Psychological Review
1993, Vol. 100, No. 2, 163–182

0033-295X/93/$3.00

Spatial Cognitive Maps in Animals: New Hypotheses on Their Structure and Neural Mechanisms

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This article provides a hierarchical model of animal spatial cognitive maps. Such maps include both topological information, which affords loose, yet operational, representations of the connectivity of space and its overall arrangement, and metric information, which provides information about angles and distances. The model holds that maps can be initially described as a set of location-dependent reference frameworks providing directional information about other locations. The addition of an overall directional reference allows for the buildup of more complete (allocentric) representations. A survey of recent neurobiological data provides some hints about the brain structures involved in these processes and suggests that the hippocampal formation and the posterior parietal cortex would act differently by handling topological and metric information, respectively.

Over the past two decades, the concept of spatial cognitive maps has gained much popularity. Historically, this concept is important because, as coined by Tolman (1948), it suggests that animals do not merely base their actions on specific stimulus–response associations but that they also internally reorganize acquired spatial information to form cognitive representations of the environment. One important property of such representations is that they allow animals to react to stimuli that are not immediately present because the relationship of such stimuli to those actually perceived is maintained in a cognitive representation, that is, a map (Ellen & Anschel, 1981). In other words, organisms can be aware of the properties of the environment beyond their field of perception. The major consequence of such a representation is that it bridges informational gaps about the environment, thus conferring greater flexibility and efficacy to behavior. Because a prominent feature of evolution is precisely the emergence of increased behavioral flexibility, it follows that cognitive maps should play a crucial role in the onset of intelligent behavior displayed by higher vertebrates.

The number of studies that support the hypothesis that, under specific conditions, animals form some kind of mental representation of their environment is quite impressive (e.g., Gallistel, 1990). This does not mean, however, that animals rely exclusively on spatial representations to orient in space. Performing specific responses, approaching particular cues, or even learning conditional associations about the sensory consequences of specific movement sequences may be efficient strategies in a number of situations. Nevertheless, in spite of their efficacy, such strategies do not confer behavior with the degree of flexibility afforded by the use of a cognitive map (O'Keefe & Nadel, 1978; Sutherland & Dyck, 1984).

The demonstration that an animal forms some internal model of its environment is not, however, sufficient evidence for the cognitive map hypothesis. As a matter of fact, the buildup of a spatial representation implies that information sequentially acquired (as a result of an animal's movements) be integrated into a maplike structure allowing for simultaneous access to all relevant information. A further step is to show that such information can be manipulated to yield the emergence of novel solutions to newly encountered spatial problems. Furthermore, the spatial extent of the representation so formed is another questionable issue. For example, the ability to represent remote portions of space and to generate novel, optimal routes when there is no overlap in the perception of the landmarks available at the origin and goal of the trajectory is still a matter of debate (e.g., Dyer, 1991; Gould, 1990; Wehner & Menzel, 1990).

To address the nature of cognitive maps, I consider both cognitive and anatomical–physiological issues. Questions concerning the type of spatial information that is preserved in the map and how such information is used during spatial behaviors exemplify the cognitive issues, whereas questions concerning the involvement of brain structures that give rise to spatial knowledge and allow the use of such knowledge exemplify the anatomical–physiological issues. The present article has two goals: (a) to present a model of cognitive maps as holistic structures that derive from a number of lower level processes and (b) to examine the plausibility of the proposed model with respect to researchers' current understanding of the neural mechanisms of spatial behavior. Before addressing these goals, I present a brief review of the properties and limits of cognitive maps. In the final section, I propose that, because of its relevance to the mechanisms of spatial behavior, this model might provide a conceptual framework likely to capture some important aspects of animal spatial cognition.

This work was supported by the Centre National de la Recherche Scientifique. I thank Simon Benhamou, Marie-Christine Buhot, Thom Herrmann, Bruce McNaughton, Bob Muller, Catherine Thinus-Blanc, Charlene Wages, and an anonymous referee for helpful comments and discussions on earlier versions of this article.

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Brief Review of Spatial Cognitive Maps

Spatial Functions

First, it is useful to address the spatial functions of cognitive maps. Broadly speaking, three distinct functions can be defined as (a) spatial recognition and identification, (b) spatial localization and memory, and (c) planning of spatial actions. Of course, these functions are not independent but rather integral components of the same system. For example, spatial planning cannot work if the animal is unable to locate itself or to locate its goal within the environment.

Recognition and Identification

The first concern regarding the spatial map is with place recognition and identification. It is a common observation that, in spite of being hungry or thirsty, animals do not exhibit consumption behavior until they have explored the environment. In other words, animals need to be familiar with their current environment. They do not behave according to hunger or thirst until they recognize and identify where they are in space. A purpose of the recognition–identification function may be to free the information-processing systems from processing already-stored information to give priority to unexpected information (Thinus-Blanc, 1988). Not as speculatively, it can be argued that, given the strong and consistent motivation that drives exploration, its result (i.e., the storage of spatial information) is an automatic process. If place recognition and identification is not accomplished, exploratory activity occurs so that the cognitive map comes to match the real environment as closely as possible, therefore providing the animal with spatial invariants. Exploration may lead either to a new representation or to the updating of a former spatial representation. An illustration of the updating process is provided by studies that show that changing the spatial configuration of objects in a previously explored arena induces a renewal of exploratory activity mostly aimed at the displaced objects (Cheal, 1978; Poucet, Chapuis, Durup, & Thinus-Blanc, 1986; Sutherland, 1985; Thinus-Blanc et al., 1987; Tomlinson, 1991; Tomlinson & Johnston, 1991).

Localization and Memory

The second function of cognitive maps, in fact the less disputed one, is to indicate where in space potentially important objects are located. Gallistel (1990) recently reviewed the different possible ways organisms extract information from their environment to infer and memorize the positions of potential goals. Most important, Gallistel stressed that the map encodes "the geometric relations among the points, lines, and surfaces that define the macroscopic shape of the animal's behavioral space" (Gallistel, 1990, p. 171) and that even when goals make suitable beacons, they are not likely to function as such. Rather, animals seem to infer goal positions on the basis of their map of the environment. Localization of the safe platform in the water maze (Morris, 1981) is a good example of this function. Because the platform is located beneath the surface of the water, it does not provide information about its location. The animal must infer its position from the array of distal cues from the environment. The localization function requires an integration of information provided by both the motivational systems and the cognitive map system, so that spatial behavior is determined in accordance with an animal's needs. This integration is particularly important when the status of location changes as a function of an animal's behavior. This is the case when an animal eats food at the end of the arms of the radial-arm maze (Olton, 1982). Subsequent visits to arms that have already been depleted from food are not rewarded. Therefore, a record of depleted arms must be kept in memory. Considerable evidence suggests that this record is based on a map of the food locations that is updated at each choice (e.g., Roitblat, 1987).

Spatial Planning

There is evidence that, in some circumstances, animals plan their displacements through space; that is, they use a global representation of the complete course of action rather than a sequential chain of responses. In a recent study by Collett (1987), gerbils were trained to orient to a goal signaled by a conspicuous light bulb close to it. As they approached the goal, this bulb was switched off and another bulb in a variable position with respect to the first bulb was turned on. In most trials, the gerbils usually changed their trajectory immediately and oriented toward the newly lit bulb, suggesting that the approach was under continuous visual control. In a second experiment, the goal was signaled by a complex array of landmarks, none of them directly associated with the goal location. When this array was shifted, animals usually tended to continue toward the previously signaled goal location and to ignore the changed location of the array of landmarks. This result suggests that, when the goal location had to be inferred from its relationship to the complex array, initial orientation was controlled by external cues, but the displacement itself was guided by an internally generated plan (see also Collett, Cartwright, & Smith, 1986). The cognitive map therefore appears to serve as a database system that allows the planning of trajectories.

The adaptive value of planning is evident because it provides a safe means of problem solving during a period of behavioral silence (Oakley, 1985). This form of internal experimentation makes behavior relatively independent from immediately available sensory information. A good illustration comes from detour and shortcut studies. These experiments generally show that the computation of locomotor movements directed at a specific goal location takes into account the structure and properties of the possible paths. Thus, spatial knowledge extends beyond information about the direct relationship between the start and goal locations to encompass more indirect relationships provided by the rest of the environment. The prototypic situation (Tolman & Honzik, 1930; see also Vauclair, 1980a) consists of blocking a path previously used to reach a baited goal to require the animal to reorganize its trajectory under these altered circumstances. It is generally observed that animals quickly select the next most appropriate path leading to the goal (see also Blancheteau & Le Lorec, 1972; Chapuis, Thinus-Blanc, & Poucet, 1983; Poucet, Thinus-Blanc, & Chapuis, 1983).

Another application of planning concerns the ordering of sequential visits to several points in space. To minimize the expenditure of energy, the successive displacements between these points must be planned so that the resulting overall trajectory is as short as possible. Examples of successful planning of this sort are documented for both rats (Bures & Buresova, 1990) and chimpanzees (Menzel, 1973).

Spatial Content of Cognitive Maps

Preliminary Remark on Place Representations

The basic units of cognitive maps are place representations. A recent account, however, proposed that cognitive maps essentially consist of stored local views of the environment, with the spatial relationship between any two points encoded as a representation of the movement (or series of movements) required to get from one local view to another (McNaughton, Leonard, & Chen, 1989). This model is compelling because it allows for the specification of the role of some brain structures thought to be important for spatial behavior. However, it does not seem to fully capture the essence of the cognitive map concept. First, it emphasizes an associationist view of spatial behavior, which does not fit the flexibility of observed map-based behaviors. Second, mere observation clearly indicates that places are often not identified on the sole basis of specific local views. For example, after a few trials of experience an animal seeking for the safe but hidden platform in the water maze demonstrates its ability to find the platform by using relatively direct trajectories from very different directions (Morris, 1981; see also Becker, Walker, & Olton, 1980, and Walker & Olton, 1984, for similar conclusions). More important, it will display a place-learning set (Whishaw, 1985), which suggests that some concept of place rather than view might be in order.

Seemingly, animals live in a coherent world that cannot be reduced to a succession of perceptual scenes. This does not mean that local views are unimportant in the building up of cognitive maps. Indeed, it is assumed that, although local views do not constitute the unit on which orientation is based, they are necessary for building place representations as an abstract product on the basis of a collection of local views.

Importance of Relational Properties

If one assumes that cognitive maps allow flexible orientation from one place to another on the basis of place representations, then an operational definition of places must be provided. A place can be objectively defined by both its relationship to the environment and its intrinsic characteristics (local cues). However, because not all places are characterized by such local cues (e.g., the hidden platform in the Morris water maze), places are most appropriately defined by relational properties. As a consequence, a place representation should encode, among other things, sufficient information about the spatial relationships between that place and the environment. Such information concerns both the global shape of the environment (i.e., its geometry) and the configuration of the discrete cues that compose it.

Geometry of Space

Evidence for abstract processing of the shape of the environment comes from the series of studies conducted by Cheng (1987) and Cheng and Gallistel (1984). In these experiments, rats were placed in a rectangular chamber and were required to visit the four corners of the chamber. Each corner contained a different amount of food and was associated with a distinctive visual insert. Two opposite corners had the most bait while the other two opposite corners had the least bait. After the animals mastered the task (i.e., visited each corner according to a decreasing order from the most-baited to the least-baited arm), a number of probe tests were conducted on the basis of transformations of the initial distribution of the inserts. These tests revealed that the rats' patterns of visits to the food locations were remarkably insensitive to the modification brought to the spatial arrangement of the inserts. Rather, the animals were using the rectangular shape of the experimental chamber as a means to locate the various food sources (see Gallistel, 1990, chapter 6, for a review).

Configurations of Cues

Contrary to the assertion of Gallistel (1990), however, animals do not base their localization of potentially important places solely on the processing of the geometry of space defined by surfaces. Configurations of distal as well as proximal discrete cues are also incorporated in the spatial representation. Spatial behavior in the water maze is a good example of the control exerted by the configuration of discrete distal cues on goal localization. Another instance is provided by experiments showing that the rearrangement of distal visual cues in an otherwise homogeneous (cue-controlled) environment markedly affects the behavior of rats performing the radial-arm maze task (Suzuki, Augerinos, & Black, 1980). The configuration of proximal cues, when available, also exerts a powerful control on spatial behavior. For example, gerbils are able to locate a hidden seed on the basis of its spatial relationship to beacons placed within the experimental arena (e.g., Collett et al., 1986). Rats are able to integrate the intramaze proximal stimuli in a maplike structure used to guide goal-directed behavior (Hughey & Koppenaal, 1987). Finally, exploration experiments reveal that animals form a representation of the spatial configuration of proximal landmarks (Poucet et al., 1986; Tomlinson & Johnston, 1991).

Relations Between Distal and Proximal Configurational Information

Animals form place representations on the basis of both the distal and proximal environments. Although these two spheres of space provide redundant information in most situations, each one presents peculiar features that are worth mentioning here because they might affect computational properties of spatial representations.

As memorial representations of space, cognitive maps must catch and hold some of the characteristics of the external world. To the extent that maps represent invariant properties of space, they must contain topographical information about the absolute locations of objects and their various spatial relationships rather than just information about egocentric locations relative to the animal, because the latter information is likely to vary as the animal moves about its environment (Hebb, 1949;

O'Keefe & Nadel, 1978). Strong evidence indicates that animals make extensive use of distal information in locating places in the environment. This might be explained by the fact that distal information retains relatively stable relationships as the animal moves about the environment and therefore can be easily used to locate specific points in relation to background cues.

In contrast with distal information, proximal information refers to information that can be gathered by close investigation and implies that, as an animal explores, it is forced to investigate the spatial relations among the elements of the situation (e.g., objects) by running back and forth between these elements. The obvious consequence is that stable relationships are much less easily extractable from proximal information than from distal information. Nevertheless, as shown earlier, there is clear evidence that animals do form allocentric spatial representations on the basis of proximal information. The question thus at hand is twofold: What are the characteristics of representations of proximal information? In other words, are there differences between the spatial parameters that are encoded about distal and proximal space? Second, are there two distinct maps or are proximal and distal information related as an overall map? Indirect answers to these questions are provided in the next section, which examines the known behavioral properties of cognitive maps.

Behavioral Properties of Cognitive Maps

The ultimate purpose of spatial maps is to provide information that allows the animal to make appropriate movements through the environment. Movements between locations that are either sufficiently distant to not be simultaneously perceived or that are separated by obstacles rely on spatial information about both the direction of the goal and the topological structure of the paths between the start and goal locations. As previously shown, information about directions is most appropriately conveyed through distal cues. In contrast, path information is necessarily conveyed through proximal cues linked to the obstacles. Path information mainly includes two parameters, the length of the paths and their directionality with respect to the goal direction.

Previous experiments with rats (Maier, 1929; Tolman & Honzik, 1930), cats (Krushinskii, 1970), dogs (Wyrwicka, 1959), and primates (Kohler, 1925) have shown that path selection is closely dependent on both length and directionality of the available paths. Attempts to dissociate the role of these two parameters (Blancheteau & Le Lorec, 1972) demonstrate that each parameter (i.e., length or directionality) can separately influence rats' path selection. More recent studies have confirmed this result for dogs and for cats (Chapuis et al., 1983; Poucet et al., 1983). In addition, it has been shown that animals tested in a situation that opposed length and directionality (i.e., the shorter path was less direct to the goal and vice versa) prefer the shorter yet less direct path when the goal is hidden but not when the goal is visible (Chapuis et al., 1983; Poucet et al., 1983). Thus, animals displayed their ability to accurately sample the various path characteristics and to behave accordingly when the goal location had to be inferred from its relation to the array of spatial cues.

These results indicate that an integration occurs between information provided by the distal and proximal environment and that both types of information are required to set up the representation needed for planning the most appropriate route. Furthermore, these data suggest that spatial knowledge is not limited to the relations of specific locations (such as the goal) to the environment but that spatial knowledge encompasses detailed information about the spatial structure as well. This conclusion is in contrast with Collett et al. (1986), who suggested that gerbils' spatial memory of a goal location consists of a set of vectors describing the distances and directions of the goal with respect to available proximal landmarks. According to this view, the goal location could be computed from two sets of vectors, one that links the subject's current location to the perceived landmarks and one that is stored and links the landmarks to the goal. This model of a goal-centered spatial memory is clearly inadequate to describe the processing of information about features not directly related to the goal location and, in particular, does not explain how the topological structure of the environment was taken into account in the route-choice experiments described earlier. It appears that the representation used by an animal during orientation is much more complete and stores information not only about the goal location but also about the structure of space (e.g., paths) in between.

Limits of Cognitive Maps

Any conclusion that cognitive maps are complete representations of the spatial environment must be moderated by a number of recent experimental data showing some of their limits. This section reviews some of these limits at two levels, which emphasize first the role of spatial experience and second the unevenness of spatial processing. A third level, namely the question of what spatial behavior (and particularly spatial errors) teaches researchers about the type of encoded spatial information, is addressed in the next section.

Place navigation in the water maze has been demonstrated to be sensitive to animals' previous experience with start locations (Sutherland, Chew, Baker, & Linggard, 1987). In this study, rats had to locate a goal platform in one half of the pool, with the physical access, visual access, or both to the other half restricted through the use of partitions. Animals were subsequently tested for navigation to the same goal platform while starting from the previously restricted half. The results showed inaccurate transfer as compared with animals previously allowed unrestricted access to all parts of the pool. Restricting the view that an animal has of an environment has also been shown to have deleterious effects on the performance of rats in the radial-arm maze (Mazmanian & Roberts, 1983). In the same vein, Ellen, Parko, Wages, Doherty, and Herrmann (1982) demonstrated that successful problem-solving performance depends on a prior exploratory experience with the test apparatus. These authors used the three-table apparatus (Maier, 1929), which consists of three elevated platforms linked to each other by a Y-shaped runway system. Obstruction screens cover the front of each platform so that animals cannot see the contents of the platforms when they are on another platform or on the runways. Following a daily period of exploration on this apparatus, the animal is fed on a platform (which differs from day to day). Following this feeding experience, the animal is then placed on one of the two unbaited platforms, and its task is to return to the platform where it has just been fed. If the daily period of exploration is not provided, rats fail to solve the problem.

Ellen, Soteres, and Wages (1984) further demonstrated that the information required to solve the problem can be acquired in a piecemeal fashion (i.e., on separate exploratory sessions). In this experiment, animals were allowed to explore only a portion of the whole three-table apparatus on each daily exploratory phase of 3 consecutive days and were tested on the 4th day after all the apparatus had been explored in this piecemeal fashion. The results showed that no rat that explored only one platform and runway per day was able to solve the problem, whereas 60% of the rats that explored two platforms and their interconnecting runways did solve the problem. All rats that explored the entire apparatus on each exploratory day were able to solve the problem. This result suggests that animals are able to combine the several elements of information acquired in a piecemeal fashion into a single cognitive representation of the problem space. However, one of the conditions required for solution behavior to occur appears to be the opportunity for the animal to have an actual experience of the connective links among the various parts of the apparatus.

It is interesting to note that in the three-table Y-shaped apparatus, the connection between the platforms invariably includes the central choice point of the apparatus. Therefore, the notion that correct orientation requires knowledge of the connective links can be stated in a different way, namely that correct orientation relies on the knowledge of the spatial properties linked to specific places where choices must be made. This proposal is supported by some of my colleagues' recent work (Poucet, Bolson, & Herrmann, 1990) on spatial problem solving using complex variations of the traditional three-table task. In this study, we showed that, under some conditions, animals prefer to use routes passing through certain places (e.g., the central choice-point of the apparatus) and leading to a substantial reduction in complexity of the problem, in spite of the availability of more direct and shorter routes (Poucet et al., 1990).

That certain places are favored by increased processing is also supported by another study in which the authors examined some properties of the trajectories used by well-trained rats when searching for the removed platform (Whishaw & Mittleman, 1986). The authors clearly demonstrated that trajectories were affected by previous experience. In particular, not only did the animals search the removed platform at its former location, but as a result of their failure to find it, they also tended to return back to previously used start-point locations, thus retracing previously used routes to the platform. Together, these results lead to the conclusion that any theory of cognitive maps should account for the fact that (a) the representation used for navigation is complete only to the extent that animals have unrestricted access to some critical parts of the environment and (b) there are some privileged locations that are better indexed than others.

Hierarchical Model of the Formation of Cognitive Maps

The present model is aimed at solving several contradictions. The first is that animals build up spatial maps that have the apparent properties of a metric (Euclidean) system of coordinates. The question is whether it is realistic to postulate such maps in organisms that experience only frontal views of that environment and which, in researchers' current understanding, do not know metric rules. The second contradiction is that there seems to be a number of limits in the way maps are formed and used. Although cognitive maps contain a lot of information about the environment, specific parts of space appear to be better processed than others. What then should be the representational characteristics that account for its limits? What are the properties of the environment that lead to selective processing about the environment?

In this section, I present the elements required for an operational spatial cognitive map. The aforementioned analysis of the spatial contents of maps shows that animals process place information as well as the spatial connections between places. Thus, any model of cognitive maps should contain these elements. The first issue to be addressed here is the type of spatial information that is likely to be encoded by animals. Then, I provide a short account of the building up of place representations that are assumed to be discrete entities resulting from increased processing at privileged locations. Lastly, I discuss how such place representations become connected into local charts and how local charts themselves can be combined to form overall spatial representations. Although this sequential presentation is convenient, it does not imply that the processing systems necessarily work in this order. For example, place representations depend on the integration of spatial relationships. Given that such relationships are extracted from the environment through perceptual and motor activity, the formation of place representations and the integration of spatial relationships are likely to be concomitant processes.

Basic Features of the Model: Topological Versus Metric Information

The aforementioned review has shown that organisms gather spatial information. Spatial information is information conveyed by the relational properties within space. Although such relational properties are, of course, extracted through perceptive and motor experience, they turn out to provide an allocentric (i.e., independent from the subject's location) frame for behavior. One assumption of the present account is that the relational properties provided by the spatial environment can be described either in topological or metric terms and that organisms are sensitive to these two types of spatial information; that is, they build both topological and metric representations. The previous sections have provided some evidence that animals are able to encode metric information (i.e., information about angles and distances) about their space. In contrast, much less attention has been paid to topological information (however, see Gallistel, 1990), in spite of the fact that virtually any movement between two portions of space can be described in topological words.

Surprisingly, although one can date the notion that spatial information can be encoded in distinct formats back to the research by Piaget and Inhelder (1956) on the development of spatial knowledge in children, only a few attempts to explore this possibility in nonhuman animals have been conducted.

The original proposal made by Piaget and Inhelder was that young children initially represent space only in topological terms, before mastering projective and Euclidean information. Although, in this psychological context, they use the word *topology* in a sense somewhat different from its mathematical meaning, the fundamental ideas of topological geometry were retained. Topology is a geometry originally based on the notions of continuity and limit, from which are derived the relations of compactedness, neighborhood, enclosure, and connectivity. In their theoretical construct, Piaget and Inhelder adapted these basic concepts to their specific purpose, which resulted in the somewhat different, yet related, notions of proximity and neighborhood, enclosure, continuity of lines, and order of succession of points (see Mandler, 1988, for a discussion of the divergence between these notions and their mathematical counterparts). The key feature of topology is that it can provide a crude description of space in which the relationships, to some extent, are not affected by metric modifications. For example, in topology, a square and a circle define a unique structure because one can transform the first into the second by a continuous distortion.

Among the few pieces of work that have attempted to interpret animal spatial representations along the lines of topological concepts are studies by Thinus (1978), Vauclair (1980b), and Poucet (1984). These authors showed that, within a certain range of metric distortions, animals are sensitive to the topological organization of space (in terms of enclosure and connectivity) and behave according to the topological, rather than to the metric, properties of the learning environment. Another example is provided by the experiments on behavior in response to spatial changes (Poucet et al., 1986; Thinus-Blanc et al., 1987), which demonstrated that, in some conditions, exploratory activity was renewed after a topological change, though this change did not affect the geometric characteristics of the initial arrangement. In contrast, metric changes that left the initial topology and geometry unaffected did not induce reexploration. Together, these studies provide some converging support that topological information, although providing a rough description of space, is an ingredient of animal spatial representations.

Consider the following study as an illustration of some of the processes at hand. This experiment was conducted with dogs in a large natural environment (Chapuis & Varlet, 1987). The animals were taken on a lead to two baited points A and B from a start location S, following the path SA–AS–SB–BS (Figure 1). Following this phase, they were simply released from S, and their way to retrieve the food hidden at locations A and B was recorded. Each of the 6 animals was subjected to 32 trials of this type, with 16 different locations for places A and B. The results showed that in 215 (96%) of the 224 trials, animals returned to A (which was the closest location with respect to S) along the path previously shown by the experimenter and then took a more or less direct trajectory (i.e., a shortcut) from A to B. A detailed analysis of these shortcuts, however, revealed a very interesting feature. Although a good deal of these shortcuts (101 out of 215, or 47%) were direct (i.e., paths deviated less than 5° from optimal direction), the remaining 114 trajectories, although still reasonably short, deviated more than 5°, a result that indicates inherent errors in the computation of the directional vector AB. These nonoptimal paths could be classified into two categories according to whether they corresponded to an underestimate (i.e., animals that used an inside shortcut) or an overestimate (i.e., animals that used an outside shortcut) of the direction of place B from place A (paths 2 and 3 in Figure 1, respectively). This analysis revealed a strong bias for inside shortcuts, which were used in 81 (71%) of the 114 indirect path trials, resulting in an unequal distribution of the computational errors around the correct direction. This metric distortion (which, however, did not prevent animals from taking the overall correct direction) is highly suggestive of an encoding of topological information about the relations between the points A, B, and S. Although such topological encoding cannot explain direct shortcutting (which requires true vectorial summation), it accounts for systematic spatial biases likely to be observed in various spatial situations.

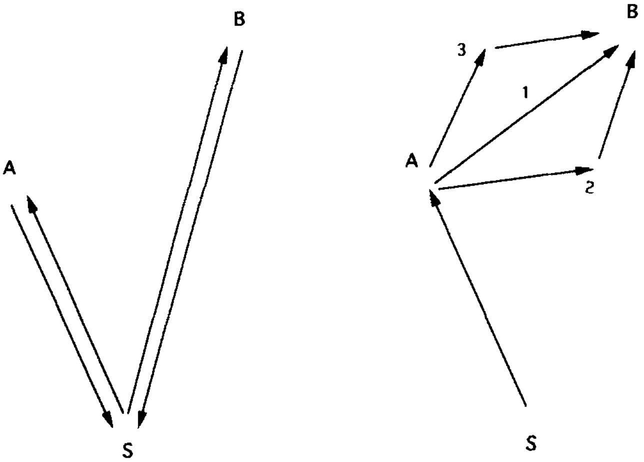

Figure 1. Illustration of dogs' shortcuts. (Dogs were taken on a lead to two baited points A and B from a start location S, following the path SA–AS–SB–BS [left panel]. They were then released from S, and their trajectories to A and B were recorded. In 215 [96%] of the 224 trials, animals first returned to A and then took a shortcut from A to B [right panel]. Of these 215 shortcuts, 101 [47%] were direct, i.e., deviating less than 5° from optimal direction [trajectories of Type 1]. On the remaining 114 trajectories, 81 [71%] were inside shortcuts [Type 2 trajectories], whereas 33 [29%] were outside shortcuts [Type 3 trajectories]. This appears to indicate systematic metric distortions in dogs' spatial representation of the situation. From "Short Cuts by Dogs in Natural Surroundings" by N. Chapuis and C. Varlet, 1987, *Quarterly Journal of Experimental Psychology, 39B,* pp. 52 and 57. Copyright 1987 by the Experimental Psychology Society. Adapted by permission.)

The view held here is that the topological and metric properties of space provide the basic information of animal spatial representations. In this system, topological information only affords a loose, yet operational, representation that specifies the connectivity of space and its overall arrangement. Topology is particularly important when possible movements are constrained by obstacles. The addition of metric information to this basic representation would allow for enhancing the grain of the spatial system by providing information about angles and distances. Although, in its most parsimonious version, the following model stresses that metric information is available only at specific locations, such information could be more readily available (i.e., independent of locations) in ultimate stages of spatial learning. In the following sections, I examine how topological and metric information are combined in spatial maps. The rationale for this approach relies on the consideration that looking at the intermediate stages of spatial learning provides an insight, not only into the nature of the final product, but also into the various means used by animals to solve spatial problems before reaching the highest level of spatial competence. As shown in previous sections, the spatial strategies animals may use are multiple (e.g., Poucet, 1985) and might provide important information about the steps of spatial encoding.

Local Views and Place Representations

I have previously argued in the Brief Review of Spatial Cognitive Maps section that animals encode places rather than views of the environment. Place representations are assumed to be abstract products that are based on the collection of local views of the environment from specific locations. Local views are spatial percepts that, once gathered, become interlinked in a place representation through the processing of sensory data acquired in the course of rotational movements while the organism is at a given location (Sharp, 1991). Such rotational movements can consist of eye movements; head rotations, with reference to the body; body rotations, with respect to the fixed environment; or all of these. The movements allow the passage from one local view to another, each percept being linked to the other through the continuity of visual space in agreement with movement parameters. The integration of visual and movement signals ultimately yields the formation of a place representation that allows place identification and recognition independent of any specific local view.

The important consequence of this integration is that, as a result of being independent of specific local views, a place representation can be activated while approaching a goal, slightly before the animal actually arrives at that goal. As a matter of fact, during the translational movements that precede arrival at a given place, the local views faced by the animal are more or less similar (i.e., have a number of common stimulus elements, in relation to distance) to those experienced while at that place. These local views can therefore be easily matched to those of the corresponding place representation, allowing the animal to unambiguously identify a place in spite of varying approach directions (Figure 2). Evidence for local-view independent place representations is provided by studies showing immediate transfer of performance when, after spatial learning from varying start points, animals are required to go to the same goal location from an entirely new direction (e.g., Becker et al., 1980; Morris, 1981; Walker & Olton, 1984).

Another important point is that the place-representation system functions according to a discrete, rather than a continuous, processing mode. This means that, initially, not all locations in a given environment are likely to be encoded as place representations. Besides the size of the explored environment, which might be a determinant factor in the rate at which place representations are formed, another crucial parameter is the complexity of space. As a matter of fact, the nature and redundancy of the local views afforded by simple, unstructured environments (e.g., an open field) cannot be compared with that afforded by more complex environments (e.g., an enclosed maze), the latter providing local views radically different from point to point. Such complexity might influence the frequency at which place information is gathered. In particular, displacements around obstacles that dramatically affect the local views faced by an animal might lead to increased processing of place information at the border of the visually distinctive environments. Turning angles that induce an inflexion in the displacement (and therefore a change in the local view) and intersections of paths that require a choice about the direction to face, might act similarly to induce increased processing of place information. In this respect, the central choice-point of traditional mazes (e.g., the radial maze or the cross maze) combines these characteristics with the additional property of being an obligatory location of passage and is likely to be used in a wide variety of situations as a reference location in the organization of vectorial information (Poucet, 1985; Poucet et al., 1990).

Connections Between Place Representations

It is assumed that spatial relationships between distinct places are encoded in polar coordinates as vectors, that is, pairing of information about distances and directions (e.g., Collett et al., 1986; McNaughton, Chen, & Markus, 1991; O'Keefe, 1991). This representational format has the advantage of fitting the ballistic nature of the planned movements required for orientation toward nonsignaled locations. Previous work has suggested that direction and distance of the goal location appear to be set from the onset of the planned movement (see the Spatial Planning section).

Because a vector consists of both a distance and a direction, there must be a mechanism that computes both parameters. It is not too difficult to imagine how distances are computed. As a matter of fact, there are a number of processing systems that provide convergent information about distances. The visual system is well equipped for evaluating distances (Gallistel, 1990; McNaughton et al., 1991), and such estimates are further confirmed by distance computations that are based on movement-related parameters derived from locomotor activity.

Although directions also involve the visual system, it is difficult to see how such directions can be useful in complex spatial computations if there is no direction of reference. One solution is to provide the animal with a compasslike mechanism, which allows the calculation of the angular deviation of the goal direction. Such a reference direction might be absolute (geocentric, such as North; see Gallistel, 1990). It also might be provided by computations about the immediate environment (e.g., a slope of the environment; O'Keefe, 1991). In spite of their relative apparent simplicity, these accounts do not say a lot about how the reference direction is extracted from the environment nor about what occurs before it is extracted. Furthermore, the notion of a unique reference direction presents the major disadvantage that if the initial reference direction is lost, so is the organism. In contrast, a highly redundant system can remedy this problem. The assumption here is that animals, in the course of learning about an environment, do not rely on an absolute frame of reference (that is based on a compass), but rather compute several location-dependent reference directions that allow them to determine directions from various individ-

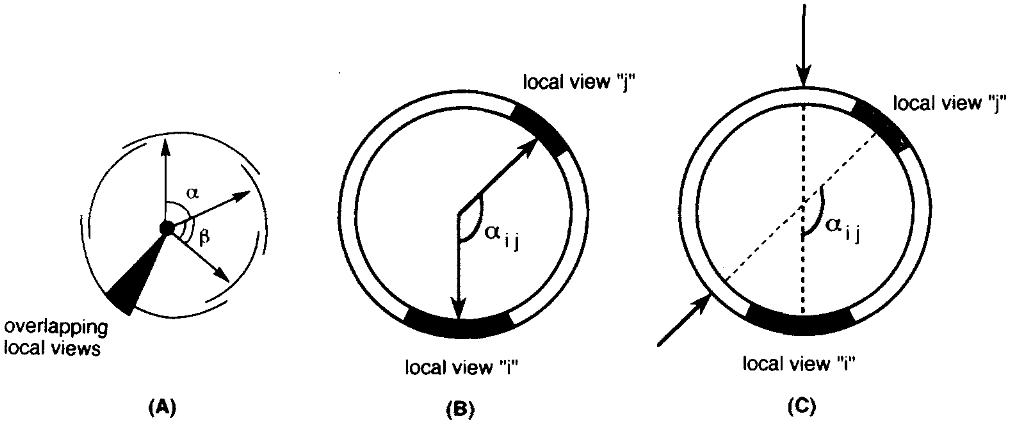

Figure 2. Integration of local views into place representations. (A collection of initially independent local views become interconnected through the processing of sensory data acquired in the course of rotational movements. The overlap between successive local views ensures the spatial continuity of the place representation and allows the specification of the angular relation between any two given local views [Panel A]. This continuity allows place identification and recognition independently of any local view, both when the organism is at the center of the locus [Panel B] or while it is approaching the locus [Panel C]. Perceptual activation of any local view reactivates the whole place representation.)

ual locations. Although this multiple-reference system presents the drawback of increasing the cost in terms of information storage, its adaptive value makes it highly recommendable for moving organisms during initial stages of spatial learning. Ultimately, however, directional information provided by the several location-dependent reference frameworks might be based on a unique reference direction.

Two different situations must be distinguished. The first one corresponds to short-distance spatial behavior, during which generally the location of origin and the goal location share a number of common stimulus elements. It is assumed that orientation, in this case, relies on the formation of local charts and on the use of spatial relationships within the local chart. The second situation occurs during long-distance displacements, when the relationship between places must be established in the absence of common stimulus elements. In this situation, orientation will rely on the representation of spatial relationships between local charts.

Local Charts

The representation of the organism's current environment will be hereinafter referred to as a *local chart.* A local chart may contain any number of place representations, but, by definition, all of these place representations must share a number of common stimulus elements provided by either the proximal or distal environment. In the present model, spatial information mainly consists of vectors (which provide polar coordinates of distant places) and topological relationships. Local charts can therefore be seen as two interlaced networks. The first (vector) network represents specific places from which direction and distance of other places can be determined, whereas the second network, more complete but looser, represents the topology (e.g., connectivity) of the environment. These two types of information are integrated together in the course of exploration.

Creation of a Multiple-Point Reference System

A main assumption of the present model about spatial learning is that one of the first steps is the construction of a *multiple-point reference system* of polar coordinates. In such a system, a number of privileged locations serve as reference points from which the direction and distance of other points can be determined. To emphasize their specific function, the representations formed at these reference locations will be hereinafter referred to as *location-dependent representations.* It is important to note that, although nonegocentric, such representations do not provide the organism with a global system of polar coordinates. Rather, each location functions as a unique frame of reference (for a similar proposal, see Benhamou, Sauvé, & Bovet, 1990).

The formation of location-dependent representations results from the unevenly distributed nature of exploration, which is usually characterized by both the coverage of a wide range of the available space and a more detailed inspection of specific locations on specific trajectories. For example, in a Y-shaped maze, animals invariably spend most of their initial exploratory activity examining the central choice-point and the distal extremities of the arms, in contrast with investigating the arms themselves. During exploration, both locomotor movements (rotations and translations) and vision of the local environment are used to form location-dependent representations. For example, homing experiments show that animals compute a direct-return trajectory to a point of origin on the basis of the integration of the path parameters of an outward circuitous route. The chosen direction of return, however, is directly affected by the presence of available visual cues, demonstrating the priority given to visual information (Etienne, 1987; Etienne, Teroni, Hurni, & Portenier, 1990).

Locomotion thus provides a continuous variation in incoming sensory information (mainly visual). If such movements take place in a small-scale environment, there are a number of common stimulus elements at the origin and goal of any trajectory. The integration of movement parameters registered during a given trajectory between two locations with place information available at the two locations therefore provides converging information. It has been previously suggested that information used by the path integration system is useful only on a short-term temporal scale, which means that such information does not enter a long-term memory store (Etienne et al., 1990). This property suggests that, once an estimate of motion parameters has been made at a given location and confirmed by correlative place information, the resulting vector is mainly based on information provided by the environment, and the path integration system can be reset for a new trajectory. A possible mechanism for linking the path integration system to the features of the environment has been recently proposed by McNaughton et al. (1991).

In this scheme, the place-representation system works in a discrete mode. Place information is processed step-by-step, at each of the privileged locations where the integration of path parameters and spatial information occurs (e.g., at the origin and at the end of the circuitous trajectory). Because spatial configurations (in particular, proximal cue configurations) vary from one place to another, at this stage, spatial information yields only a location-dependent framework in which the perceived environment at each location provides its own reference direction as a means to orient the vectors (Figure 3). It is convenient to imagine that, initially, the reference direction at each location would be provided by the organism's orientation with respect to the environment during its first visit to that place.

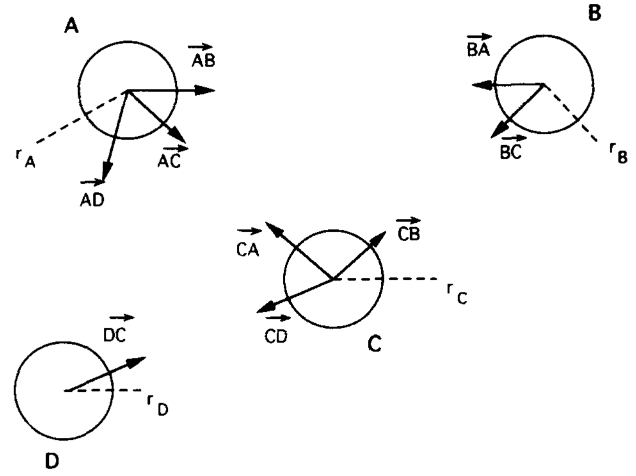

Figure 3. Schematic representation of a location-dependent reference framework. (Each place [indicated by A, B, C, or D] provides its own reference direction [r_A, r_B, r_C, or r_D]. Vectorial information about distant places is therefore location dependent. Note that the availability of vectorial information about a distant location [e.g., about location D] from another location [e.g., from location A] does not imply the availability of vectorial information about the latter location from all other distant locations [in the given example, there is no vector from D to A]. Yet, some locations may provide vectorial information about all other locations [for example, as a result of their central position in space, Location C].)

However, it is assumed that with greater experience (i.e., after having experienced various approach directions to a single place), more than one reference could be used to identify the direction of distant places so that, ultimately, a given location could function as a reference point from which the direction and distance of other encoded places can be determined on the basis of several independent reference directions. This particular feature will prove important in later stages of spatial learning when information contained in the local chart will be referred to by a reference direction common to several location-dependent representations.

Topological Relationships Between Places

As described earlier, the multiple-point reference system provides polar coordinates that are sufficient for planning routes in most localization tasks within open environments (e.g., water maze). Yet, it is clearly different from a Cartesian system of coordinates. First, not all points in the explored space are represented in the local chart. Second, the availability, at a given location, of vectorial information about other locations does not imply that vectorial information about the former location will be available from these other locations. Therefore, the system does not provide enough information for the emergence of shortcut and detour behaviors nor for the generation of novel routes from unknown locations (e.g., Sutherland, Chew, Baker, & Linggard, 1987).

Such abilities require the addition of information about the topology of space. Topological information (i.e., proximity, connectivity, inclusion, and order) is extracted from the regularities resulting from the combination of elementary movements, because such movements are highly constrained by the obstacles and physical connections of space. One source of topological information comes from the fact that spatial movements take time. Thus, processing of spatial information can be accomplished concomitantly with the processing of related time information, therefore resulting in time and order estimates about the relationships between spatial locations. It is of some importance to note that because such knowledge is acquired through repeated exploratory learning, it yields a network of connected places, a result quite different from the memory of a route (O'Keefe & Nadel, 1978), which only requires the memory of a fixed sequence of locations. The interesting feature of this topological network is that new information can be obtained by combining existing information.

As an illustration, consider the network of locations shown in Figure 4, Panel A. An arbitrary topological transform of the actual arrangement is displayed in Figure 4, Panel B. This topological map is sufficient by itself to plan reasonably short trajectories between its connected elements. For example, when starting from e, a left turn at c leads to a, whereas other movements result in longer trajectories. Thus, although the trajectory e–c–a is equivalent to more complex combinations of movements (e.g., e–c–b–a) with respect to the issue of getting to a from e, the topological information gathered during the two trajectories is clearly different in terms of order and proximity between the various points traversed. The point is that, on the basis of topological information, such differences can be usefully translated in general rules about space concerning the as-

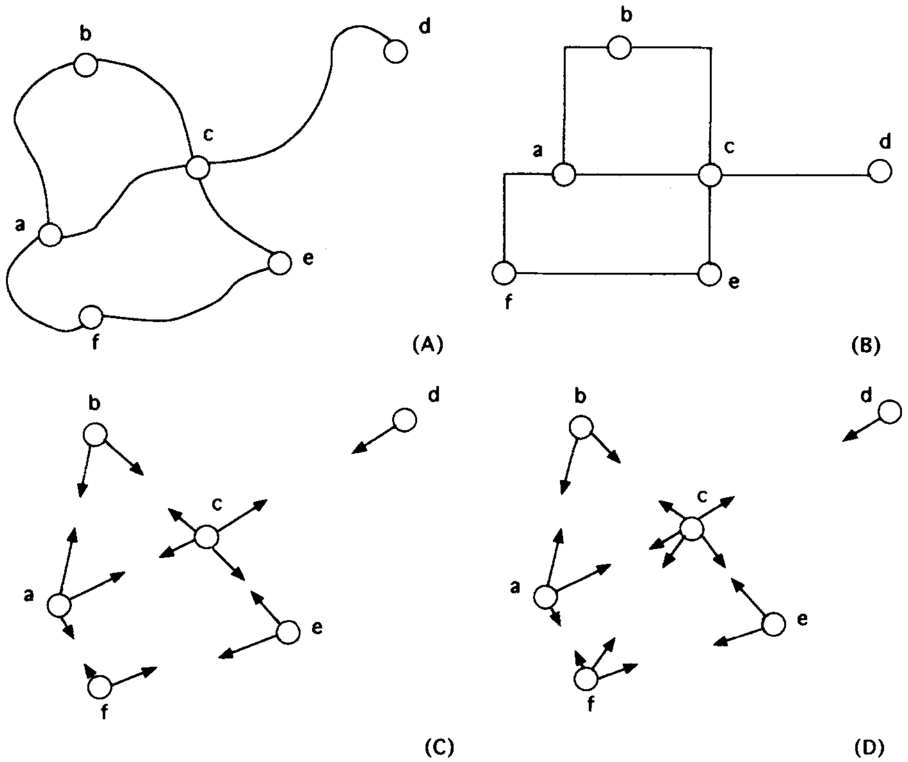

Figure 4. Complementarity of topological and location-dependent reference frameworks. (Panel A shows an actual network of spatial locations, linked together by specific trajectories that result either from constraints by physical obstacles or from incomplete experience. An arbitrary topological transform [which distorts metric relationships but not topological relationships] is displayed in Panel B. The vectorial map corresponding to the actual network [Panel C] contains vectorial information only about the locations connected in the topological map. Additional vectorial information can be computed provided that a single reference system is used [in Panel D, Location c is used as a reference for vectorial computation].)

sociativity and transitivity of trajectories (see Piaget & Inhelder, 1956). Because of their relevance in terms of economy of energy, rules of transitivity and associativity are essential for minimizing the cost of displacements, and animals likely possess the ability to infer such rules from experience. In particular, because exploration is usually characterized by a pseudorandom activity (with back-and-forth movements, retracings, shortcuttings, etc.), it ultimately leads to the canceling of the temporal sequence of information gathering, with the result that simple notions of proximity and connectivity of space become readily available to the organism. Generally, any combination of two (or more) elementary movements between distinct places can be replaced by a single and shorter one (shortcutting) and conversely (detour behavior).

With the addition of sufficient vectorial information, the use of such rules permits more efficient shortcutting. Figure 4, Panel C displays a vectorial map of the actual network. Note that this figure shows only the vectors that join the locations connected in the corresponding topological network (see Panel B). Additional vectorial information can be computed provided that a single reference system is used. Panel D shows the result with location c used as the system of reference for vectorial computation. Although the result of these computations adds a good deal of information to the original network, it still does not map the complete set of relationships between all the locations of the network. Such complete mapping requires that vectorial summation is conducted within a system of reference common to all locations. This, in turn, implies the extraction of an overall reference direction.

Computation of an Overall Reference Direction

The ultimate step in the buildup of local charts is that vectorial information contained in each location-dependent representation be combined into a more global (location-independent) representation. This problem has recently received some attention and has led to two different hypothetical constructs. One has been proposed by Gallistel (1990), who assumed that animals might process the geometry of space. This proposal holds that a purely spatial module would handle information about the general surfaces and lines provided by the environment and that such information would be useful in providing an allocentric, absolute reference framework. Although it is not difficult to imagine how such extraction of geometric information is possible in laboratory settings that usually provide a geometric environment, it is much harder to see how this system could work in more natural environments. The other proposal solves this difficulty by postulating that animals compute a slope (i.e., a general reference direction) of the environment on the basis of the overall distribution of cues (O'Keefe, 1991). One problem with the calculation of the overall slope is that it is based on the computations of partial slopes between pairs of cues, which already require the animal to maintain a constant orientation in an absolute geographical framework at each computational step. Because the overall purpose of the slope computation is simply to allow such absolute orientation, it is not easy to see how it is calculated.

Although there is no simple answer to this question, one solution is to suggest that computing a single reference direction is based on the spatial properties of the environment derived from the organism's own experience, rather than on abstract properties of space. This proposal relies on the consideration that space is not homogeneous. It is not only that some places may have more value than others, but also that the animal is more likely to engage in exploration between these places than to use routes between either nonuseful or potentially dangerous places. As a result of increased familiarization with the environment, this differential attention to certain areas of the environment would lead to the emergence of an environmentally defined overall reference direction, allowing for vector summation by providing a common reference to all places. As stated earlier, such overall reference direction is more or less related to the preferred axes of movement, themselves influenced by gross asymmetries in the environment. Note that the passage from the multiple-point reference system (in which vectorial information about a distant place depends on the animal's location) to a more global representation of the local chart (in which vectorial information is location independent) requires a concomitant process for updating vectorial information derived from the location-dependent reference frameworks. For the sake of simplicity, it is assumed that such updating does not operate continuously as a function of the moment-to-moment computed reference direction but operates only when the final overall reference direction has been calculated. In a location-independent reference framework, the reference direction is common to all places and is computed from the spatial properties of the environment derived from the organism's own spatial experiences.

One consequence of this hypothesis is that the reference direction may vary over animals. As a matter of fact, the final orientation of the reference direction is critically affected by individual spatial experience (i.e., by encoded locations, usual trajectories, and location-dependent vectorial contents). Although each of these parameters is in turn affected by the structure of space, and therefore might lead to some common reference across different individuals, it is nevertheless clear that very different computations can emerge as a result of different exploratory patterns and experiences. However, provided that different individuals are consistent in their computations, their overall performance in orientation will be quite comparable in spite of relying on distinct reference directions.

Connections Between Distinct Local Charts

The problem of long-distance orientation, that is, of how place representations from distinct local charts are connected, is more complex because, by definition, such place representations do not have any stimulus elements in common. In addition, such a capacity has never been demonstrated unambiguously. Although reference can be made to work emphasizing the existence of an absolute geographical framework (e.g., Gallistel, 1990), evidence for this higher level of spatial processing is far from convincing. I would like here to briefly comment on another possibility. The hypothesis rests on the two following postulates. First, local charts of distant environments are interconnected. Second, an animal seeking a distant place orients, in fact, to that distant region of space by accessing the local chart of the goal location. The question, therefore, is how local charts are interconnected.

There are two solutions to this problem. The first is that the representation of the distant environment could be associated with a representation of a *linking place*, defined as a place in the current environment that is on the border between the two environments (recall that natural borders and obstacles are assumed to lead to additional processing of specific place information). Therefore, the problem of orienting to a place in a distant environment could be reduced to the single problem of orienting to a linking place in the current environment and then orienting to the goal on the basis of a local chart of the distant environment (Figure 5, Panel A). This problem has been examined in some detail in the previous section and is not developed further here. This strategy can be extended to more complex problems (Panel B). Application of this type of solution, however, leads to indirect trajectories when there is no linking place between any two environments and therefore cannot account for the emergence of a truly novel solution.

The second solution is either that topological information is extracted from long-distance displacements (resulting in a connected network of local charts) or that some general (geocentric) reference direction is extracted. In the former proposal, a specific region of space could serve as a reference framework providing vectorial information about other distant regions (much in the same way as a location-dependent representation provides information about other locations; see Figure 3). Thus, local charts would work more or less as tables of orientation (Benhamou et al., 1990) providing information about direction and distance of other local charts and therefore leading to a successful solution only when such information is available. The latter proposal requires that the distinct reference directions provided by different local charts be combined into a single, local chart-independent, overall direction so that a two-stage vector summation would be sufficient for correct orientation to a distant environment (Figure 5, Panel C). As mentioned earlier, evidence for such a capability is still controversial and clearly requires some additional research.

Summary and Comments

A behavioral review suggested that spatial representations, although capturing some essential aspects of the environment, can nevertheless be hardly assimilated to maplike, Euclidean

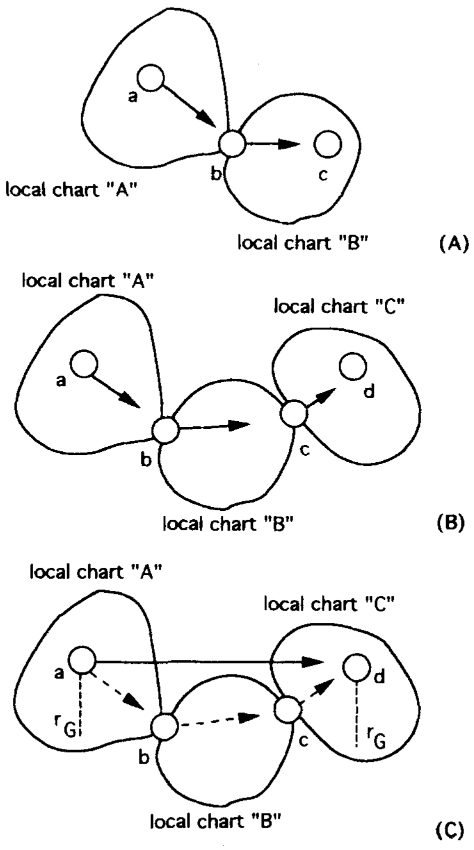

Figure 5. Connections between distinct local charts. (In Panel A, the problem of reaching Location b [local chart B] from Location a [local chart A] is solved by using local chart A as a location-dependent reference framework that provides information about the linking place b between the two nonoverlapping environments. Panel B shows how such operations can be combined to solve spatial problems [e.g., reaching d from a] between two nonoverlapping environments A and C with no linking place. Note that the resulting trajectory is not direct. In contrast, the availability of a general reference direction [r_G], independent from any location or environment, allows for the computation of a direct path from a to d [Panel C].)

representations. Accordingly, two main points can be made about the present model of spatial knowledge. First, I posit that more than one type of spatial information might be encoded in the spatial representations acquired by animals. More specifically, such representations might be conceived as a dual network, consisting of a loose (but extended) representation of the topology of space and a more precise (though less complete) vectorial location-dependent representation of distant places.

Second, the model emphasizes a hierarchical organization of space that is based on the necessary steps required for building cognitive maps. To summarize, learning about an environment would involve (a) the integration of local views into place representations; (b) the formation of local charts of contiguous regions, in which vectorial information is initially conveyed by location-dependent reference frameworks; and (c) the computation of an overall (location-independent) reference direction for each local chart.

The interesting properties of this hierarchical organization are the following. First, it permits the optimization of cognitive resources. For example, on the basis of a mathematical formalization of the problem, Yoshino (1991) recently demonstrated that a hierarchical organization of spatial knowledge leads to a substantial reduction in the cognitive resources required to form, store, and use spatial representations. Second, near-optimal spatial performance is allowed without having to resort to a cartographiclike map. However, increasing the ability of the system to process more abstract spatial information (e.g., by making the reference direction independent of the subject's location) results in enhanced precision and flexibility. Third, in spite of a difference in information manipulated at each stage, the number of computational processes required is limited to three main operations: (a) a classification device allowing the categorization of sets of incoming information; (b) a comparison–updating system, which guarantees the stability of encoded information; and (c) a set of experience-derived rules (transitivity and associativity), which allow spatial reasoning. Each of these distinct processes operates at the several steps of spatial cognition. Furthermore, a number of recent neural network models describe how some of these processes could come to work in a manner making them biologically plausible (e.g., Sharp, 1991). In the next section, I briefly examine how researchers' current knowledge of brain functioning converges with these ideas.

Neural Mechanisms of Cognitive Maps

Brief Review of the Literature

There is no recent account of spatial cognitive maps in animals that does not emphasize the role played by the hippocampal formation. The amount of evidence that supports a spatial function for the hippocampus should not obscure the fact that this structure could have a number of nonspatial functions. For example, hippocampal damage in rats affects odor discriminations (Eichenbaum, Fagan, & Cohen, 1986), timing of events (Olton, Meck, & Church, 1987), and performance on configural problems (Sutherland, McDonald, Hill, & Rudy, 1989). Thus, the spatial function of the hippocampus can be viewed as a particular instance of the involvement of the hippocampal formation in a broader category of memory tasks. With respect to this point, recent theories have argued that the hippocampus would be essential for declarative memory (Squire, 1992; Squire & Zola-Morgan, 1991) or for the formation of configural associations (Sutherland & Rudy, 1989). It is important to emphasize here that none of these theoretical constructs is incompatible with a particular involvement of the hippocampal formation in the learning of spatial relationships. With respect to the current discussion, the question here is, therefore, how researchers' understanding of hippocampal functioning fits with the present conception of spatial cognition; that is, what could be the role of the hippocampus in this scheme?

In spite of the prominent role assigned to the hippocampal formation, however, some investigators have suggested that other cortical structures such as the parietal cortex (e.g., Hyvarinen, 1982; Kolb & Walkey, 1987) and frontal cortex (Kolb, 1984) are critical to spatial functions as well. Although it is not in the scope of the present article to review in detail either the extensive evidence that supports the spatial function of the hippocampal formation (for reviews, see Barnes, 1988; O'Keefe & Nadel, 1978) or the somewhat weaker evidence for parietal and frontal involvements, it is worth summarizing the main arguments.

Lesion Data

Hippocampus. Lesion studies show that damage to the hippocampus or its associated structures (fimbria-fornix, septum, entorhinal cortex, and subiculum) induce severe and permanent deficits in a wide variety of spatial abilities (Rasmussen, Barnes, & McNaughton, 1989), such as water-maze navigation (Kelsey & Landry, 1988; Morris, Hagan, & Rawlins, 1986), cross-maze orientation (O'Keefe & Conway, 1980), and spatial memory in the radial-arm maze (Olton, 1982). Hippocampal lesions also induce strong deficits in exploration. Hippocampal rats are often hyperactive in the open field and usually do not display a normal pattern of habituation (Foreman & Stevens, 1987, for a review). Although simple sensory discriminative abilities are left intact, hippocampal rats are also impaired in terms of their reactions to novelty (Markowska & Lukaszewska, 1981; Poucet, 1989; Thinus-Blanc, Save, Buhot, & Poucet, 1991).

Hippocampal damage, however, does not affect evenly all spatial capacities. There are at least two distinct circumstances in which spared spatial abilities are observed. First, hippocampal dysfunctions do not affect retention of well-learned spatial information, even though acquisition of new spatial information does not occur (Kubie, Dayyani, Sutherland, & Muller, 1989; McNaughton, Barnes, Rao, Baldwin, & Rasmussen, 1986; Poucet, Herrmann, & Buhot, 1991). Such observations suggest that the hippocampus is not a long-term store of spatial information; instead, it is critical during initial acquisition. Second, hippocampal animals can learn to navigate to a single fixed goal if their start location is kept constant, although they take longer than normal animals to reach asymptotic performance (Eichenbaum, Stewart, & Morris, 1990). However, in spite of this ability, hippocampal animals do not transfer navigational performance if other start locations are used. This suggests that, although specific vectorial information can be computed without the hippocampus, it cannot be combined with other vectorial information.

Parietal cortex. Parietal lesions in rats also produce deficits in spatial navigation (DiMattia & Kesner, 1988a; Kesner, Farnsworth, & DiMattia, 1989; Kolb & Walkey, 1987; review in Kolb, 1990a) and spatial working memory (DiMattia & Kesner, 1988b). Although no deficit is observed in habituation of exploration, parietal animals fail to react to topographical rearrangements much in the same way as hippocampal animals (Save, Poucet, Foreman, & Buhot, 1992). One important difference between hippocampal and parietal animals is that, although both are impaired in water-navigation performance, only hippocampal animals are able to use a nonmapping strategy to reach the hidden platform, that is, engage in a searching behavior characterized by swimming in circles at about the appropriate distance from the pool wall (DiMattia & Kesner, 1988a). In contrast, parietal animals display random swimming patterns, resulting in a lengthening of the latency to find the platform as compared with hippocampal animals. Also, parietal damage, unlike hippocampal damage, appears to affect both initial acquisition and retention of spatial information (DiMattia & Kesner, 1988a). The trajectories of parietal animals are always poor, even with extended training and pretraining (Kolb, 1990a). This difference could be partly explained by the fact that the spatial deficit displayed by animals with hippocampal damage is temporally graded so that the impairment is more important if the lesion is made soon after initial training than if it is made after some time has elapsed following initial training (Sutherland, Arnold, & Rodriguez, 1987). In general, these results are consistent with the notion that the hippocampus and posterior parietal cortex make important, although distinct, contributions to spatial performance.

Frontal cortex. Lesions of the medial frontal cortex result in impairments in a number of spatial tasks such as spatial delayed alternation, radial-arm maze, spatial navigation, and spatial problem solving (see Kolb, 1984, 1990b). Although their behavior in response to a spatial change is qualitatively different from that of normal animals, frontal animals react adequately to topographical rearrangements and are not impaired in exploration (Poucet, 1989). It has been previously proposed that most of the spatial deficits observed in frontal animals can be explained by an impaired working memory for specific items of information, precluding them from appropriately planning complex sequences of actions such as those required for accurate navigation (Poucet, 1990).

Electrophysiological Data

Electrophysiological studies relevant to the analysis of the neural correlates of spatial behavior have mainly focused on single-unit recordings in the hippocampal formation. So far, similar data from parietal (e.g., Chen & McNaughton, 1988) or frontal (e.g., Batuev, Kursina, & Shutov, 1990) cortical areas are too scarce to allow for drawing significant conclusions.

Hippocampal recordings have revealed that a number of single pyramidal neurons in the CA1 (cornus ammonis) and CA3 areas of the hippocampus fire in relation to the animal's location within the environment. Such so-called *place cells* are active during both exploration and spatial localization behaviors (Muller & Kubie, 1987; Muller, Kubie, & Ranck, 1987; O'Keefe & Nadel, 1978; O'Keefe & Speakman, 1987; Olton, Branch, & Best, 1978). Even though the firing of such cells may be modulated by nonspatial variables (e.g., speed of movement, Wiener, Paul, & Eichenbaum, 1989), Muller, Kubie, Bostock, Taube, and Quirk (1991) have convincingly demonstrated that the most consistent correlate of the activity of these cells is the animal's spatial location. Another important problem, still a matter for debate, is whether, in addition to location, the direction faced by the subject also accounts for increased firing of place cells. With respect to this point, conflicting results have been reported. For example, in some situations place cells have been shown to have strong directional correlates, that is, to fire whenever the animal faces a particular direction at a given location (Jones Leonard, McNaughton, & Barnes, 1988; Leonard, McNaughton, Barnes, & Marquis, 1990; McNaughton, Barnes, & O'Keefe, 1983). This observation is important because it shapes the way one sees the hippocampal involvement in spatial representations. For example, it led Leonard and McNaughton (1990) to propose that the hippocampus would mainly serve to store local views of the environment as well as their associations. In contrast, other investigators have found little, if any, evidence for directional selectivity of place-cell firing (Muller et al., 1991; O'Keefe & Speakman, 1987), a negative result that led them to formulate entirely different opinions about the spatial function of the hippocampus. Although there is no definitive answer to this question, some hints as to why some situations would induce directional firing of place cells have recently been proposed by Sharp (1991). The basic idea is that the emergence of directional properties in place cells would result from mechanical constraints on the possible directions faced by the animal when at specific locations. Sharp implemented this idea in a model where the hippocampal place cells were at the output of a neural network aimed at classifying local views on the basis of their similarity and found that directional properties were emerging under specific circumstances (e.g., in the radial-arm maze or during initial learning) but that place cells were pluridirectional in most conditions. Although this result does not constitute a formal proof that directionality is unimportant for place-cell firing (and actually, it could well play a modulatory role), it suggests, at the least, that direction is not the best indicator to predict place-cell firing. Accordingly, in the following, I favor the position that place cells have truly locational, rather than directional, correlates.

The properties of hippocampal place cells are too complex to be fully described here (for a review, see Muller et al., 1991). However, at least two of these properties are important for consideration here. First, when rats are exposed to a new stimulus situation in an open field, place cells become progressively active while the rat is at a given location (Muller & Kubie, 1989) and, once established, the locations of their firing fields are stationary. Second, although in some way the firing fields of hippocampal cells are controlled by the environment (e.g., rotating the cues induces a corresponding rotation of the location of the firing field), such a control is more complex than a mere sensory triggering. When the controlled cues are removed, most place cells display firing fields remarkably similar to those observed when the cues were present. Such similarities concern their size, shape, and radial distance from the center of the circular arena used for recording, with the noticeable exception that their angular location within the arena becomes unpredictable (Muller & Kubie, 1987). In some occasions, however, place cells can retain all aspects of their original characteristics in the absence of the controlling cues, including their actual location of firing in the environment. This occurs particularly when the animal has the opportunity to sample the environment before the cues are removed or the lights are turned off. Together, these results suggest that place-cell firing is not triggered in a simple sensory fashion (for converging conclusions, see Muller & Kubie, 1989; O'Keefe & Speakman, 1987; Quirk, Muller, & Kubie, 1990).

There is another recently discovered population of neurons that is also relevant to the spatial computations performed by the hippocampus. These so-called *head-direction* neurons, unlike place cells, are postsubicular cells, whose firing activity is tightly related to the orientation faced by the animal with regard to the environment, irrespective of its location (Ranck, 1984; Taube, Muller, & Ranck, 1990a, 1990b; see Muller et al., 1991, for a review). In some occasions, two such head-direction cells were recorded simultaneously. Although their preferred directions of firing were clearly distinct, they were affected in the same way by a rotation of the available environmental cues; that is, the preferred direction of each cell shifted the same magnitude and sign. One additional property that head-direction cells have in common to place cells is that they maintain their activity when either the environmental cues are removed or the lights are turned off, provided the animal has been in the recording chamber for awhile before the environmental manipulation (Taube et al., 1990b). This memory property suggests that postsubicular head-direction cells as well as hippocampal place cells are not simply sensorially triggered, but rather represent some aspect of the environment.

Reexamination of Hippocampal and Fronto-Parietal Spatial Functions

In this section, I present a speculative account of how the neural systems discussed earlier could cooperate for processing spatial information along the lines of the hierarchical model of spatial cognition. The point here is that, although the spatial model primarily stemmed from a behavioral analysis, it seems to receive some support from researchers' current understanding of central processing by neural systems. The two main suggestions of the behavioral model were, first, that spatial representations can be viewed as the result of a dual mode of encoding emphasizing both topological information and vectorial (metric) information and, second, that several levels of spatial organization are likely. The review of neural data clearly showed the crucial importance of the hippocampal formation and parietal cortex and to a lesser extent of the frontal cortex. The following is an attempt at examining the respective contributions of these structures to spatial processing. It should not be viewed to constitute a rigid and definitive scenario but rather as a possible framework for further empirical studies and theoretical elaboration.

Briefly, the circuitry for spatial information processing is based on that proposed by Mishkin, Ungerleider, and Macko (1983) for visual outflow in primates (see Figure 6). The circuitry consists of two cortical pathways stemming from the occipital visual cortex. One of these pathways is directed at the posterior parietal cortex (hereinafter referred to as the occipito-parietal [OP] pathway) and carries spatial data, whereas the other is directed at the infero-temporal cortex (hereinafter referred to as the occipitotemporal [OT] pathway) and carries data pertaining to object recognition. In the present hypothesis, it is assumed that these two outflows then converge onto the entorhinal cortex, with each one carrying specific signals corresponding to its specific mode for processing spatial information. Furthermore, information is assumed to be processed in parallel along these two pathways, contrary to Pandya and Yeterian (1984), who posited sequential, rather than parallel, progressive elaboration of spatial information. It is important to realize that, although this circuitry was originally described in the primate brain, some of the corresponding connections have been evidenced in the rat brain. Kolb and Walkey (1987) described connections between the visual areas and the posterior parietal cortex of the rat. This area is a multimodal sensory association region that receives projections from striate, extra-

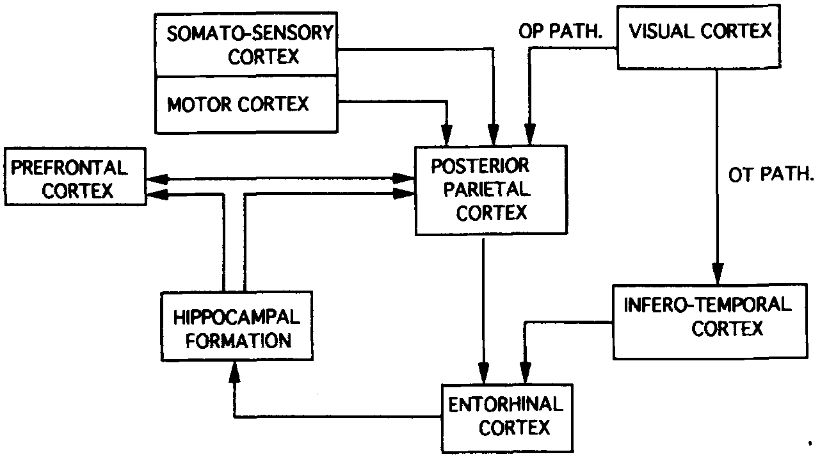

Figure 6. A schema of the hypothetical circuitry involved in spatial processing. (OT path. = occipitotemporal pathway; OP path. = occipitoparietal pathway [see the text for an explanation]. From "Object Vision and Spatial Vision: Two Cortical Pathways" by M. Mishkin, L. G. Ungerleider, and K. A. Macko, 1983, *Trends in Neurosciences, 6,* p. 414. Copyright 1983 by Elsevier Science. Adapted by permission. Also from "Cortical-Hippocampal Interactions and Cognitive Mapping: A Hypothesis Based on Reintegration of the Parietal and Inferotemporal Pathways for Visual Processing" by B. L. McNaughton, B. Leonard, and L. L. Chen, 1989, *Psychobiology, 17,* p. 237. Copyright 1989 by the Psychonomic Society. Adapted by permission.)

striate, and somatosensory cortex. It is also reciprocally connected with the medial frontal cortex. Although connections between the visual and temporal cortex are much less documented in rats, such connections do exist in primates (e.g., Ungerleider & Mishkin, 1982). Accordingly, it will be speculated that rodent brain contains similar projections. Lastly, the entorhinal cortex is itself a site of convergence receiving inputs from higher level association cortexes through the perirhinal cortex (Deacon, Eichenbaum, Rosenberg, & Eckman, 1983; Witter, Groenewegen, Lopes da Silva, & Lohman, 1989).

In the course of this dual outflow, visuospatial information (i.e., local views of the environment) is subjected to parallel processing leading to two distinct representations. The OP pathway participates in the formation of a composite representation of visuospatial information and somatosensory information (Leonard & McNaughton, 1990; McNaughton et al., 1989). Ultimately, these composite representations will be combined in the posterior parietal cortex to build a metric spatial representation on the basis of correlative processing of movement parameters and visuospatial information (see the following paragraphs). The OT pathway leads to the formation of a representation of specific, highly processed, visuospatial material that consists of local views. The high-grain representation of individual local views in the OT pathway allows for their precise identification. Both sets of information converge onto the entorhinal cortex (Mishkin et al., 1983), which receives highly processed information from all sensory modalities, and is reciprocally connected to the amygdala. It can therefore be suggested that information stemming from the OP and OT pathways is combined in the entorhinal cortex, where it is tagged according to its value for the organism, so that only significant information is conveyed to the dentate gyrus and then to the hippocampus proper.

The hippocampus would serve two main functions in spatial processing. First, it would build place representations of specific locations on the basis of the combinatorial arrangement of distinct local views gathered across different temporal episodes. This function would be handled by complex-spike cells, whose activity is highly related to an animal's current location, therefore providing a neural representation of specific locations in space. As mentioned previously, such place representations could be based on the integrated collection of local views of the environment (see Sharp, 1991). Inasmuch as such representations point to current locations, they indicate where the organism is located in space. However, as the animal moves within space, more and more place information enters the hippocampus through the entorhinal gate, and the second function of the hippocampus, recently suggested by Muller et al. (1991), is to provide information about the topological relationships (e.g., proximity and connectivity) between the selected locations that are subject to elaboration as place representations. The incorporation of existing place information into the topological framework would result from the integration of place cells into a neural network that is based on the strengthening of the synaptic weights between place cells (Muller et al., 1991). Synaptic strengthening would be the consequence of the closer temporal association in firing activity of pre- and postsynaptic place cells that arises from movement between close locations than that arises from movement between more remote locations. The result of this process is that topological relationships such as proximity and connectivity between place representations are built by the hippocampal network.

With respect to the proposed model of spatial knowledge, the present account makes the following additional proposals. First, the population of postsubicular head-direction cells would represent the full 360° range of angular directions, thus providing a whole set of reference directions readily available at any time and in any environment. Recall that such reference directions are used to compute vector orientation in the location-dependent reference frameworks provided by place cells. The postsubiculum therefore would serve as a database system providing information useful for computing directions. If one assumes that such directional information can be combined with the locational information provided by place cells, then the combined system provides full information for further processing by other systems.

A possible candidate for the output of hippocampal processing is the posterior parietal cortex. This parieto–hippocampo–parietal loop is required to incorporate metric information by combining the hippocampal topological representation with locomotor-pattern-related information to enhance the grain of the spatial representation. This enhanced grain is induced by extensive computation of distance information correlative of animal displacements, with the result that the representation handled by the parietal cortex acquires metric properties. It is important to note that, because of this disposition, spatial information processed by the parietal cortex comes to rely heavily on extensive locomotor experience within the environment. In this hypothesis, therefore, the spatial representation finally handled by the parietal cortex requires more time for its building up than the hippocampal representation. Conversely, however, the correlative advantage of the slower elaboration of spatial information within the parietal cortex is that the grain of the representation finally achieved is greater than that of the hippocampal (topological) representation. Another consequence of the differential rate of spatial processing within the parietal cortex and within the hippocampus is that the latter structure would provide useful spatial information early in the time course of familiarization with the environment, whereas the former would provide useful information only at later stages (Kametani & Kesner, 1989; Meunier, Jaffard, & Destrade, 1991). This property could account, at least partly, for the spared spatial capacities displayed by animals with hippocampal lesions when tested for retention of well-learned spatial information in highly familiar environments.

Lastly, the use of spatial information for solving tasks that require the computation of trajectories would involve the prefrontal cortical area. Spatial information could reach the prefrontal cortical area as a result of convergent activity from the output flow of either hippocampal (topological) information, parietal (finer-grained) information, or both. Notice that functional connections from the hippocampus and posterior parietal cortex to the medial frontal cortex have been recently documented (Kolb & Walkey, 1987; Laroche, Jay, & Thierry, 1989). This converging input to frontal cortical areas would allow for the computations required for planning spatial movements, on the basis of both the working-memory functions assigned to the medial prefrontal cortex (Poucet, 1990) and the rule-learning functions assigned to the more dorso-lateral (and possibly orbital) areas of the prefrontal cortex (Winocur, 1991; Winocur & Moscovitch, 1990).

Conclusion

Comparison With Other Models and Implications

As stated earlier, this neural view of the formation of spatial representations does not pretend to achieve a complete explanation and certainly does not exhaustively examine all the brain structures that might be relevant to spatial processing. Rather, it should be considered as a possible theoretical framework that attempts to account for the contributory participations of several brain structures to the complex problem of spatial processing. In that respect, the main characteristic of the framework is that it emphasizes the cooperativity of two structures, the parietal cortex and the hippocampal formation. Before concluding, it is useful to briefly examine the relation of the present account to other similar proposals. First, on the basis of an analysis of the main properties and limits of spatial representations in animals, the present account draws a distinction between several distinct levels of spatial representations. Second, contrary to other models, it emphasizes the possibility that spatial information can be encoded in multiple formats (e.g., topological and metric), rather than a single one (e.g., McNaughton et al.'s, 1989, sensory-motor associative matrix or O'Keefe & Nadel's, 1978, Euclidean map). At this point it is interesting to focus on these two models.

The model proposed by McNaughton et al. (1989) holds that an animal's spatial representation can be seen as an associative matrix constructed so that an animal's spatial choices are based on the selection of the motor response triggered by the current local view of the environment and a stored local view of the desired goal. Such a matrix of associations between local views and motor responses would be created as a result of an animal's previous experience within the problem space. In previous sections, I have suggested that this model has two drawbacks. First, the behavioral flexibility it affords is limited (novel solutions are unlikely to occur rapidly) and is certainly less than what is revealed by behavioral observation (see the Brief Review of Spatial Cognitive Maps section). Second, it emphasizes local views as the psychological units on which spatial decisions are based. Although local views may be essential ingredients of spatial representations, available evidence suggests that animals do form place representations that have the property of being relatively independent of sensory data. Furthermore, the neural properties of place cells fail to provide strong support for directional selectivity of firing (Electrophysiological Data section).

The model posited by O'Keefe and Nadel (1978), recently updated by O'Keefe (1991) on computational grounds, assumes that animals build a metric representation of their environment. This assumption, of course, removes any difficulty in terms of the computation of new trajectories and therefore provides the animal with a more flexible system than McNaughton's model. One problem, however, is that a metric representation cannot account for errors in spatial computation. With respect to this point, it is interesting to note that, even in humans, such errors are often suggested to result from a failure of the spatial representational system to be guided only by metric rules. Another problem is that, as such metric computations and representations are assumed to take place in the hippocampal formation, the model does not make serious assumptions about the contribution of other brain regions. In particular, the posterior parietal cortex is not assigned any specific function in the map elaborated in the hippocampus, whereas current literature clearly suggests a fundamental contribution both in animals (Hyvarinen, 1982; Kolb, 1990a) and in humans (Andersen, 1988).

In contrast, the present conceptualization emphasizes the existence of several levels of spatial knowledge. It is first assumed from this conceptualization that place representations are formed within the hippocampus. The hippocampus, through its role in configural learning, also creates a topological map, which specifies the main properties of space in terms of connectivity. No spatial computations, except for the extraction of such topological information, would occur in the hippocampus. Rather, such computations would involve the posterior parietal cortex. Moreover, if it is assumed that metric encoding relies to a large extent on movement-related information, then such metric encoding could arise in the parietal cortex, because it collects both visuospatial information and information linked to movement parameters. Overall, the cooperative action of the hippocampus and parietal cortex would allow for flexible spatial behavior, although still not relying on the emergence of a Euclidean map.

The consequence of this cooperativity is that there is a partial redundancy in the type of information that is likely to reach the neural systems for planning spatial actions, that is, the frontal areas. I assume here that it is this redundancy that makes possible the sparing of some spatial capacities in spite of either hippocampal or parietal damage.

With respect to this point, the present conceptualization has some specific implications. One prediction is that, although the hippocampus is necessary for the buildup of a complete spatial representation because of its central role in the processing of place and topological information, its importance should decrease as a function of an organism's experience with the environment. There is already some evidence that animals with hippocampal damage are not impaired in retention of well-learned spatial information (see the Neural Mechanisms of Cognitive Maps section). Such evidence is consistent with the notion that the parietal cortex would be sufficient by itself to support the use of an accurate navigational strategy in well-trained animals, provided that place information has not changed as a result of a modification in the task requirements. Conversely, the parietal cortex would be essential both at acquisition and at retention of spatial information because it is located at the heart of a loop circuit connecting it with the hippocampus.

In previous sections, I reported evidence for a crucial role of the parietal cortex in these two stages of spatial learning. I also pointed out that a particular aspect of the parietal deficit in spatial navigation tasks is the apparent failure of damaged animals to use a nonmapping strategy such as that observed in animals with hippocampal damage. The latter observation could be taken to strengthen the hypothesis that hippocampal animals, although deprived of topological and place information, retain some ability to use metric information to navigate a certain distance from the wall of the pool and that this ability would be definitively disrupted by parietal damage, resulting in the adoption of a random strategy. When considered together, these data therefore provide some evidence in support of the general model of cooperative contribution of the parietal cortex and hippocampus in the processing of spatial information. However, direct comparisons of the deficits induced by each type of lesion is clearly required to determine with greater precision the respective contribution of either structure in the course of spatial learning and in retention of spatial information. For example, according to the present scenario, a corollary of the observation that animals with hippocampal lesions retain some ability to deal with metric information is that parietal lesions should not impair spatial behavior on the basis of topological information.

Finally, on a purely behavioral ground, one implication of the model is that locations close in space are more easily related to each other than are locations more distant in space, with the result that accuracy of spatial behavior should depend on the actual distance to be traveled. This property stems from the fact that the topological information handled by the hippocampal formation is dependent on the connections between hippocampal place cells and that the strength of the synaptic connections is itself a function of the physical proximity between places (Muller et al., 1991). One important consequence would be that the mechanisms for long-distance and short-distance orientation could be partially dissociated. More specifically, short-distance orientation would be easier and more accurate than long-distance orientation, by taking advantage of the topological information provided by the hippocampal formation.

Final Comments

Most of the interest in neural models of animal spatial cognition is based on the discovery, two decades ago, of a specific class of hippocampal cells whose firing is highly correlated with the actual position of the animal in space (O'Keefe & Dostrovsky, 1971). One assumption, which is logically derived from this finding, has been therefore that spatial behavior should rely, at least partly, on the activation of such cells. This assumption has led to another assumption, namely that the hippocampus, which contains these cells, is responsible for most of the computations required for adaptive spatial behavior to occur.

It has only recently been realized that, although place cells indeed are important for encoding spatial locations and for building up more complete spatial representations, spatial behavior clearly requires additional ingredients (e.g., for accessing relevant information about hidden places or for computing trajectories). Thus, cognitive mapping cannot be reduced to psychological processes presumed to be implemented by hippocampal place cells. In other words, the mere existence of a spatial representation does not ensure that intelligent spatial behavior will occur. Therefore, a comprehensive view of animal spatial cognition requires an understanding of both the type of internal representation used and the computations involved in the maintenance of the map and in the setting of trajectories. Accordingly, recent years have witnessed the separate development of neurobiological models of spatial representations and of psychological–behavioral accounts of such representations. Still more recently, some attempts to reconcile both aspects have been made (e.g., Leonard & McNaughton, 1990). However, the position taken here is that such attempts either failed to capture the essence of the cognitive map concept or did not prove sufficiently general to account for the increasing bulk of data from the literature. Accordingly, in the present article, which is based on a consideration of the logical steps involved in spatial learning, I proposed a hierarchical model of spatial representations. This model was then examined in the light of researchers' current understanding of how different neural systems could cooperate to implement spatial knowledge. I hope that some of these ideas will be confirmed by further theoretical and empirical work or that some of these ideas at least will be useful in solving the puzzling issue of animal spatial cognition.

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Received November 12, 1991
Revision received August 12, 1992
Accepted October 1, 1992 ■