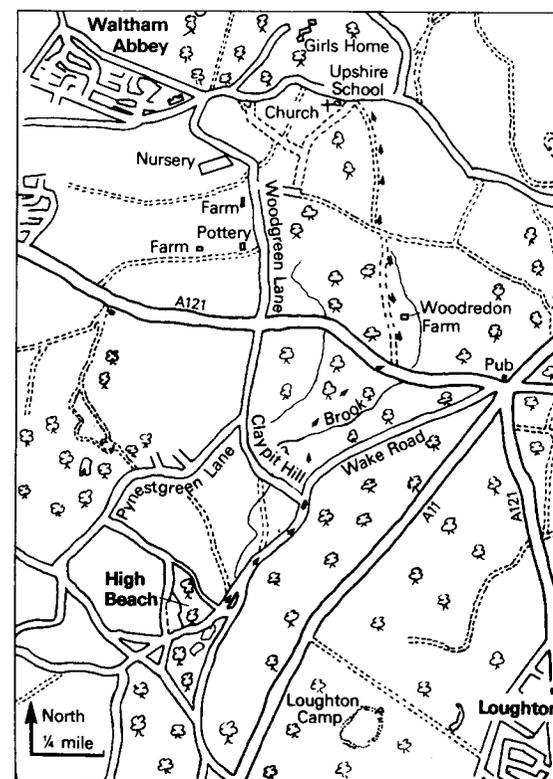


FIG. 2. A map of north-east London showing the area referred to in the *London Country Walks* (1971) route. (Based on the Ordnance Survey Map with the sanction of Her Majesty's Stationery Office).

almost ½ mile, when you may hear the sound of main-road traffic ahead. After crossing one or two little forest brooks you will reach the road at the top of a hill, near a bus stop (if you strike the road lower down, simply turn right to the top of the hill). Almost opposite, at the crest of the hill, you will find a metalled drive that leads through the trees to Woodredon Farm. Do not miss the pretty Georgian house on the right as you pass the iron lodge gates (and the notice that keeps the next mile of your walk free from cars and bicycles). After passing the mansion on your left, the drive winds left-wards, then twists right again to emerge, after ½ mile, at Upshire.

Upshire is a wayside settlement near the forest's edge. St. Thomas church was built in 1902 but looks much older. The spire is a useful landmark' (p. 37).

Route instructions, as this example shows, are a list of stimulus-response-stimulus (S-R-S) commands which lead the rambler from one sight to another, from the feel of walking on uneven ground to the sound of distant cars, from babbling brook to bus stop. To get from one landmark to the next he must strike obliquely left, bear slightly right, pass between

* A rambler is a country walker.

beeches, keep forward, cross, continue, go. Careful examination shows that within each S-R-S instruction the emphasis can be on the stimulus or cue component, on the one hand, or on the response requirement on the other. We shall call the former type of instruction a *guidance* and the latter type an *orientation* or *direction*.*

A guidance directs attention to a particular landmark or object and requires that the rambler approach it or maintain a certain egocentric relationship to it, regardless of the behaviour involved. Guides are often localized and stationary. The most obvious guide is the destination itself, but this is often only perceptible just before it is reached. More often a guide is a prominent object or stimulus at the goal or before it: a tall building, mountains, the distant sound of traffic; 'the spire (of St. Thomas church) is a useful landmark'. Guides need not be localized or stationary; they can be extended (in *one* dimension) as are streams and trails, or they can be mobile. The best guide of all is a fellow rambler who knows the way to Upshire.

No specific motor behaviours are selected by guidance instructions. Rather, any behaviour can be used which, in the case of the fixed localized landmark, reduces the distance between it and the rambler or, in the case of mobile or extended guides, maintains their distance within certain narrow limits: thus, 'follow this trail regardless of how it twists and turns', 'keep near the upper slopes of the woods', not too close, not too far. To reach those massive beeches at the beginning of our journey might require either a very shallow left turn or a virtual about-face, depending on where one chose to 'strike . . . into the forest'.

The second type of route instruction, the orientation or direction, focuses on the response requirement to the neglect of the cue aspect. Orientations can be interpreted as sets of instructions for aligning the egocentric body axis relative to some other axis. In the simplest case this involves a rotation relative to the present orientation, i.e. a simple turn and continuation straight on. Our route to Upshire tells us to 'bear slightly right', 'strike obliquely left'. One of the problems with orientations is the difficulties organisms have in going straight solely on the basis of interoceptive and proprioceptive cues. Thus, we find that accompanying an orientation there is often a reference to a landmark and how to use it in order to 'keep straight'. The best such landmark is one which is distant and in a straight line with the starting point and the goal. By heading towards this landmark one can keep on this straight line and eventually intersect with the destination. This directional cue is similar in some respects to a guidance, but there are important differences which will become clear when we discuss the different problems each presents to

* The reader should be warned that we are giving these and similar geographic terms rather restricted definitions and they are not to be understood in the more general senses used in common parlance.

the traveller who gets lost or is faced with an obstacle.

Usually one is not fortunate enough to find a directional cue directly behind the destination; instead, one must make do with one off to the side. This can be used in an approximate fashion: 'keeping the lower ground on your left', 'passing the mansion on your left'. A more sophisticated use of such a landmark to describe a straight line would involve calculations as to how fast the landmark ought to sweep across egocentric space for the speed at which the traveller is moving. Very distant stationary objects need only be kept in the same part of egocentric space. The use of the compass for direction finding is a good example of this strategy. The needle always points to an imaginary distant object which acts as a landmark for the North-South-East-West framework, and any given direction is measured as so many degrees rotation of the body axis relative to this distant framework. Finally, if the distant reference object is not stationary but moves in a predictable fashion, as does the sun for example, internal or external clocks can be used to calculate the relationship between the reference and the external axis. Homing pigeons and migratory birds clearly do this in reference to the sun, as we have seen.

2.2.2. ROUTES

Before turning our attention to maps we can outline some of the positive and negative features of route. One thing is clear: routes *imply goals which imply motivations*. Why do you want to go to Upshire? The second stimulus in each S-R-S link can be looked on as a subgoal in the overall goal directed chain.

Routes direct attention to particular objects or specify turns within egocentric space. They are inflexible, must be used in the correct sequence, and only rarely allow freedom of choice to the traveller. Three circumstances in which some choice exists come to mind: (1) the trivial one in which all possible routes converge on the goal (or subgoal) either because of their shape or the size of the goal; (2) the more common one exemplified in our passage where the goal is an extended guide crossing all possible routes, 'pick your own way through the trees . . . you will reach the road'; finally, (3) alternatives are sometimes provided in case one set of guide instructions proves inapplicable. As we shall see presently it is this general lack of flexibility in the face of an ephemeral environment which is one of the main drawbacks of routes.

The knowledge required to follow a route is usually quite simple. In the case of a guidance one must be able to identify it under its various aspects and tell how its distance is changing, usually by monitoring its size or intensity.* Orientations are equally simple, involving rotations within

* This 'simple' knowledge, of course, is just that specified by Poincare and others as lying at the base of spatial representation. We have already argued that identifying objects requires, at least in developmental stages, a spatial framework similar to a map.

egocentric body space and maintaining stimuli in a particular part of that space. One result of this simplicity is speed. The actual pace of movement does not figure in any of these instructions and is limited only by other considerations such as the endurance of the traveller and the speed at which he can access and process information at the subgoals. During the remainder of the link the traveller is operating on information which is already available.

The major drawback of routes, their inflexibility, leads to another vulnerability. Consider the following ways in which one can get lost. The route instruction can be physically or mentally degraded (smudged word, forgotten orientation), landmarks or other guides may be destroyed or changed (snow, fallen trees), the translation of the instruction into behaviour may go awry (an elm is mistaken for a beech), a momentary lapse of attention leads to a subgoal being missed. It will be instructive to consider the strategies available when one loses the way or is forced to detour while following a route, because it is here that the differences between routes and maps are most clearly revealed. Getting lost is such a problem that routes often attempt to foresee possible lapses of attention or deviations and provide appropriate cautions, 'the old track ... is now elusive', or corrections, 'if you strike the lower road, simply turn right'.

Deviations from the intended route while following a guide can only be corrected by random wandering until the guide is located again. In the case of a prominent fixed guide this is often successful; extended guides such as trails or streams, on the other hand, will only be found if the appropriate direction of search is used or if a sophisticated strategy such as moving in ever-widening circles is adopted. Finally, it is almost impossible to find a lost moving guide without the most sophisticated communication strategies. Note that in all cases it is important to find not just any mountain or any stream, but to find the same mountain or stream. This brings up the problem of re-identification again, as discussed before. An additional problem with an extended guide is once having located it to follow it in the correct direction.

Orientations are even more difficult to re-establish once they have been lost. It is not enough merely to re-adopt the original orientation, since this was only appropriate along the original axis. Once off that axis an entirely new orientation is required. Thus, orientations are only useful when both the position of the traveller (the body axis) and some external axis are specified; they are purely egocentric tools. If one is forced off one's route by an obstacle, rather sophisticated geometric calculations would be required to regain the original orientation and axis. Landmarks are also useless since, again, they mark the orientation only in conjunction with the original axis. The farther away the landmark, the more the goal will be missed. One of the major problems with an orientation is simply knowing whether one is lost or not. Many readers will have had the experience of

driving several miles along a road looking for a turn-off indicated by the route instruction with a mounting feeling of panic that it had been missed. Here, some indication of distance, no matter how crude, is useful.

Finally, there is the question of reversibility of operation. Given a map or route, one might ask if it can be used as easily in the reverse direction from goal to start. We have already seen the importance of this property of reversibility in discussing Poincare and Piaget, both of whom consider reversible displacement groups to lie at the root of spatial concepts. As we shall see, maps are unambiguously reversible, since they provide a means of getting from any place to any other place. For routes the answer is more complex and requires closer analysis. Let us start at the end of our route instruction, at Upshire, and see if we can transform it to take us towards High Beach. Such a reversed set of instructions might read as follows:

'Upshire is a wayside settlement near the forest's edge. St. Thomas church was built in 1902 but looks much older. The spire is a useful landmark. From Upshire, a metalled drive goes for 1/2 mile, first twisting left, then winding right-wards before passing a mansion on your right. Pass the iron lodge gates of Woodredon Farm (and the notice that has kept the last mile of your walk free from cars and bicycles); do not miss the pretty Georgian house on the left. The drive leads through the trees away from the Farm to the crest of a hill opposite a bus stop (on a road)'.

We can examine this reversed route and see how it was done and how useful it would be. It is immediately clear that extended guides such as the metalled drive remain useful, while distant landmarks such as the church spire are of little value. Walking away from such landmarks is hardly the reverse of walking towards them from a particular starting point.* Even with the extended guides there may be some trouble finding them. It is easy to find a large area such as Upshire when entering it from any one of many metalled drives; however, it would be quite difficult to find the correct metalled drive leading away from Upshire without additional information. In order to use orientations in the reverse direction it was necessary to make certain substitutions: left for right, retreat from for approach towards. In general these substitutions are successful and provide the primary basis for the reversibility of route statements. In our later discussion of language (cf. pp. 391-410) we shall compare this limited reversibility of routes with the syntactic transformations rules of Chomsky and others for transforming the surface structure of sentences (as in active to passive modes). Routes, then, are rapid and easy to use, but because of their inflexibility very vulnerable and easily rendered inoperative by changes in the route statement or the environment. Under certain

* We have already seen, in our discussion of the South Sea island navigators, that two landmarks aligned in a certain way can give a direction which is equally useful both in approach and retreat.

circumstances transformation rules can be applied to them which allow them to be used in the opposite direction.

2.2.3. MAPS

In marked contrast to these properties of routes are those associated with maps. As with our discussion of routes it will be helpful to have in front of us a particular map to illustrate the discussion. We have chosen the map which corresponds to the previously used route instruction to facilitate comparison (see Fig. 2).

The simplest definition of a map is that it is the representation (usually two dimensional) of a part of space. The constituents of space are places, and thus an alternative definition of a map is the representation of a set of connected places which are systematically related to each other by a group of spatial transformation rules. The notions of place and space are logical and conceptual primitives which cannot be reduced to, or defined in terms of, other entities. Specifically, places and space are not, in our view, defined in terms of objects or the relations between objects. The absolute space defined by Kant exists in the absence of objects. It is sometimes convenient to locate a place by reference to the object occupying it, 'she was standing over there where the desk is now', but this is only a convenience. This freedom from reference to any specific object or set of objects is one of the most important properties of maps and is easily demonstrated by reference to our map. Consider two maps of the same terrain (and therefore containing the same places) which could be derived from this map. In the first, only man-made artifacts such as roads and houses would be represented; in the second, only natural objects such as trees, hills, and lakes would appear.

There are two broad classes of maps, *topographic* and *thematic*. Topographic maps are used for finding one's way around a part of the world and will be of primary interest to us here. In the topographic map the entities which are located in space are symbols for objects. The system for placing items on this type of map usually tries to preserve the Euclidean relationship between angles and dimensions, although there may be some compression in one dimension and small objects such as roads are often made disproportionately large so that they may be seen easily. The thematic map is a specialist map used to display or emphasize particular selected features or concepts such as the distribution of rainfall or the percentage crop yield over an area:

'Thematic maps represent not only facts, but ideas, hypotheses, and the results of analysis and synthesis' (Miller and Voskuil 1964, cited by Board 1967, p. 713).

Only rarely is the thematic map used to guide the traveller from place to place, and there can be a relaxation of the spatial transformation rules to suit the particular purpose of the cartographer. For example, some thematic maps represent the

relative concentration of some feature by the area given to it, such that there is no relationship between space on the map and space in the real world.

Reading maps is a more complicated affair than following route instructions. Let us assume one is at High Beach and wants to get to Upshire. First, it is necessary to locate one's place and one's orientation on the map. This can be done by identifying several surrounding landmarks which can be seen (or heard) from one's position, and looking for these on the map (or vice versa). Two such objects and their spatial relationship will place the observer on the map. Here we have a complicated process in which the objects and their relationships in egocentric space are translated into three objects in unitary, or absolute, space. Alternatively, one need only identify one object together with a direction. Usually this latter can be obtained from a compass reading or from the location of a distant object such as the North star. In this process of locating a place on the map there is a considerable amount of surmise and conjecture. 'If that is Loughton in the distance, then there ought to be a church in this direction, but since there isn't then that can't be Loughton, but there is a church in this other direction, so that built-up area must be Waltham Abbey'. Additional predictions of objects to be seen from that position can be made, and the position further verified. When one's place on the map has been ascertained, along with the relative orientation of the map to the terrain, the next step involves locating one's destination on the map and calculating its direction from the starting point. Thus, Upshire lies almost directly to the north of High Beach. Now, one has the choice of many different routes which can be derived from the map, all of which converge on Upshire. Some are more direct than others, some go through wooded areas, others along country lanes, some are beautiful, others mundane, all end in Upshire.

The first striking feature of a map is its flexibility. Whereas a route specifies a starting point, a goal, and a particular direction of movement from the former to the latter, a map specifies none of these, either in its construction or its usage. It can be used with equal facility to get from any particular place to any other. Additional flexibility derives from the freedom from specific objects and behaviours. If one path is blocked another can be easily found and followed. If a storm destroys a prominent landmark, an alternative is readily available. As we have noted, unless these calamities are foreseen and alternatives specifically included in the route statement, they usually destroy the usefulness of the entire route.

This flexibility means that any given map can be used for a variety of goals and purposes. The map itself may have been designed with a purpose, as we have seen with thematic maps, but the heavy rainfall in London is no more the focus of a weather map than is the light rainfall in Birmingham. Furthermore, even if the map had been designed with a purpose in mind (the cartographer secretly held stocks in a London umbrella firm),

it could be used for an entirely different purpose (the Royal Society of English Rainmakers cancels its annual convention in Birmingham). More often,

'the natural development of the map is the desire which necessity, or curiosity, imposes on mankind to explore the earth's surface, and to move from one part of that surface to another—working from the known to the unknown—on the path of experience and enquiry' (Fordham 1921, p. 1).

Another feature of maps is their high information content, which is equivalent to all of the possible routes between the places depicted on it. Consider, in addition, the way information is stored in a map. Each new item which is located on a map is automatically related to every other place and item already on the map. A change in a feature of the landscape occasions only a single alteration in a map, yet it changes every route statement in which that feature occurs. It has been estimated that the amount of information contained in a medium-sized map of the United States of America is 100-200 million bits (Roberts 1962).

A further, related, feature of maps is their high safety factor and their great resistance to degradation, both of which are achieved without any marked redundancy of information. The high information content of a map enables the traveller to constantly monitor his position by checking predictions from the map about the location of objects. Furthermore, a map can suffer a considerable loss of information, either through changes in objects in the environment or through deletion of information from the map, before it becomes useless. Thus, the problems of getting lost or being forced to take a detour, which presented such formidable challenges to the traveller relying on route instructions, are not significant for the map reader.

The disadvantages in using a map are associated with the necessity of using special codes for constructing them by placing items in specific locations, on the one hand, and reading routes off it on the other. The large number of routes from any place to another can also serve as a disadvantage. The decision as to which route to use, coupled with the time needed to employ the coding system, greatly increases the time required to read a map in comparison to that needed to follow a route. Yet another disadvantage of a map is that the information contained in it cannot be as exact as that contained in a route. As we have seen, there is inevitably some distortion in a map. Route statements, on the other hand, can be made as detailed as possible. If a flexible, yet detailed, system for finding places was desired, one could not do better than to use a map to decide which route to take to get there and then to have a series of route statements to give the final details required.

Before turning to an examination of how neural cognitive maps might work, it would be useful to summarize the differing properties of routes and maps. This summary is given as Table 1, and the information in this

table will serve as the basis for translating the geographic concept of a map into a potentially useful psychological tool.

TABLE 1

Properties of routes and maps

| | Route | Map |
|---------------------|--|--|
| Motivation | The final stimulus is the goal; the route is built with this in mind | No object or place on the map is a goal; the map is usually built out of curiosity |
| Flexibility | Routes are rather rigid; they are rendered useless by any damage, or by the loss of a guidance, or direction | Maps are extremely flexible, and relatively invulnerable to noise and damage |
| Speed | Very fast | Relatively slow |
| Information content | Relatively little; each route contains only a small amount of data | Maps are one of the most efficient information storage devices known, with very large capacity |
| Access | No specialized knowledge is required for access; no coding strategies | Special knowledge of coding strategies required |
| Manipulation | None | Maps can be compared; places on maps can be compared |

2.3. The psychological basis of cognitive maps

In the previous section we discussed two basically different ways of moving from one part of the environment to another involving the use of maps or routes. Maps were viewed as sets of connected places which provided the traveller with a large choice of possible paths between any two points in the environment. Because they do not rely on particular cues or behaviours maps were seen as flexible and relatively resistant to the effects of environmental change. In contrast, routes were best described as lists of guidances and orientations, the guidances acting as landmarks to be approached or followed by any available behaviour and the orientations specifying a particular movement to be made in the presence of a particular cue. Routes, unlike maps, were seen as inflexibly leading from one point to another and easily disrupted by alterations of relevant cues.

In this section we shall translate these theoretically derived notions into psychological mechanisms which could explain the types of spatial behaviour we described at the start of this chapter. The end point of the

chapter will be the assertion that the hippocampus acts as a cognitive mapping system, which we shall call the *locale* system and which generates place hypotheses and exploration. Loss of this system forces an animal to rely on the remaining extra-hippocampal systems. In addition to discussing the properties of the mapping system, therefore, it will also be necessary to sketch in enough of the properties of the route, or *taxon*, systems to enable us to predict the behaviour of animals deprived of the hippocampus. The reader is warned, however, that our main emphasis is on the hippocampal locale system and that our treatment of the taxon systems may suffer from this perspective. For instance, we shall not attempt a detailed differentiation of guides and orientations, though it is likely that important differences exist between the two. Our main emphasis will be on the difference in the way that the locale system and the taxon systems store information. This difference, when combined with some simple assumptions about changes in synapses with use, will enable us to predict differences between the two systems which will be reflected in the place and route hypotheses generated by them and ultimately in the animal's behaviour based on these hypotheses.

Temporal changes after synaptic activation. We will assume that in both locale and taxon systems there are synapses which change with activation. When such a synapse is activated it undergoes both short-term and long-term changes in potency. These changes will differ in different synapses and will depend to some extent on the 'success' of the hypothesis based on the brain areas containing those synapses (see below). A hypothetical set of changes might be as follows: after activation of a synapse, the presynaptic element has a decreased efficacy for some time, perhaps due to transmitter depletion. With time, this decreased efficacy is reversed and the presynaptic element returns to normal potency or even slightly increased potency. In contrast the post-synaptic element is left more excitable after activation. This change also decays with time but may not reach the previous baseline or may even cross it to leave a long-term raised threshold for activation. Depending upon the relative time courses of these two changes, attempts to reactivate the synapse at different times subsequent to activation might find it hyper- or hypo-excitability. Furthermore, different afferents to the same postsynaptic cell might have different access to it. For example, shortly after activation by one pathway the cell might be poorly activated by another input on the same pathway but hyper-responsive to an input on a different pathway. We will discuss the evidence for these sorts of changes in greater detail when we discuss habitation in the taxon system (see pp. 244-7). Our main point here is that hypotheses will differ in the degree to which they show temporal changes in efficacy after activation in so far as they rely on the same synapses each time they are activated. As we shall see, this only applies to *taxon* hypotheses.

Reinforcement. Within our theory, reinforcement acts at two different levels. At the level at which different hypotheses compete for control of the output systems, reinforcement serves to maintain the ascendancy of the currently dominant hypothesis. Non-reinforcement by contrast, results in a tendency to switch away from the dominant hypothesis. At this level, then, reinforcement affects all hypotheses equally. Reinforcement also acts within each hypothesis system, and it is here that its action differs from system to system. Within the locale system, the role of reinforcement appears to be purely informational. Biological rewards are encoded just as any other stimuli would be; they are represented as occupying particular places in specific environments. This representation is encoded during exploration and is unaffected by the motivational state of the organism at that time (latent learning).^{*} If the animal is subsequently motivated, this information can be read off the map and used in the form of a place hypothesis to obtain reward.

Within the taxon system, reinforcements might serve to strengthen the recently active synapses or to counteract the normal reduction in efficacy discussed above.

2.3.1. HYPOTHESIS BEHAVIOUR

In some learning situations the change in an animal's behaviour reflecting learning occurs slowly over trials, while in others there is an abrupt jump in the learning curve from near-chance performance to near-perfect performance. Typical of the former are such things as lever pressing or wheel turning, while the latter is seen in choice situations such as a simple T-maze or Y-maze (cf. Mackintosh 1974, pp. 147-50). Thus, the choice of the correct alley in a T-maze often goes from 50 to 100 per cent abruptly, while lever-pressing rates increase in a smooth, negatively accelerated fashion. It is reasonable to suppose that in the lever-pressing situation the neural changes underlying learning are incremental, while those in the maze are discrete and non-incremental. These discrete processes could involve the switch from one *hypothesis*, or strategy, of behaviour to another. 'Learning' occurs abruptly when the switch is from an incorrect to a correct hypothesis. The early work of Hamilton (1911) and Lashley (1929), and the subsequent, more elaborate, studies of Krechevsky (1932, 1933) clearly demonstrated such hypothesis behaviour. Krechevsky (1932) found, for example, that in a linear maze with four successive choice points a rat might choose to go through the left door at all four points on one trial, through the darkest doors on the next, then alternate right and left doors, and so on. Hypotheses can also be maintained across a number of trials. In a T-maze brightness discrimination most rats will choose either the left or right arm for a number of trials, and only then the darker or brighter

^{*} High levels of motivation will compete with, and curtail, exploration, leading to meagre maps, but will not affect the nature of the information stores in these maps.

arm. Careful testing in this situation shows that some of these 'position hypothesis' choices involve the use of places and others the use of body turns, or orientations. Thus, if one rotates the starting arm 180° one puts into opposition a place and an orientation hypothesis. If the animal returns to the same arm it is using a place hypothesis, because it had to make a different body turn to get there. In addition to simple orientation (body-turn), guidance, and place hypotheses, animals occasionally alternate left and right turns.

In the early, pre-solution stages of learning animals typically switch from one hypothesis to another with regard to its form; that is, they might switch from an orientation to a guidance, rather than to another orientation. Switching within modes, as stressed by Sutherland and Mackintosh (1971), occurs only after considerable learning, typically in reversal situations (see pp. 281-2) where one particular hypothesis has been consistently associated with reward. As we shall see later, this can provoke the so-called 'overlearning reversal effect' in which animals given added training show an increased ability to switch behaviours when the reward contingencies are changed; that is, when reward is switched from black to white in a two-choice brightness discrimination, for example. The fact that this effect is not usually seen in tasks requiring a position hypothesis (either place or orientation) is important, and will be discussed at length later (pp. 281-2).

As Restle (1957) has pointed out, the probability of a particular hypothesis being chosen depends on the lay-out of the experimental situation.* The availability of extra-maze cues, together with a large number of choices, favours the use of place hypotheses; a strong cue biases the animal towards guidance learning, while a paucity of cues coupled with a minimal choice of behaviours favours orientation hypotheses. In an environment which does not provide enough structure to activate strongly any hypothesis (e.g. uniform, closed, multi-choice mazes) all hypotheses will be weak and the animal might choose semi-randomly from trial to trial, approximating the type of behaviour described by Hull (1943). There are many factors which influence the selection of a hypothesis, such as rearing conditions, personality, previous experiences, inter-trial intervals, and so on. Some of these will be discussed at greater length when we describe the properties of the locale and taxon systems in detail below. In general, though, too little is known about the factors controlling selection. To use contemporary terminology, one would like to know the precise conditions under which one hypothesis *overshadows*, or dominates, others; this should prove a fruitful area for research. Though we cannot specify precisely the factors controlling hypothesis selection, there is a lot that can be said about the properties of the different hypotheses.

* We do not accept Restle's suggestion that place learning is equivalent to distal cue learning (see pp. 73-4)

2.3.1(a). PLACE HYPOTHESES

The notion of place. Place hypotheses are based on information contained in the hippocampal cognitive-mapping system. In the next section we shall provide some speculations concerning the anatomical and physiological bases of this system. There, we shall define a place in an environment in terms of the activation of a specific array of hippocampal neurones. Here it will be more useful to speak of a *place representation*; this can be taken as a part of a cognitive map, while conversely a map can be viewed as a set of ordered, connected places. Such a place representation can be activated in either of two ways: (1) externally, by the simultaneous occurrence of two or more sensory inputs with the appropriate spatial co-ordinates in egocentric space; (2) internally, by an input from another place representation coupled with a signal from the motor system concerning the magnitude and orientation of a movement. Let us consider these in turn.

The first mode of activation involves a particular arrangement of external cues. When an animal is in a particular place the cues it perceives will have a unique spatial relationship with one another. This set has two important properties. First, no individual cue is *necessary* to the relationships among the rest of the set; places are *not* specified by complexes of cues in any simple sense. Any cue, or group of cues, can be removed from the total array without preventing the remainder (so long as at least two or three remain) from uniquely specifying, by their relations, a particular place. This property lies at the root of the difference between cue learning and place learning. Second, the spatial relationships among a set of cues remains constant when the animal stays in place but engages in rotational movements. Thus, when an animal sits in a place there is a unique spatial arrangement of the various stimuli available to it, and this arrangement is independent of the animal's specific orientation in that place. If the animal rotates its eyes or head the angular relations between these cues remains invariant. As Eriksson (1974) pointed out, sense data is sufficient to specify the relative spatial arrangements of things in the environment (see p. 48).*

When the animal moves, however, the problem of identifying a place becomes more complex. Here, not only is there subjective movement to be taken into account, but the sensed spatial angles between the objects in the environment change. As we have seen, the input from motor feedback processes enables the organism to map these objects accurately even though their angles are changing. Thus, some interaction between sensory data

* Eriksson also pointed out that in order to obtain information about absolute distances some further information was needed. In the same way, though the relative arrangement of cues remains invariant through rotational movements, the position of the objects in question changes in terms of the egocentric space of the organism. Though the angles are the same, they are falling in a different part of the field. In order to reach out and grab one of these objects after a rotational movement the organism does require input from the systems which locate it in egocentric space.

and movement feedback is required to identify the procession of places as an animal moves through its environment. The vital importance of active exploration in the construction of maps, as we shall see shortly, rests on this observation.

The alternate mode of activating a place representation is an internal one. Here, inputs from other place representations are coupled with those from an internal 'dead-reckoning' system; this latter calculates the expected translation/rotation in space concomitant with a potential movement. During the building of a map motor feedback information is crucial in assigning representations of things to their appropriate 'place' in locale space. When an animal is in a familiar environment the activation of the system, without real movement, will enable the animal to predict what should appear in what place.

The cognitive-mapping system is assumed to contain a map for each environment the organism has experienced. These maps are built up in the following way: The animal brings to a new situation a *tabula rasa* of potential place representations. One of these is chosen to represent a specific location in that environment; this automatically determines the way in which the remainder of the locations in the environment will be represented. As the animal moves, the 'internal navigation' system will shift the focus of excitation within the map to other place representations appropriate to other locations. This is done, as we have suggested, on the basis of information about distances generated from both sensory and motor inputs. In order for the distances to be 'correct' in both the internal sense (that is, purely between the locations) and in the external sense (that is, between the framework of the observer and the locations) both these sources of input must contribute. There need be no representation within the map itself of the behaviours which moved the organism through the environment and which were instrumental in constructing the map.

According to the theory, exploration is behaviour designed initially to build and subsequently to update cognitive maps. When there is a mismatch between some sensory input to a place representation and the predicted sensory input, a set of *mismatch* detectors is triggered, the output of which activates and directs the motor systems involved in exploration. This behaviour is directed towards the incongruence and new information can be incorporated into the map as a result of it. When the animal first enters a novel situation all the mismatch detectors will be activated and exploration will continue until sufficient information is incorporated into the map of that environment. Thus, our theory accords curiosity the status of a major motivation, the driving of information incorporation into cognitive maps.

Properties of place learning. Given that an animal has built a map of an environment, it can subsequently use this information in its attempts to

solve a wide variety of problems. Safety or danger can be attributed to environments, or places within an environment; approach or avoidance responses can be directed towards, or away from, places; places can be reached from any other place, by any available behaviours, even when landmarks are unavailable; new paths can be generated when old ones are closed, as in detour behaviour. Thus, the behaviour of Tolman's rats in his complex mazes is attributable to the workings of the cognitive map. The map is responsible for an animal's sensitivity to novelty in its environment, but at the same time it enables the animal to behave (in the molar sense of the term) in a consistent fashion in spite of occasional changes in the environment since the alteration of any particular feature of the environment does not destroy the usefulness of the map in identifying places.

On the other hand, the mapping system is sensitive to constant variability in the environment; such variability makes it difficult, if not impossible, to build a useful map. The novelty-seeking properties of the mapping system, so important to its function, have the disadvantage of pre-empting the output systems whenever novelty occurs.* Thus, in a continuously changing environment the mapping system becomes useless as a device for problem solving. In practice this means that such variability could block the locale system from directing behaviour and bias the organism towards other hypotheses. We shall suggest later that this effect of environmental variability is partly responsible for the marked persistence often seen in the behaviour of animals in such situations; the taxon hypotheses they are forced to use are inherently persistent, as we shall see shortly.

Unlike the extra-hippocampal systems the locale system is relatively free from the effects of time and repetition. Whenever an organism attends to an object it is encoded in the map. Subsequent attention to that object will have no further effect on the representation of that object in the map. In fact, by virtue of the workings of the misplace system the locale system will act in such a way as to direct the animal's attention away from objects whose presence it can predict towards those whose presence was unexpected. In this sense it is, as we noted, a novelty-seeking device. Incorporation of information about stimuli occurs in a non-incremental fashion. The map itself can become richer and more distinct (i.e., there is better and finer differentiation of places) but it is not altered in any fundamental sense with repeated exposures to the same environment. Since each representation of a stimulus is encoded in terms of its spatial relations to other stimuli, an identical stimulus occurring in different parts of the same environment, or in totally different environments, will have distinct, and differentiable, representations in each case. This, of course, is the way in which a spatio-temporal framework solves, by its very structure, the problem of re-identification so central to our philosophical discussion.

* We shall suggest later that one of the possible advantages in the delayed, or postnatal, maturation of the hippocampus (pp. 112-16) lies in the fact that exploration could be quite maladaptive in infants.

This structure guarantees that there will be relatively little interference between the activations of traces representing the same stimulus in different contexts. On the other hand, some interference could arise within the mapping system between maps of an environment formed before and after some slight change. The up-dating of maps, consequent to such change, does not imply that the old map is literally erased. Some representation of every experienced state of the environment must be maintained, along with information as to which representation is current and which is no longer so.

In most situations place learning is unaffected by inter-trial intervals; this is not the case with route learning. In general, the insensitivity of the locale system to time factors can be attributed to the fact that a place representation can be activated by any of several *different* sensory inputs and that place hypotheses can be effected by any of several *different* motor programmes. *Thus neither the synapses on the input side nor on the output side need be re-used with successive activations of a place hypothesis.* Consequently the strength of a place hypothesis does not suffer from the temporal after-effects which are characteristic of taxon hypotheses. As we shall see shortly, guidance hypotheses involve the consistent reactivation of the input or sensory component while orientation hypotheses require the continual use of the same synapses in the output or motor side. Activation of a route then becomes dependent upon the momentary state of its various links and this state will depend on how recently it has been used. We shall discuss all this at greater length in the next section.

2.3.2. THE TAXON SYSTEMS

The taxon systems generate routes, which can be viewed as lists of guidance and orientation hypotheses.* Both of these rely on egocentric spatial systems. In a guidance hypothesis a positive or negative valence is attached to a specific cue, or item, and this can be approached or avoided by any available behaviour. In this mode the motor system acts as a goal-directed device, reducing the distance between the organism and the desired item, or, conversely, increasing the distance between the organism and its nemesis. In orientations the emphasis is on the specific form of behaviour which is to be executed in the presence of a cue. This type of hypothesis usually involves behaviours which include a change in orientation of the body axis relative to some aspect of the external world (e.g. a right turn at the corner).

In this context it is of no major importance whether the hypotheses within a particular route list are *unordered*, *ordered*, or *concatenated*. In an ordered list subsequent items can only be activated after the earlier ones.

* We are using the terms guidance and orientation hypotheses to refer to what have traditionally been termed *cue* and *response* hypotheses. Since there are cues and responses involved in both forms of hypothesis, the traditional nomenclature is misleading.

In a concatenated list there are actual links between the items such that the first facilitates the second, and so on. From our point of view the ordering of items in the chain may be due to factors such as the physical layout of the environment (e.g. the stimuli for response 2 are revealed by response 1) or the mapping system. In other words, many of the interpretations put on behaviours which seemed to involve interactions between the individual links in a chain (such as Hull's backwards chaining) can be seen as ways of avoiding the notion of a mapping system. Once the latter is accepted, these 'explanations' become both laborious and unnecessary.

2.3.2(a). *Some possible principles underlying taxon hypotheses.* In the absence of a body of pertinent data we must limit ourselves to a few tentative statements about the properties of guidances and orientations, without attempting to differentiate strongly between them. Our basic assumptions concerning the properties of taxon hypotheses rest upon the best guesses we can make concerning the physiological impact of activation within the taxon systems. It must be stressed that the 'taxon systems' embrace the vast majority of the central nervous system, including both sensory and motor systems, and the generalizations put forward here can scarcely be expected to apply at all levels of this set of systems. The force of this caution will be made clear in what follows.

The activation of a taxon hypothesis, or a representation within the taxon systems, can result in any of several independent physiological processes with different time courses, including potentiation and depression of both short-term and long-term significance. The complexity and multiplicity of these phenomena will be conveyed by a consideration of the following facts, all of which we would attribute to the action of the taxon systems:

- (1) The activation of a representation in the taxon system elicits, immediately, a reduction in the threshold for re-activation of the same representation. For instance, with a brief inter-stimulus interval (ISI) the elicitation of a reflex can undergo sensitization rather than habituation (e.g. Pearson and Wenkster 1971, Szabo and Kolta 1967); the ISI in these studies was 10 and 15s, respectively. Similarly, the perception of a word, or any item, in a tachistoscopic presentation temporarily lowers the threshold for perception of the item, the so-called *priming effect* (e.g. Neisser 1954). Finally, perception of one version of an ambiguous figure transiently biases the observer towards perceiving the same version again (Leeper 1935).
- (2) The continued activation of a taxon representation, or several successive activations (with some ISI longer than 10-15 s) usually increases

the threshold for subsequent re-activation. For instance, constant perception of one version of the ambiguous figure, such as a Necker cube, leads to a spontaneous reversal of perception of the other version. Similarly, repetition of any action will lead to its eventual habituation. Thus, there are short-term effects resulting in either potentiation or depression, depending perhaps on the rate of activation.

- (3) The accumulation of activations of any representation over a long period will lead to a more or less permanent reduction in the threshold for its activation. An example of this is seen in the easier recognition of familiar *versus* unfamiliar items in tachistoscopic tests; another example is seen in the ease with which well-learned habits are elicited.
- (4) The repetition of any taxon habit *can* lead to the build-up of inhibition; this occurs readily when reinforcement is absent, but can be seen even when it is present (Kendrick 1958).

This perplexing picture arises, as we have noted, partly because we are considering within the same context the action of a variety of systems from the periphery to the depths of the central nervous system. These undoubtedly have potentiation and depression processes with quite different decay rates, such that the net outcome of the interaction of several of these systems could be just about anything, depending upon the consistency of input (cf. Kimble and Ray 1965) and the interval between activations. This latter point is worth stressing; in contrast to the locale system, the taxon systems are particularly sensitive to temporal factors. The temporal effects most prevalent in animals, and which we shall stress here, are those of short-term depression and long-term potentiation. Later, in discussing humans, we shall amplify our discussion of short-term potentiation effects.

2.3.2(b) Some properties of taxon hypotheses. The reader should bear in mind that one of the major premises of the present theory is that the behaviour of animals bereft of their hippocampus (and locale system) is largely determined by the properties of the remainder of the brain (and its taxon systems). Thus, the mode of action of the taxon systems is part of what one sees after hippocampal lesions and becomes important in any understanding of the effects of such lesions.

Because of the possibility of activation-produced depression in taxon hypotheses, they are more sensitive to the rate at which they are activated than are place hypotheses. At short intervals there will be a rapid buildup of depression, leading eventually to a blockage of the taxon hypothesis. Thus, as the inter-trial interval in a given situation shortens, there will be a bias towards the use of place hypotheses. Further, in the absence of other

mechanisms inhibiting behaviour only the rapid repetition of the same taxon hypothesis will enable the animal to cease using an inappropriate hypothesis when conditions have suddenly changed, as in reversal and extinction (see pp. 281-4 and pp. 337-48). This principle is central to an understanding of the abnormal persistence often seen in animals totally dependent upon taxon hypotheses and the concomitant mechanisms by which they can be inhibited when necessary. While similar principles of potentiation and inhibition might be working in the locale system's short-term reaction to activation, they would not lead to persistence in the same fashion as seen in the taxon systems, owing to the multiple channels available for activation of any representation. Thus, the persistence associated with taxon hypotheses is correlated with their inflexibility.

As we noted, representations in the taxon systems should, in the long term, be strengthened with repeated activation; such an effect does not occur within the locale system. Thus, all things being equal, repeated exposure to a situation in which both place and taxon hypotheses are appropriate will see a shift in favour of the taxon hypothesis with continued training (assuming the inter-trial interval is not too brief). This is one way of conceptualizing the autonomy, and stereotypy, of habits after many repetitions. Here, it becomes important to note a difference between guidance and orientation hypotheses. The former involve *any* response directed at a particular cue, and thus need not involve the repetitive activation of the same output channel. Different movements might be involved on repeated approaches to, or avoidances of, a given cue. On the other hand, orientation hypotheses, by definition, involve similar or identical responses, even if these are defined at the micro-level. Because of this such hypotheses could be particularly prone to long-term potentiation effects, leading to marked stereotypy in their execution. Some such process is probably involved in *autonomous habits*, which are remarkably persistent and progressively less dependent upon any particular eliciting cue. Thus, there are differences in the long-term effects of repetition on these two types of taxon hypotheses. With a guidance hypothesis a variety of responses can be used to act persistently relative to a given cue; with orientation hypotheses stereotyped responses are emitted with little regard to the cues offered by the environment.

The mechanisms preventing serious interference effects in the place system are lacking in the taxon systems. Representations in the latter do not incorporate the (spatial) context which could differentiate one presentation of a guide from another. Consequently, there can be considerable confusion, expressed as interference between behaviours appropriate in different contexts. The best way of avoiding this kind of confusion is through the provision of cues which specify the appropriate taxon hypothesis, thus acting as substitutes for the context normally provided by the locale system. This interference effect, based on the lack of information

defining the appropriate interpretation of a guide, might be less prevalent with orientations.

The general absence of context information characterizes the memory storage properties of the taxon systems. Concepts and categories, the look, the feel and the sound of things, the goodness or badness of objects: all these are represented within the taxon systems. What is missing is the spatio-temporal context within which this knowledge was acquired; this is provided by the locale system, where representations from the taxon systems are located within a structure providing such context. Behaviour which can proceed without contextual information, and there is much that belongs to this class, will not require more than intact taxon systems. However, such behaviour will be subject to the principles of those systems; the meaning of this will be made clear when we analyse the effects of hippocampal lesions upon behaviour.

2.3.3. CONCLUSIONS

In this chapter we have discussed the evidence for cognitive-mapping behaviour and its translation into place-learning mechanisms. Cognitive maps were contrasted with routes, and the types of behavioural strategies dependent upon the two were derived from the properties of maps and routes, as defined by geography on the one hand and physiology on the other.

Our thesis is that place hypotheses are dependent upon the hippocampal cognitive-mapping system, and that guidance and orientation hypotheses do not require the hippocampus. The primary effect of dysfunction in the

TABLE 2

Properties of the taxon and locale systems

| | Taxon | Locale |
|------------------------------------|--|---|
| Motivation for learning | Biological need: to obtain reward or avoid punishment | Cognitive curiosity: to construct and update a map of the environment |
| Learning change | Incremental or decremental | All-or-none |
| Persistence | High esp. orientation hypotheses | Low |
| Temporal changes after activation | Marked changes in threshold and strength as a function of time after activation: sensitive to inter-trial interval | Minimal changes with time after activation; insensitive to inter-trial interval |
| Interference between similar items | High | Low |

locale system should be the loss of the two functions dependent upon cognitive maps: exploration and place learning. However, the radically different properties of the locale and taxon systems confer quite different characteristics on behaviour based on these. Place hypotheses allow for flexibility, rapid change, and the retrieval of context-specific information; taxon hypotheses lack all of these properties. Some of the differences between the properties of the two systems are summarized in Table 2. Before moving to an analysis of the effects of hippocampal lesions, where these principles are brought out most clearly, we shall discuss the way in which the anatomical structure and physiological functioning of the hippocampus can be understood in terms of the cognitive-mapping system described above.

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