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Unpacking the Cognitive Map: The Parallel Map Theory of Hippocampal Function

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In the parallel map theory, the hippocampus encodes space with 2 mapping systems. The *bearing map* is constructed primarily in the dentate gyrus from directional cues such as stimulus gradients. The *sketch map* is constructed within the hippocampus proper from positional cues. The *integrated map* emerges when data from the bearing and sketch maps are combined. Because the component maps work in parallel, the impairment of one can reveal residual learning by the other. Such parallel function may explain paradoxes of spatial learning, such as learning after partial hippocampal lesions, taxonomic and sex differences in spatial learning, and the function of hippocampal neurogenesis. By integrating evidence from physiology to phylogeny, the parallel map theory offers a unified explanation for hippocampal function.

The cognitive map theory articulated by John O'Keefe and Lynn Nadel in 1978 not only was the first unified theory of hippocampal function but also has been the most influential (Best & White, 1999). This theory postulated that the hippocampus creates a mental representation of allocentric space. This representation, the cognitive map, is more flexible than other mental representations of space and allows the navigator to create novel routes between familiar sites.

O'Keefe and Nadel's (1978) cognitive map theory was supported by a diversity of empirical results, such as the impairment of spatial navigation by hippocampal lesions (Jarrard, 1983; Morris, Hagan, & Rawlins, 1986). It was also supported by two remarkable discoveries. The first was the elucidation of the hippocampal place unit by O'Keefe (e.g., O'Keefe & Dostrovsky, 1971). O'Keefe found that activity of these hippocampal pyramidal cells was localized to specific locations in a test environment and that they retained their specificity even in the absence of visual input (O'Keefe & Conway, 1980). This provided concrete evidence for the role of the hippocampus in coding locations in space.

A second discovery was the demonstration of a hippocampal mechanism for rapid, long-lasting, synapse-specific associative learning. This is the process of long-term potentiation (LTP; Bliss & Lomo, 1973). LTP mediation by the *N*-methyl-D-aspartate (NMDA) receptor provided a physiological theory of the Hebbian synapse (Bliss & Collingridge, 1993). Evidence that spatial learning and hippocampal LTP are impaired by NMDA-receptor antagonists provided new support for the cognitive map theory (Morris et al., 1986).

Twenty years later, however, the cognitive map theory remains controversial. Although it laid the foundation for current theories of how the hippocampus encodes space (McNaughton et al., 1996; O'Keefe & Burgess, 1996; Redish, 1999), the present theories differ from one another, and no one model of spatial encoding has received universal acceptance. There are also critics of the cognitive map theory itself (Eichenbaum, Dudchenko, Wood, Shapiro, & Tanila, 1999). The disagreement about hippocampal function is fueled in part by different approaches to the question (e.g., nonhuman vs. human studies) and in part by paradoxical results. Results from the rodent literature include the recovery of place learning after hippocampal lesions (Whishaw, Cassel, & Jarrard, 1995), the tuning of hippocampal cells to nonspatial information (Wood, Dudchenko, & Eichenbaum, 1997), the ameliorative effects of maze pretraining on place learning in the presence of blocked synaptic plasticity (Bannerman, Good, Butcher, Ramsay, & Morris, 1995; Saucier & Cain, 1995), and other dissociations of synaptic plasticity and spatial learning (Abeliovich et al., 1993; Huang et al., 1995; Nosten-Bertrand et al., 1996; Richter-Levin, Thomas, Hunt, & Bliss, 1998).

Research guided by questions of hippocampal function in humans has focused on the hippocampus's role in universal cognitive processes, such as intermediate-term memory (Rawlins, 1985), declarative memory (Squire, 1992), contextual processing (Gluck & Myers, 2001), episodic memory (Burgess, Maguire, & O'Keefe, 2002; O'Keefe & Nadel, 1978; Squire & Zola-Morgan, 1991; Vargha-Khadem et al., 1997), or relational processing (Cohen & Eichenbaum, 1993; Eichenbaum et al., 1999). For example, Eichenbaum et al. proposed that the hippocampus's role in spatial

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learning is an application case of its function for a more general learning process, the learning of relations. Here, spatial representations do not constitute a map of space but instead contribute to the general principle of "linking events within episodes" (Eichenbaum et al., 1999, p. 216). As a consequence, this "memory space" (Eichenbaum et al., 1999, p. 218) codes spatial and nonspatial relations among events, processing spatial relations for navigation and serial relations for solving more abstract, nonspatial stimulus relations, such as those found in transitive inference (Dusek & Eichenbaum, 1997).

Spatial models of the hippocampus, in contrast, often take a bottom-up, computational approach to the question of how the rodent hippocampus maps space. These models have included new generation models from O'Keefe and Burgess (1996), the multiple chart theory of McNaughton et al. (1996; Samsonovich & McNaughton, 1997), and the multiframe theory of Redish and Touretsky (1997). For example, the Redish and Touretsky model on spatial navigation combines four different navigation systems (taxon, praxic, locale, and route) and five spatial representations (local view, head direction, path integrator, place code, and goal memory). The anatomical realization of the model is provided by the connections among the several brain structures assumed to mediate these representations (Redish, 1999). We cannot review all of the models in detail, and the interested reader is referred to the above citations for more information.

At present, no one theory, whether spatial or nonspatial, qualitative or quantitative, modeling human or nonhuman behavior, has gained universal acceptance. Instead, the different approaches appear to be developing in parallel (Best & White, 1999; Cohen & Eichenbaum, 1991; McNaughton, 1996; Nadel, O'Keefe, Shapiro, McNaughton, & Disterhoft, 1998). It is clear that the rodent hippocampus plays some critical role in spatial orientation and that this role is not fully understood. If neurobiology cannot be understood except in light of behavior (Shepherd, 1994) and, as Dobzhansky (1951) argued, biology cannot be understood except in light of evolution, then to understand the hippocampus, we must understand both its evolution and its role in spatial navigation. We begin with a reexamination of this behavior.

The Nature of Spatial Navigation

We start by defining spatial navigation and discussing what is commonly accepted as spatial information. We do this because there is much confusion over terms and it is important for us to specify exactly what we mean by a word such as *landmark*. We then outline a new theory of navigation based on the idea that the cognitive map is composed of parallel component maps. We then address the origins of the dual nature of navigation in vertebrates and the development of a more powerful representation of space, the cognitive map, in birds and mammals. Because we propose that different classes of maps are constructed by the mammalian hippocampus and that these maps rely on different cues, we are also required to introduce new terminology to define experimental conditions precisely in terms of such cues.

Navigation can be defined as purposive movement through absolute space. For absolute space, we ascribe to O'Keefe and Nadel's (1978) original definition:

> Absolute space embodies the notion of a framework or container within which material objects can be located but which is conceived as existing independently of particular objects or objects in general. Objects are located relative to the places of the framework and only indirectly, via this framework, to other objects. Movement of a body (including the observer) changes its position within the framework but does not alter the framework or the relationship of other objects to the framework. In contrast, relative space designates a set of relationships amongst objects or sensory inputs which in themselves are inherently nonspatial. Objects are located relative to other objects and relative space does not exist independent of the existence of objects. (p. 7)

Further, O'Keefe and Nadel distinguished between the mental representations of *psychological space* and its complement, *physical space*, defined as "any space attributed to the external world independent of the existence of minds" (pp. 6–7).

Thus, there is physical space, and there are mental maps of that space. A map can be defined in diverse ways; we ascribe to Neisser's (1976) broad definition: "not pictures in the head, but plans for obtaining information from potential environments" (p. 131). Hence, the defining characteristic of the class of mental representations known as a map is that it provides a navigator, moving in space, with an expectation of the sensory input given a certain movement in a certain direction at a certain speed or around a certain obstacle. With a cognitive map (i.e., a mental map of absolute space; O'Keefe & Nadel, 1978, p. 2), the navigator can place itself within the framework and navigate directly among objects.

This ability is also known as *place learning*. This differs from orientation in relative space, such as egocentric or orientation to a simple cue. In an experimental setting, an animal is said to demonstrate place learning when it automatically creates a new route to the goal, and this new route is constructed from new egocentric relations to objects. Thus, a rat that can spontaneously chart a direct course in the water maze, regardless of its release position in the pool, is said to demonstrate place learning (Morris, 1984).

Sources of Spatial Information

As an animal explores, it uses internal and external cues to relate its current position to its start point in the environment. Internal cues such as *self-generated movement cues* inform the navigator how far and in which direction it has moved from a given position. External cues such as landmarks can be used in two different ways, both for direction and for position (Collett, Cartwright, & Smith, 1986; Leonard & McNaughton, 1990), as illustrated in Figure 1c and 1e.

Self-Generated Movement Cues

Locomotion generates a dynamic sensory flow in diverse modalities (proprioceptive, tactile, auditory, olfactory, and visual). The navigator integrates some or all of this information to update the current position relative to the start point. Path integration is the outcome of the process that regularly updates a directional vector. The vector is generated by the animal's movement during an exploratory bout and is based on this dynamic sensory flow and the efferent copy of the intended action. The path integration vector encodes the distance and direction from the start point of exploration, where the vector is apparently reset. Thus, path integration allows the navigator to beeline to its most recent start position at any time. It appears to be an ancient component of

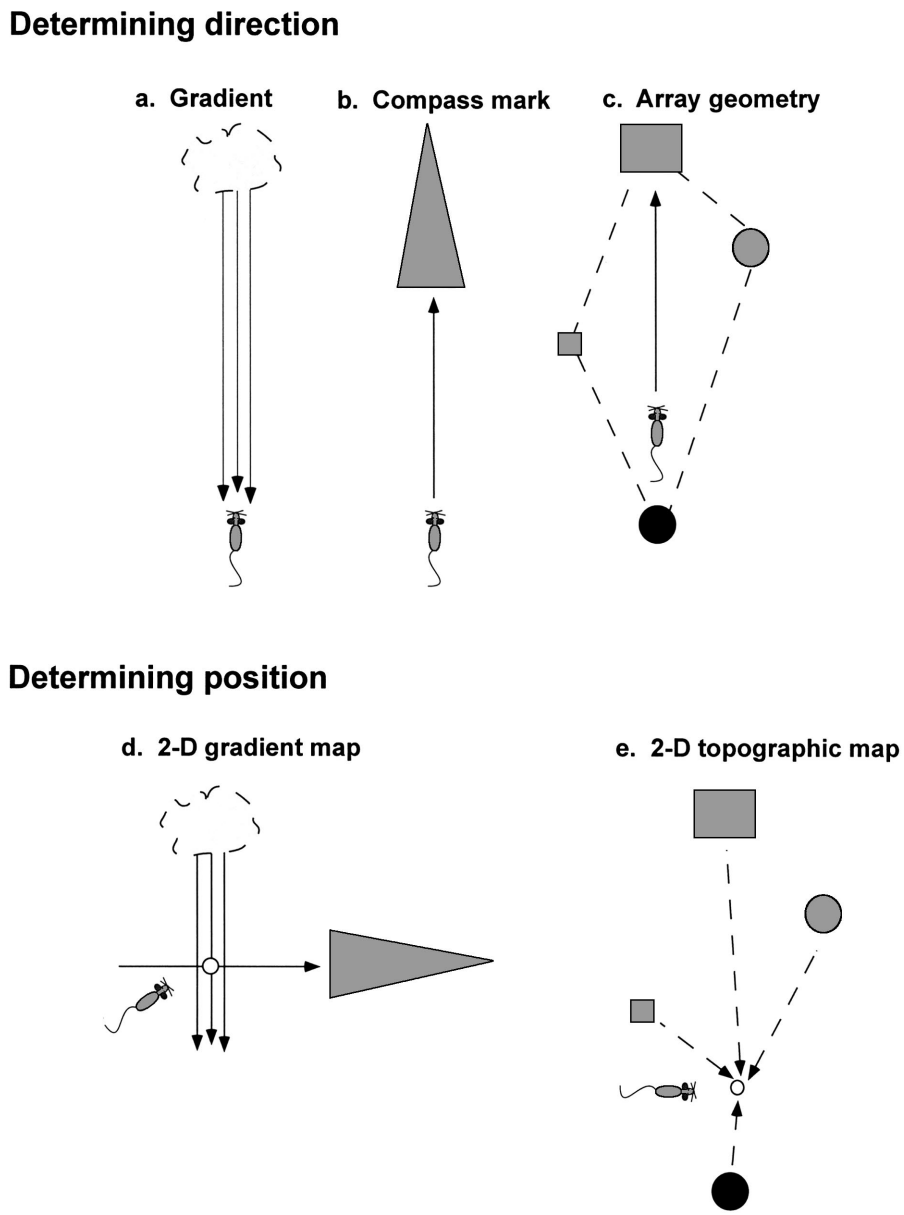

Figure 1. Determining direction and position with spatial cues. a: Gradient—A field of graded intensity. b: Compass mark—A distal landmark that can provide only directional information; it is too distant to provide positional information. c: Array geometry—Direction deduced from the polarization of an array of positional landmarks. d: Two-dimensional (2-D) gradient map—A 2-D map constructed from directional cues. e: 2-D topographic map—A 2-D map constructed from positional cues.

spatial orientation, as it is found throughout invertebrate and vertebrate taxa (Leonard & McNaughton, 1990; Maaswinkel & Whishaw, 1999; Wehner, Michel, & Antonsen, 1996).

We point out one caveat: Although we can define path integration, it is much less clear when and how it is combined with other spatial information. We suggest there is an important distinction between pure path integration and the reliance of the hippocampus on path integration. Perhaps path integration itself (a single, one-dimensional gradient produced from vestibular and external sensory feedback) is simply a vector that is exported to the hippocampus, which then assigns meaning to this vector. In this case, path integration would not be a property of the hippocampus but a process whose output is used by the hippocampus in constructing one-dimensional (1-D) and two-dimensional (2-D) maps. The vector obtained from path integration could be a primitive working memory representation, one that is reset at the start of every exploratory bout. It might then acquire more dimensions when it is associated with external points, such as an identifiable start position. This association of the working memory vector with external landmarks would lead to a richer representation of space, one that

cannot be computed without the path integration process. The properties of such a representation would exceed those provided by pure path integration.

Directional Cues: Gradients and Directional Landmarks

In general, directional cues polarize the navigator's environment rather than identifying a specific position in space (see Figure 1a–1c). An example of a visual directional cue is a compass mark, such as a mountain range: It is a landmark that is too distant to provide accurate positional information but can nonetheless provide an accurate direction (Leonard & McNaughton, 1990). Gradients of distributed cues (e.g., odor, sound, polarized light, magnetic fields) emanating from a source are also directional cues. A directional cue may be static or dynamic. When the navigator is not moving, a directional cue provides static directional information when its size and aspect do not change. It is also static when the cue is too distant for the size or aspect to change with the navigator's movement.

Directional cues can be provided by the geometrical shape of the contiguous visual space or panorama (e.g., experimental room, cage, or forest clearing) or by the arrangement of salient objects (see Benhamou & Poucet, 1998). Asymmetrically shaped spaces provide directional information. In contrast, symmetrical or regular shapes (e.g., square, rectangle, equilateral triangle) can be spatially ambiguous (Benhamou & Poucet, 1998; Cheng, 1986). These details of the cue environment have important implications for the encoding of space in our theory of parallel maps.

Positional Landmarks

In contrast to directional landmarks, a *positional landmark* is a local object that can be used to deduce position from the relative distances and positions of objects within an array (see Figure 1e). Here, movement of the navigator causes the cue's appearance to change quickly, allowing the navigator to deduce the distance between landmarks (or between a landmark and the navigator). In contrast, a directional cue generally does not change with small movements of the navigator. For example, a pigeon walking on the ground might perceive a tree at a 100-m distance as a directional landmark but treat it as a positional landmark if the pigeon is flying 100 m above the same tree.

Positional landmarks in an array can be processed separately, as unique objects. In an array composed of multiple positional cues, however, each cue has a spatial relation to at least one other cue. This relationship forms the basis of relational coding. When different objects form a symmetrical geometrical figure, the figure is identifiable even if the identity of each component object is not learned (Benhamou & Poucet, 1998). This creates ambiguity among symmetrical positions in a configuration, even when each corner is uniquely identified by local cues (Cheng, 1986; Cheng & Gallistel, 1984).

In contrast, rodents pay attention and learn the identity of a single directional cue if it is part of a symmetrically shaped array and if an additional directional cue is placed on the periphery of the arena (for studies of rats, see Poucet, 1989; for studies of hamsters, see Poucet, Chapuis, Durup, & Thinus-Blanc, 1986). Thus, it appears that objects can either provide directional information as a part of a geometrical figure or be recognized as unique objects, but not both. Hence, the information that is extracted from a landmark depends critically on the observer and the context and implies that direction and position are processed individually, according to context. This interpretation has important consequences for the analysis of place units, as we discuss later.

Evolution of Spatial Orientation Mechanisms

"Just as the human body represents a whole museum of organs, each with a long evolutionary history, so we should expect to find that the mind is organized in a similar way. It can no more be a product without history than is the body in which it exists" (C. Jung, 1964, p. 67). We begin with a discussion of the evolution of spatial navigation.

The environment in which the hippocampus evolved was not that experienced by terrestrial mammals. The vertebrate forebrain evolved underwater, with limited capacity for visual or auditory processing (Northcutt, 1996). The sensory modalities that were well developed depended instead on distributed fields and gradients of stimuli, such as chemical, light, or magnetic gradients (Northcutt, 1996). Such gradients are used for orientation by all mobile animals, even unicellular species (Dusenbery, 1992; Schöne, 1984). In a sensory world composed of such gradients, location is defined not by discrete landmarks but by changes in the amplitude or sign of a sensory input (i.e., the input becomes larger, brighter, louder, etc; see Figure 1a–1b). Of these, characteristics of the earth's geomagnetic field (polarity, inclination, intensity) are perhaps most universally exploited, and orientation to magnetic fields is found in insects (Collett & Baron, 1994; Frier, Edwards, Smith, Neale, & Collett, 1996), fish (Walker et al., 1997), amphibians (Phillips & Borland, 1994), reptiles (Light, Salmon, & Lohmann, 1993; Lohmann & Johnsen, 2000; Lohmann & Lohmann, 1996a), birds (Wiltschko & Wiltschko, 1996), and rodents (Kimchi & Terkel, 2001; Olcese, 1990). Magnetic fields have also been shown to influence spatial learning ability in rodents (Kavaliers, Eckel, & Ossenkopp, 1993; Kavaliers et al., 1996; Levine & Bluni, 1994).

Using Gradients

Orienting to simple gradient maps, such as to a magnetic field, has both advantages and disadvantages. The animal must move up and down the gradient to construct its crude representation of space with repeated sampling and by knowing its rate of movement. The animal must precisely calibrate changes in the single perceptual dimension (i.e., the polarity of sensory input, whether increasing or decreasing) to its own rate of movement (Schöne, 1984). Once an animal can do this, it can predict the sensory input that it will experience at a future location. Thus, as it travels up or down this gradient, it creates a 1-D map, as the term was used by Neisser (1976; see Figure 1a). With careful and discrete sampling of the gradient (e.g., sniffs) and precise knowledge of its own movements, an animal can extrapolate a vector through unexplored territory and continue to navigate accurately on the basis of this simple 1-D map. An animal can also use this gradient map to calculate distance from its knowledge of time spent traveling.

The abstract nature of the gradient map, which allows animals to navigate accurately through unknown terrain, also has its disadvantages. If the gradient is unevenly distributed or the animal loses

track of its rate of sampling or its rate of movement, the map is no longer reliable, and there is little opportunity for self-correction. The value and reliability of a simple 1-D map can be enhanced, however, when it is combined with other 1-D maps, the intersection of which yields a Cartesian coordinate (i.e., 2-D) map (see Figure 1d). Once this 2-D map has been created, it can be used to predict the length and orientation of a vector through untraveled space.

Evidence for Gradient Maps

The hypothesis that vertebrates create 2-D maps from distributed stimuli has generated much discussion but few rigorous tests (Wallraff, 1996). There is indirect support for this hypothesis, however, from studies on orientation to plumes of olfactory cues by homing pigeons (Papi, 1992) and magnetic field orientation in sea turtles (Lohmann & Lohmann, 1996b).

Green sea turtles (*Chelonia mydas*) migrate as adults to their place of hatching, Ascension Island in the southern Atlantic Ocean, a site thousands of kilometers from the location to which they initially dispersed. They navigate through the southern Atlantic Ocean using traditional paths, even on their first return to the island after many years (Luschi, Hays, Del Seppia, Marsh, & Papi, 1998). Therefore, on the basis of little experience and in the absence of obvious landmarks, the turtles solve an oceanic water maze, returning to a tiny island in the middle of the southern Atlantic. A population genetic analysis of Ascension Island turtles has shown that their genotype is unique to this island. Because no turtle of a different genotype has ever been found on the island, this suggests that the population has been genetically isolated, perhaps by the unique navigational algorithm they use to return to the island (Lohmann, Hester, & Lohmann, 1999). Such genetic programming of long-distance orientation has also been demonstrated in migrating birds (Helbig, Berthold, & Wiltschko, 1989; Wiltschko & Wiltschko, 1996).

Lohmann et al. (1999) and others (e.g., Akesson, 1996) have suggested that the mystery of this precise orientation lies in the turtles' ability to decode the geomagnetic map in this locale. The angle of inclination of the earth's magnetic field and the geomagnetic field strength are close to orthogonal in the south Atlantic. Ascension Island's location can therefore be specified with some precision by the intersection of these magnetic gradients (Lohmann et al., 1999). In the laboratory, loggerhead sea turtles can deduce direction both from magnetic inclination and from field strength (Lohmann & Lohmann, 1996a). Hence, it is feasible that wild turtles can read location from the bicoordinate grid formed by this intersection (Lohmann et al., 1999). As in other cases of extraordinary migration, such abilities have probably evolved slowly, as animals adapt their movements to slowly shifting patterns of resource distribution (Alerstam, 1990).

Despite the widespread use of orientation to distributed stimuli in animals (Dusenbery, 1992), this class of stimuli has been absent from previous models of spatial navigation in mammals and from models of hippocampal function. To anticipate our later argument, we note that the hippocampus's ability to create vectors from distributed stimuli is at the heart of its ability to encode the cognitive map. Our proposition that the cognitive map is based on such directional, 1-D maps forms the basis of our theory. Only by encoding gradients can the hippocampus create the mental representation of a novel short cut between locales that have not been previously connected in the animal's spatial experience. We begin by discussing hippocampal function among vertebrates.

The Evolution of the Hippocampus

The hippocampal formation (HPF) is the mammalian homologue of the medial pallium, one of three regions (dorsal, medial, and lateral) of the vertebrate telencephalon or pallium (Northcutt, 1995). The medial pallium is found in all jawed vertebrates and, hence, is a remarkably conserved structure (Bruce & Neary, 1995). The homology of structures derived from the medial pallium in birds, mammals, and reptiles has been established by converging lines of evidence, including patterns of embryology, connectivity, histochemical boundaries, and homeotic gene expression (Fernandez, Pieau, Reperant, Boncinelli, & Wassef, 1998; Medina & Reiner, 2000). Although a medial pallium homologue can also be defined in fish and amphibians (Butler & Hodos, 1996), there are no studies of its functional or behavioral significance in these groups. Thus, at present, we can discuss medial pallium function only in those taxa for which studies of spatial learning exist: reptiles, birds, and mammals. Our goal here is to present a brief synthesis of the vertebrate literature, tempering our conclusions with the knowledge that much research remains to be done.

Cognitive traits leave few fossils. The accepted method of elucidating the function of an ancestor is to compare function and structure across extant taxa. If contemporary groups share a common trait, one can parsimoniously conclude that the similarity arises from common descent. Hence, the shared trait may be ancestral and may have been present in the common ancestor (Harvey & Pagel, 1991). The common ancestor of birds and mammals, for example, existed over 200 million years ago (Romer, 1977). It is possible that the similarities seen in extant species are thus homologies of structure and function.

Despite other differences in telencephalon structure, in both birds and mammals the relative size of the hippocampus is predicted by the spatial behavior of the species under natural conditions. For example, in both songbirds and rodents, the fitness of individuals of certain classes (e.g., females vs. males, scatter hoarding species vs. larder hoarding species) may depend more heavily on spatial memory or spatial exploration. These individuals have larger hippocampi, relative to the remaining telencephalon, than do individuals not subject to these selection pressures (Jacobs, Gaulin, Sherry, & Hoffman, 1990; Jacobs & Spencer, 1994; Sherry, Forbes, Khurgel, & Ivy, 1993; Sherry, Jacobs, & Gaulin, 1992; Sherry, Vaccarino, Buckenham, & Herz, 1989). Lesions of the hippocampus in birds and mammals also produce similar deficits in locating a place in an array of distal cues (Bingman, 1990; Bingman, Bagnoli, Ioalé, & Casini, 1989; Morris et al., 1986; Sherry & Vaccarino, 1989; Strasser & Bingman, 1997). Thus, the function and physiology of the medial pallium homologue appear to be similar in birds and mammals.

At first glance, the function of the medial pallium homologue, the medial cortex, in reptiles appears to parallel that seen in birds and mammals. The relative volume of the medial cortex, for example, is larger in a lizard species that forages actively for prey compared with a species that waits for prey to arrive (Day, Crews, & Wilczynski, 1999). As we discuss below, a more recent behav-

ioral study by Day, Crews, and Wilczynski (2001) paints a slightly different picture of the role of the medial cortex.

Homology of Structure

The evidence for homologies at the level of hippocampal subfields—that is, the dentate gyrus (DG) or the hippocampus proper (HP)—is somewhat speculative at this point. Comparative studies of medial cortex structure in reptiles suggest that the small-celled area of the ventral medial cortex is homologous to the DG, the ventral-most region of the mammalian hippocampus (Hoogland, Martinez-Garcia, Geneser, & Vermeulen-Vanderzee, 1998). Likewise, the reptilian dorsomedial cortex may be homologous to the entorhinal cortex (EC) and the subiculum (Hoogland & Vermeulen-VanderZee, 1990; Martinez-Garcia & Olucha, 1990). Subfield homologies are less clear in birds. Szekely (1999) has concluded, on the basis of a comparison of intra-and extrahippocampal projections between birds and mammals, that the HP homologue in birds is ventral to the DG homologue. Because this dorsal–ventral orientation is the opposite of that seen in mammals and reptiles, we suspect the final definition of subfield homologies in vertebrates awaits further research, preferably informed by patterns of embryology (Striedter, 1997) and gene expression (Fernandez et al., 1998; Medina & Reiner, 2000).

Because the phylogenetic history of birds, reptiles, and mammals separated hundreds of million of years ago, one could speculate that the spatial function of the medial pallium predated the separation of these lineages and, hence, can be back dated at least this far. This does not mean that all hippocampal function is homologous in birds and mammals. Because cognitive mapping ability requires association structures (e.g., mammalian neocortex) and these areas are not homologous in birds and mammals, the ability to construct a cognitive map must be the result of convergent evolution in these groups. What may be homologous among birds, mammals, and reptiles is, instead, the role of the medial pallium in allocentric orientation to distributed stimuli. The similarities among these taxa thus would have arisen from this ancestral trait, even if the expression of this trait has diverged widely among vertebrates with the further evolution and specialization of the forebrain. It is possible that all the similarities are the result of convergent evolution, although this is not the most parsimonious explanation in light of the evidence for homology of structure. This question can only be resolved with further comparative studies of medial pallium structure and function.

Homology of Function: Spatial Learning in Reptiles

Despite patterns of medial pallium allometry (i.e., size relative to telencephalon) that are similar to those seen in birds and mammals, new studies by Day et al. (1999) suggest that reptiles may not use visual cues for spatial orientation in the same way as do birds and mammals. Reptiles, of course, represent a diverse group that includes the order of turtles and the suborders of snakes and lizards (Romer, 1977). There have been few studies of spatial orientation in reptiles. Three studies published recently represent almost the entire body of work on the use of cues during spatial navigation in reptiles (Day et al., 2001; Holtzman, Harris, Aranguren, & Bostock, 1999; Lopez et al., 2000). It is unfortunate that these new studies were each conducted by a different laboratory, using a different task and studying a different reptile group (snake, turtle, and lizard). On the other hand, the studies do have an important feature in common, as each task measured reference memory for a single location.

In the first study, by Holtzman et al. (1999), corn snakes (*Elaphe guttata guttata*) searched for an escape hole among a ring of nonescape holes in a reptilian version of the Barnes (1979) maze, a hippocampal task in rodents. The circular arena was surrounded by a high wall, and the only landmark was a single, conspicuous cue card; the pathway of the snake from a central release point was used as evidence that it had learned the correct location for escape. The snakes did orient more quickly to the escape hole over repeated trials. Although this was interpreted as true place learning (Holtzman, 1998; Holtzman et al., 1999), in the published search paths, all initial orientations of the snakes were first directed toward the single cue card. Thus, the snakes' performance could also be ascribed to an egocentric encoding of a cue location rather than to true allocentric place learning.

Day et al.'s (2001) study of two species of lacertid lizard (*Acanthodactylus boskianus*, *Acanthodactylus scutellatus*) also failed to find evidence for orientation to a landmark array. In this study, the goal was a single heated rock in a ring of seven unheated rocks. Although lizards decreased their latency to the goal, their movements were not affected by any landmark rotation or removal, as assayed by probe tests with eight cold rocks. Medial cortex lesions did not alter the lizards' nonresponse to landmarks, as might be expected. Thus, lizards did not orient in the same way as birds and rodents given similar experimental conditions (Suzuki, Augerinos, & Black, 1980; Vander Wall, 1982).

In contrast to the snake and lizard studies, allocentric place learning was recently demonstrated in turtles (*Pseudemys scripta*). In this study, the goal was a food bait in one arm of a water-filled plus maze (Lopez et al., 2000). Experimental groups learned to associate either a cue or a place with the bait. Probe trials were conducted in which part or all of the maze was curtained, blocking distal cues. When distal landmarks (e.g., lab furniture, distinctively colored room walls) were blocked by a curtain, only turtles in the place group showed a decline in performance.

The negative findings from the lizard study contrast sharply with the positive findings from the turtle study, which the authors rightly described as the first demonstration of unequivocal place learning in reptiles. Rather than concluding that this ability is special to turtles, however, we suggest an alternative explanation that also explains the results from the other groups. We propose that in all studies, reptiles oriented primarily to directional, not positional, cues, whether visual or nonvisual. In the snake study, the evidence is their initial orientation to the single cue card. In the lizard study, the authors concluded that the lizards were learning to orient to a goal but that the experiment did not control the cues the lizards were using (Day et al., 2001). We suggest that the lizards could have been orienting to directional cues, such as magnetic fields or gradients of auditory or light cues, as these types of stimuli are used by reptiles.

Results from the turtles orienting on a plus maze are also consistent with this hypothesis. There are two ways to solve a plus maze: choose the correct arm, as defined by an array of positional landmarks (see Figure 1e), or choose the correct direction, as defined by directional landmarks (see Figure 1a–1c). Thus, accurate performance on a plus maze could be the result of orientation

to a directional cue or to an array of positional landmarks. In this study, the walls of the experimental room differed in color, and these distinctively colored walls could have functioned as coarse directional landmarks. Turtles could thus have oriented using this directional information and accurately chosen the correct arm, with no knowledge of place (a correct choice was scored as entry into the arm). As we discuss later, this interpretation may also explain the residual spatial learning seen after genetic lesions of the hippocampus in mice when orienting in a water-filled plus maze (Silva, Paylor, Wehner, & Tonegawa, 1992).

Role of the Septum

In all jawed vertebrates, the medial pallium receives significant input from the septum (Butler & Hodos, 1996; Swanson & Risold, 2000). Because of extensive homologies between the septum in mammals and in reptiles (Font, Lanuza, Martinez-Marcos, Hoogland, & Martinez-Garcia, 1998), theories of the behavioral function of the septohippocampal connections in mammals may be relevant to spatial navigation in reptiles. In particular, Numan's (2000) theory of septal function dissociates the contributions of the septohippocampal system from that of the corticohippocampal system in spatial navigation. He concluded from physiological and behavioral evidence that "it is possible that the hippocampus and its connections with surrounding cortical areas encode the relations between external stimuli, and that the hippocampus and its relations with the septum encode and maintain the self-motion cues" (Numan, 2000, p. 316) We suggest that the septohippocampal system, which is highly developed in reptiles (Hoogland & Vermeulen-Vanderzee, 1990), plays a critical role in their spatial navigation. Like a mammal with lesions in the corticohippocampal system, intact reptiles may rely heavily on egocentric orientation to cues, orienting primarily to directional cues such as gradients and visual beacons but not encoding the relationship among external stimuli.

In conclusion, we suggest that studies of spatial orientation in reptiles are consistent with the hypothesis that reptiles orient to directional cues but not to landmark arrays. Striedter (1997) has shown that the medial cortex in adult reptiles is structurally similar to the hippocampus of mammals or birds at an earlier embryological stage. This is interesting in light of the striking similarity in behavior between juvenile rodents and adult reptiles. Both show a dependence on directional cues (Schenk, Grobety, Lavenex, & Lipp, 1995), and this may reflect a rough equivalence of hippocampal development. More research is needed to test this hypothesis of the role of the medial cortex in directional cue-based orientation in reptiles. If confirmed, studies of medial cortex function would support our hypothesis for the ancestral gradient-encoding function of the medial pallium.

The Parallel Map Theory

The term *cognitive map* was first introduced by E. C. Tolman (1948) to describe what he saw as mental representations in the rodent, and it is a term he coined for his bold reply to the tenets of strict behaviorism. The cognitive map is currently understood as the mental representation that conveys the ability to compute shortcuts through untraveled terrain (Gallistel, 1990; O'Keefe & Nadel, 1978). To date, cognitive maps have been found only in groups that have evolved significant associational structures (i.e., birds and mammals) but not in reptiles (as reviewed above) or insects (Dyer, 1994). Within mammals, hippocampal organization increases in complexity in groups with greater development of the neocortex (Schwerdtfeger, 1984; West, 1990; West & Schwerdtfeger, 1985).

The concept of the cognitive map is usually assumed to be a unitary mental representation. We propose instead that the cognitive map is constructed from two parallel maps that, when integrated, allow the navigator to calculate cognitive map shortcuts. These parallel maps differ in how they represent space, what cues are used to represent space, and what hippocampal structures are involved in creating the representation (see Table 1). We call this new formulation of the cognitive map the parallel map theory (PMT) of spatial navigation.

The Maps

The first parallel map is the *bearing map.* It is constructed from the integration of self-movement cues and directional cues. These cues are used to form a mental representation of a 1-D vector. The bearing map is created from the intersection of vectors, which forms a 2-D coordinate system (see Figure 2a). Because the bearing map can be based entirely on gradients, the navigator can use a simple movement algorithm to accurately navigate over long

Table 1
The Parallel Components of the Integrated Map

Parallel component	Hippocampal structure (must be intact)	Environmental stimuli (must be present)
Bearing map	Subcortical channel	Directional cues
	Dentate gyrus	Compass mark, or
	CA3	Gradient of distributed cues, or
	Medial septum	Asymmetric room or arena, or
	Fimbria fornix	Polarized landmark array
Sketch map	Cortical channel	Positional cues
	CA1	Array of perceptually unique local landmarks
	NMDA receptor in CA1	
Integrated map	Both channels intact	Both directional and positional cues available
	Subiculum	

Note. CA = subfields of the hippocampus proper; NMDA = *N*-methyl-D-aspartate.

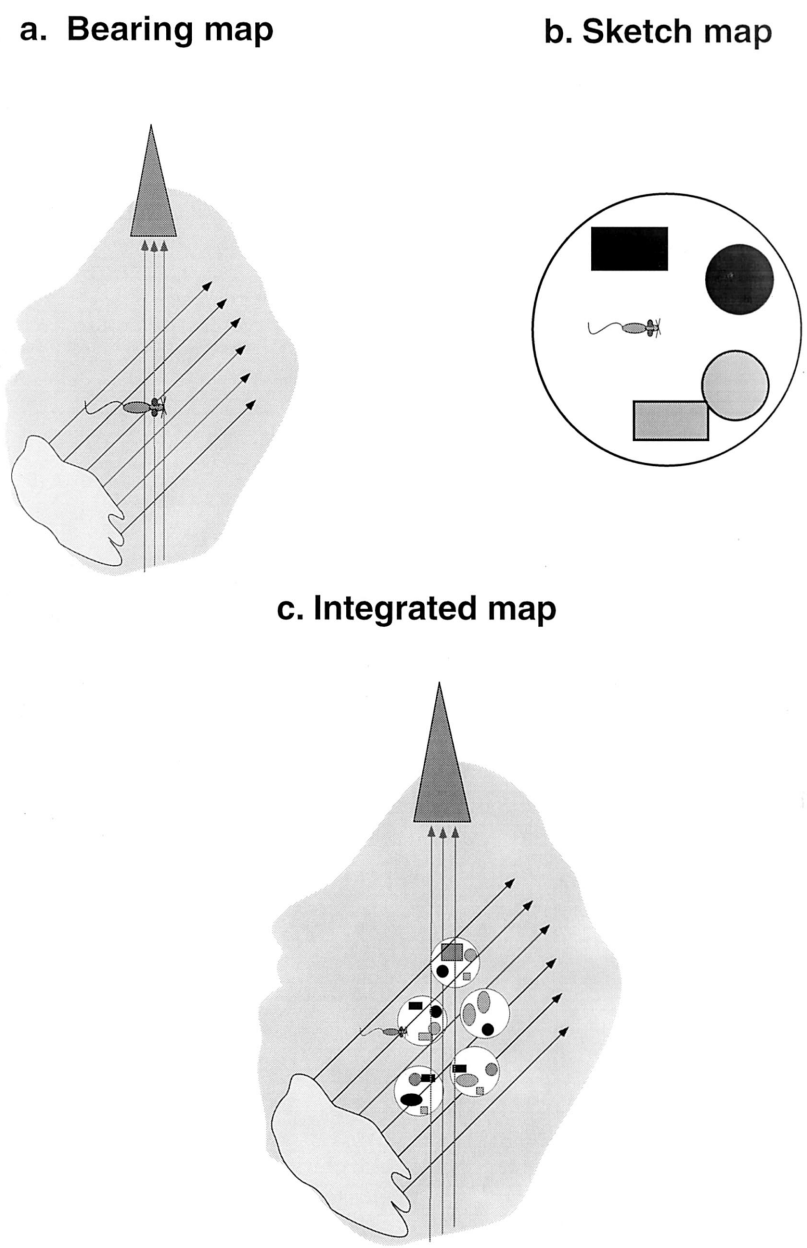

Figure 2. A schematic of the parallel map theory. a: Bearing map—This map is constructed from directional cues such as compass marks and gradients. Here, the bearing map is formed from the transection of two gradient maps: a chemical gradient based on odorant concentration and a visual gradient based on a distant compass mark. Arrows indicate the axis of the gradient map. The solid triangle represents a visual beacon, the smaller shaded cloud in the lower left represents a source of odorant, and the larger shaded cloud represents allocentric space that is mapped by the bearing map. b: Sketch map—This topographic map is constructed from the relative position of fixed positional landmarks. Solid and patterned shapes represent unique positional landmarks. c: Integrated map—This map is constructed from the integrated bearing and sketch map. By linking all sketch maps onto the single bearing map, the rat can compute novel routes among them. The solid triangle represents a directional landmark such as a visual beacon, the smaller shaded cloud in the lower left represents a directional cue such as an odor source, solid and patterned shapes represent positional landmarks, and the larger shaded cloud represents the boundaries of the integrated map.

distances. The navigator must only calibrate self-motion cues with changes in the intensity of a distributed cue to extrapolate its future position in the coordinate system. Thus, the bearing map allows the navigator to maintain an accurate representation of its position, even in unknown territory. Starting with a primitive gradient algorithm, the bearing map creates a coarse-grained mental representation of space that nonetheless provides a powerful tool for spatial navigation, particularly long-distance navigation.

The second parallel map is the *sketch map*. It is constructed from an arrangement of positional cues. These unique local landmarks are encoded relative to each other as a topographic map (see Figure 2b). The sketch map differs in fundamental ways from the bearing map. First, all landmarks in the map must be individually learned, and thus, there can no extrapolation or generalization across novel terrain, as in the bearing map. The relations (distance, direction) among landmarks must also be learned. The sketch map is thus a fine-grained mental representation that is best suited for local navigation. The positional codes within sketch maps are allocentric, as each cue refers to another component of the sketch map.

PMT can be described at several levels of analysis. What we have just described is the first level, the conceptual account of two maps. In this account, one map is based on directional cues, some of which may be extrapolated, and the other is based on a set of memorized positional cues. The concept of the bearing map has no real predecessors in theoretical models of spatial navigation in mammals, including previous formulations of the cognitive map. In contrast, the second, topographic sketch map has much in common with previous cognitive map theories, as we describe below. PMT thus describes two new concepts, the bearing map and the idea that the cognitive or *integrated map* is composed of parallel maps (see Figure 2c). We use the term *integrated map* instead of *cognitive map* because the original term was never precisely defined by Tolman in 1948, which has led to different usages in different disciplines (see review by Bennett, 1996).

Anatomy of the Parallel Maps

A second level of analysis is the physical scaffold underlying the three mental representations (bearing map, sketch map, and integrated map). Despite recent progress (Amaral & Witter, 1995; Deadwyler & Hampson, 1999; Witter, Wouterlood, Naber, & van Haeften, 2000), the full complexity of hippocampal anatomy has yet to be mapped onto a complete theory of its function. What Swanson, Köhler, and Björklund said in 1987 remains true:

> It appears safe to say that nowhere is the gap between structure and function greater than in this region [hippocampus]. The major reason for this is that while the hippocampal formation contains the simplest cortical fields from an anatomical point of view, it receives, processes, and transmits the most complex array of information of any cortical region. (p. 126)

Keeping this in mind, we present a working model of the hippocampal structures underlying the encoding and use of the parallel map system (see Figure 3). We propose that the maps are mediated by different neural structures: The bearing map is mediated by subcortical hippocampal channels projecting to the DG and the CA3 subfield of the HP, the sketch map is mediated by the CA1 subfield and its cortical connections, and the integrated map is mediated by the synchronization of activity between these two channels. The anatomical basis of the parallel maps is shown schematically in Figure 3.

The assignment of map to structure is an important feature of PMT, as is its emphasis on separate functions of the DG and the HP, which create parallel and independent maps. Although the hippocampal subfield functions have received some attention, having been modeled (e.g., Deadwyler & Hampson, 1999; Granger, Wiebe, Taketani, & Lynch, 1996) and empirically disassociated (Gilbert, Kesner, & Lee, 2001; McNaughton, Barnes, Meltzer, & Sutherland, 1989; Mizumori, McNaughton, Barnes, & Fox, 1989), these studies have proposed complementary functions rather than parallel ones. We are taking this line of reasoning in a new direction, first by proposing that DG and CA1 mediate parallel maps, and second by adding the concept of the gradient map. PMT, based on parallel maps and representations of gradients, thus leads to a set of unique predictions (see Tables 2 and 3).

In summary, the integrated map relies on the presence of two parallel map processes. It emerges from the simultaneous activation of the parallel bearing and sketch maps and, hence, from the synchronization of physiological activity between the DG and the HP. When both maps are active and accessible, the navigator can create the integrated map by double labeling positional cues within and between sketch maps, as outlined in Table 4. The emergent properties of the integrated map supply an ability that neither map alone can accomplish: navigation among familiar locations that involves movement across unfamiliar terrain. With this, the navigator can extrapolate its movement beyond the knowledge of memorized landmarks. The strength of this system lies in its redundancy, a design feature found in spatial navigation throughout the animal kingdom (Keeton, 1974). Because the maps work in parallel, if one is impaired then the navigator may continue to orient accurately, using the residual ability afforded by the remaining map. It cannot, of course, use the integrated map, but it may retain a considerable ability to navigate, as is apparent from the literature on partial lesions of the hippocampus. Because the integrated map is an emergent property of the coactivation of the bearing and sketch maps, all three maps can be isolated with a variety of techniques (e.g., cue manipulation, lesion, unit activity), allowing each element of the theory to be tested (see Tables 2 and 3).

The final level of analysis for PMT lies beyond experimental tests of its predictions, however, and that challenge is to map concept to structure with computational models. PMT narrows the search for such a model by mapping specific functions to different subfields, and now feasible and realistic computational models of the parallel maps need to be developed from knowledge of the anatomy and topography of the HPF (Amaral & Witter, 1995; Witter et al., 2000). We are currently working with collaborators to develop a model of a hippocampal parallel mapping process.

We now discuss each map in turn, describing its characteristics and its physiological properties and reviewing the evidence for the effect of its experimental dissociation on spatial navigation in the laboratory rodent.

Predictions From a Parallel Map System

Our theory proposes that spatial abilities depend not only on the integrity of two independent brain mapping systems but also on the

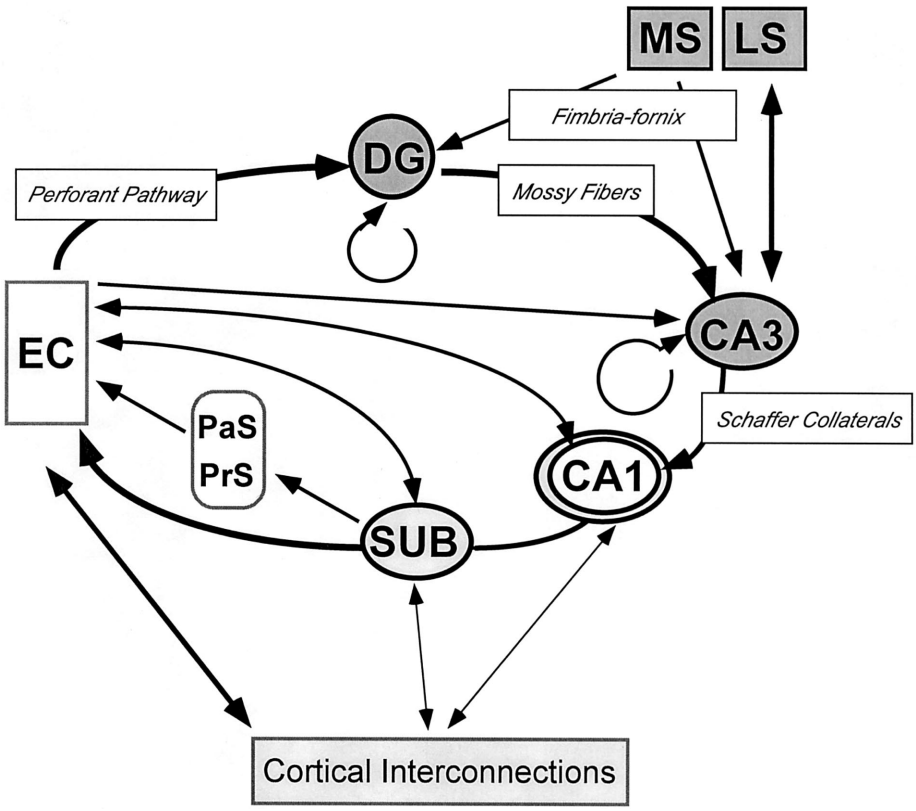

Figure 3. Major intrinsic connections of the hippocampal formation, adapted from Amaral and Witter (1995). The direction of connections leads to the stepwise assembly of the integrated map. Fiber tracts are shown in italics. A unidirectional connection is indicated with a single-headed arrow, and a reciprocal connection is indicated with a double-headed arrow. Circular fields represent the hippocampal structures. Rectangular fields represent extrahippocampal structures. Dark shading indicates a structure involved in the bearing map, no shading represents structures involved in the sketch map, and light shading represents a structure involved in the integrated map. MS = medial septum; LS = lateral septum; DG = dentate gyrus; EC = entorhinal cortex; CA1 and CA3 = fields of the hippocampus proper; PaS = parasubiculum; PrS = presubiculum; SUB = subiculum. From "Hippocampal Formation," by D. G. Amaral and M. P. Witter, in *The Rat Nervous System* (p. 449), 1995, San Diego, CA: Academic Press. Copyright 1995 by Academic Press. Adapted with permission.

type of information that is available in a given environment. This leads to several corollaries. If a class of orienting cues is missing, then the map that requires that class will be impaired. Alternatively, if one mapping system is more developed than the other, then the navigator's orientation will be biased toward using that system. If the anatomical structures underlying one map are lesioned or otherwise impaired, the corresponding map will be impaired. Impairment of one map should reveal residual spatial learning by the other map. Finally, cognitive mapping abilities (e.g., one-trial spatial learning in working memory tasks, new detour strategies in reference memory tasks) should be impaired following damage to any of the structural channels underlying these mapping systems. Hence, the resulting behavioral phenotype is the consequence of two factors: data coming in from the environment, and the capacity of the hippocampus to process different types of data (e.g., directional vs. positional cues).

The corollaries of PMT lead to testable predictions, according to the certain variables (see Tables 2 and 3). These are (a) cues available in the experimental room or *task environment*, defined below; (b) the state of development of different hippocampal structures; (c) the state of impairment, due to age, lesion, or pharmacological treatment; and (d) potential for synaptic plasticity (e.g., NMDA receptor availability).

Task Environment

We define *task environment* as the environmental stimuli that are available to the navigator at a given time to solve a particular task (see Table 1). This concept is critical in PMT because the bearing and the sketch maps use different types of cues. Thus, maps (and, hence, behavioral phenotypes) are controlled and dissociable by task environment. For example, a curtain surrounding an arena or maze eliminates visual directional landmarks and should selectively impair the bearing map. If positional landmarks are removed or rearranged, however, the sketch map is lost, altered, or impaired, and now the rat appears amnesiac for position. If one structural component of each map is impaired, the integrated

Table 2
Predictions of the Parallel Map Model When the Bearing Map Is Impaired (rS Phenotype)

Cause of reduced representation	Experimental conditions during water maze testing	Behavioral phenotype
Impaired DG, CA3, medial septum, or fimbria fornix	Open room: Local and directional cues present.	Unable to organize search from new release point. Swims in a disorganized pattern until it enters the correct quadrant, then searches locally, producing daisy loop pattern.
	Open room: Platform is visible or cued.	Rapid learning of direct path to platform; no impairment.
	Curtained maze: Local cues are available within curtain; no directional cues.	Intermediate performance, which is impaired if local cues are rearranged. With additional training, performance again reaches an intermediate level.

Note. rS = residual sketch; DG = dentate gyrus; CA = subfields of the hippocampus proper.

map becomes impaired, which eliminates cognitive mapping ability (see Tables 2 and 3).

Map Phenotype

By knowing the task environment (i.e., the input to the mapping system) and the locus of impairment (i.e., the residual mapping system), we can predict the behavioral phenotype of the navigator, or *map phenotype.* We define this as an animal's spatial strategy in a given experimental condition. A particular strategy may be intact or absent; if it is the remaining intact strategy, it will underlie any residual spatial learning observed (see Tables 2 and 3).

As discussed earlier, if directional cues are removed, even in an intact animal, the bearing map is impaired. The map phenotype for this navigator is then a *residual sketch map* (rS; see Table 2). As illustrated with the example of the Morris water maze task in Figure 4, the rS rodent should concentrate its search in the correct quadrant of the water maze but should not be able to organize straight trajectories toward the platform from any starting position. In contrast, removing positional landmarks impairs the sketch map and hence should result in the expression of the *residual bearing map* phenotype (rB; see Table 3). The rB rodent should search for the platform by moving along parallel transects but should express a reduced accuracy in locating the platform location (see Figure 4).

Sex Differences in Spatial Strategy: A Natural Dissociation of Bearing and Sketch Maps

Females and males of several polygamous species, such as humans (Kimura, 1999; Moffat, Hampson, & Hatzipantelis, 1998; Sandstrom, Kaufman, & Huettel, 1998; Sherry & Hampson, 1997), laboratory rats (Williams, Barnett, & Meck, 1990), and kangaroo rats (Langley, 1994), differ in spatial navigation strategy. They appear to use different sets of visual cues to orient. In laboratory rats, male performance on the radial arm maze is severely disrupted if the maze is curtained, even if positional landmarks are still visible. Female performance is only slightly impaired under this condition. In contrast, if the positional landmarks are removed or randomized, female performance is severely impaired, whereas this manipulation has less effect on male performance (Williams et al., 1990; Williams & Meck, 1991, 1993). As Williams and Meck (1993) have discussed, sex differences in spatial behavior are small in comparison with other sexually differentiated behaviors, such as reproductive behavior or learned bird song. The sex differences may also disappear if the task is well learned, and they are difficult to detect if the task is too simple (Williams & Meck, 1991). Experimental evidence for the sexual differentiation of the hippocampus and spatial strategy (Isgor & Sengelaub, 1998) continues to accumulate, however, lending strong support to the hypothesis that sex differences in spatial behavior are the result of hormonal mechanisms similar to those seen in behavior classically defined as reproductive.

Recouched in terms of PMT, females and males rely more heavily on different mapping systems, with males extracting their primary orientation information from the bearing map and females extracting this information from the sketch maps. In a typical laboratory test room, the bearing map is constructed from room geometry, distal cues, and stimulus gradients. The sketch map is based on unique positional landmarks. Therefore, even with the

Table 3
Predictions of the Parallel Map Model When the Sketch Map Is Impaired (rB Phenotype)

Cause of reduced representation	Experimental conditions during water maze testing	Behavioral phenotype
Impaired CA1 or blockade of NMDA receptors	Open room: Local and directional cues available.	Swimming is organized into long transects across pool, with little or no local searching. Latency decreases slowly with extended (more than 2 days) training. Latency increases if directional cues are manipulated.
	Open room: Platform is visible or cued.	Rapid learning of direct path to platform.
	Curtained maze: Nonvisual directional cues available.	Intermediate performance, which is impaired if directional cues are manipulated.

Note. rB = residual bearing; CA = subfields of the hippocampus proper; NMDA = *N*-methyl-D-aspartate.

Table 4
Steps in the Construction of the Integrated Map

Step and locus	Process	Representation
1. MS	Self-movement cues calibrated with theta rhythm as pacemaker. Derives rate of movement and location relative to prior point.	1-D algorithm, stored in working memory.
2. DG	1-D map calculated from medial septum input and sensory input from entorhinal cortex.	1-D map, stored in working memory.
	Autoassociative network within DG recalls 2-D bearing map and adds new 1-D map, creating a newly expanded 2-D bearing map through pattern completion. Transmits updated bearing map to CA3.	2-D bearing map, stored in reference memory.
3. CA3	Localizes current position on the 2-D map from DG by matching pattern with current EC input. Transmits position to subcortical structures through bilateral projection to lateral septal nuclei and to cortical structures through Schaffer collaterals to CA1.	Local aspect of the bearing map, stored in working memory.
4. CA1	Creates a minimap of the local panorama, computing within-sketch vectors on the basis of head direction input.	Sketch map, stored in working memory, and integrated map, also stored in working memory.
	Receives bearing map position from CA3; localizes current sketch map on bearing map. Transmits this part of the newly computed integrated map to subiculum.	Integrated map, an emergent map from the integration of bearing and sketch maps, stored in working memory.
5. Subiculum	Updates reference memory of integrated map with new information from CA1. Computes final position of this fragment on the integrated map. Transmits integrated map to associative cortices.	Current integrated map, stored in reference memory.

Note. This is a proposed account of how the parallel map theory could be assembled by components of the hippocampal formation. The schema must be considered speculative, as we cannot yet even incorporate the CA2 field. MS = medial septum; 1-D = one-dimensional; DG = dentate gyrus; CA = subfields of the hippocampus proper; 2-D = two-dimensional; EC = entorhinal cortex.

same task environment, females and males may differ in how they map the space: Females learn and remember the relations among unique positional landmarks, whereas males perceive positional landmarks as points in the shape of an array. Perhaps for this reason, reducing the ambient light after acquisition produces an immediate and severe impairment in female but not male orientation on the radial arm maze (Williams & Meck, 1993). Thus, even in the same environment, there are two ways to encode the space, with females and males showing a natural dissociation of these two strategies and of the parallel mapping systems.

This sex difference has certain implications for studies of spatial navigation in polygamous rats and mice. If a study uses all male subjects, because males rely more heavily on distal cues and room geometry, this could lead to a bias in defining spatial navigation in that paradigm as highly dependent on such directional cues. This might be particularly evident in studies in which cues are in conflict. In such studies, a male's use of cue hierarchy should show greater reliance on directional cues. For example, a recent study of cue use in male rats found a significant preference for directional over positional landmarks in orientation. The rats were also more likely to extract directional than positional information from the configuration of positional landmarks. They oriented first to the geometry of the landmarks and only then to the identity of the positional landmarks (Benhamou & Poucet, 1998). In this case, positional objects appear to serve as directional landmarks. In another study using all males, rats used the geometrical relationship of proximal landmarks to deduce direction (Greene & Cook, 1997). We do not question the validity of these results but only point out that it is possible that the same study repeated with females might find a different set of rules, such as orientation primarily to landmark identity and only secondarily to array geometry.

Dissociating Parallel Maps

We now turn the remaining discussion to experimental evidence in support of PMT. We first discuss the functional and structural characteristics of each map, its development and plasticity. We then discuss how task environments and specific lesions of hippocampal structures should result in predictable map phenotypes. Finally, we will discuss patterns of unit activity in the hippocampus and their relation to PMT.

The Bearing Map

Oliver Wendell Holmes (1889) once wrote, "I find the great thing in this world is not so much where we stand, as in what direction we are moving" (p. 127). It is no less true for spatial than for conceptual navigation. The bearing map supplies the direction and the global location. It is the locus of primary mapping, and the anatomical channel underlying it is the permanent scaffold of this primary map. Because it is the scaffold, we postulate that it necessarily increases in size and complexity as an animal matures, explores new territory, and adds knowledge about new gradients and directions in its environment.

The bearing map is constructed from simple 1-D gradients. Structures in the bearing map channel create a 2-D coordinate system from this 1-D input (see Figure 2a and Table 4). These external gradient maps are calibrated to internal gradient maps supplied by path integration. The 2-D coordinate system of the bearing map becomes the scaffold not only for all directional information but also for encoding the relative position of sketch maps. Once a sketch map has been defined in relation to the bearing map, the distance and direction of vectors that connect disparate sketch maps can be computed. This is the integrated map

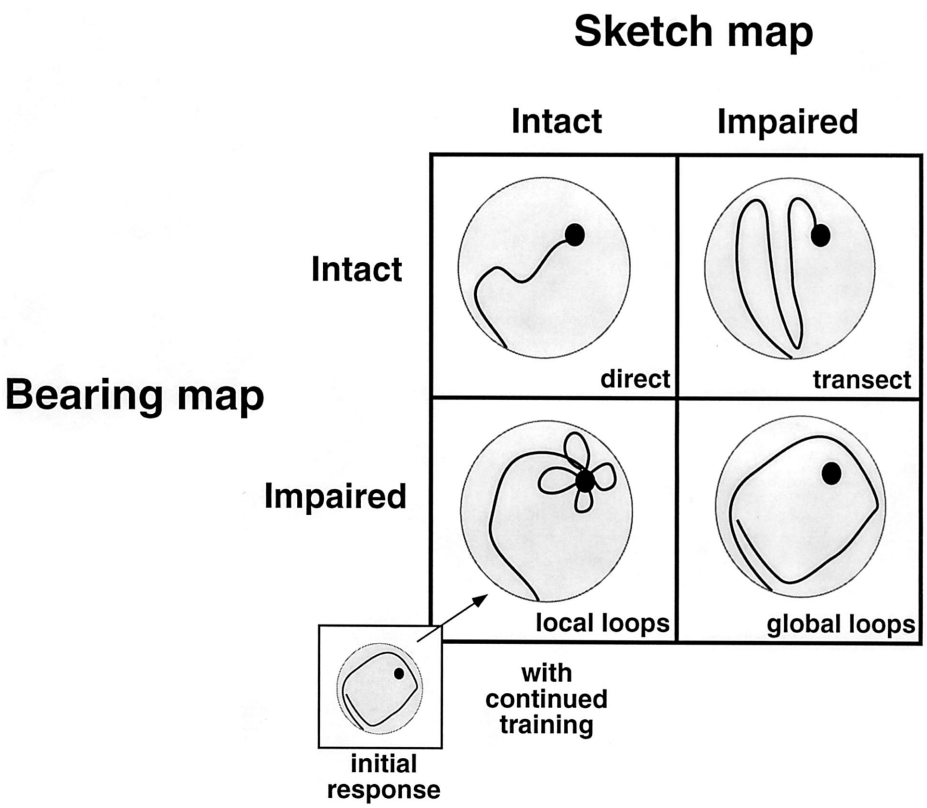

Figure 4. Predictions of the parallel map theory for the Morris water maze. The four patterns of spatial performance result from the presence or absence of the parallel maps. Residual learning, resulting from the loss of a single map (bearing or sketch), allows the rat to solve the maze, using transects when the bearing map is intact and local loops when the sketch map is intact. The residual sketch map phenotype is expressed in two stages: initial impairment of orientation and recovery to local loops with additional training. With both maps impaired, the rat shows a permanent loss of spatial orientation, represented by global loops; performance improves only with the development of nonspatial algorithms. With both maps intact, the rat encodes an integrated map, which allows it to choose a direct path to the platform, regardless of start point. The solid circle represents a hidden platform; the thick line represents a predicted swim trajectory.

representation, and, using this map, the navigator can set out on novel routes among known locales (see Figure 2c).

Structural Components of the Bearing Map

Navigators create gradient maps when they can calibrate their movements relative to regular changes in stimulus intensity. This requires three components: an input from internal movement (e.g., vestibular input), a sensory input, and a neural structure that can create 1-D maps and 2-D maps from such gradient information.

We propose that these roles are mediated in stepwise fashion by the septal nuclei, DG and CA3. Rather like an assembly line, each component adds a new piece to the bearing map (see Figure 3 and Table 4). The medial septum (MS) coordinates the input from internal movement by supplying the pacemaker needed to assess self-movement along a gradient. The pacemaker of this process may be the hippocampal theta rhythm, a rhythmical, slow activity pattern (Hasselmo, 2000). Theta occurs during active locomotion, and its frequency and amplitude are related to the many parameters associated with movement, such as speed (O'Keefe, 1993), anticipation of movement (Morris & Hagen, 1983), and type of body movements (Whishaw & Vanderwolf, 1973). Theta ceases when the animal is immobile or engaged in other behaviors that do not involve movement in a trajectory (Vanderwolf, 1969). Given its close relationship to movement, it is not surprising that the MS and its modulation of theta are important in spatial navigation (Whishaw, 2000).

Given the pacemaker's input, the next step is the integration of external sensory input in the DG. The DG is the locus of a convergence of subcortical and cortical (i.e., EC) inputs. It also has a complex internal structure, in which projections from the polymorphic layer synapse within the molecular layer, which contains projections back to the polymorphic layer (Amaral & Witter, 1995). This complex internal structure could underlie the function of the DG to create the 2-D bearing map. After the sensory input from EC is integrated with self-movement by calibration to the theta rhythm to create the 1-D map, this autoassociative structure in the DG completes the pattern of partially intersecting 1-D maps, creating a 2-D representation. This is then used to create or update the bearing map. This new information is then projected out of the DG to the CA3 through the mossy fiber projection.

CA3 has long been a focus of theoretical models because of its unusual autoassociative architecture (Kali & Dayan, 2000; Marr, 1971; McNaughton & Morris, 1987; Rolls, 1996). We speculate that one function of this architecture could be to convert gradient map information to data that can be incorporated into a topographic map (see Figure 1d–1e). This process may be necessary to integrate the bearing and sketch maps. Because CA3 is the conduit between DG and CA1, this could be a role it plays. CA3 would thus translate the current location on the bearing map into a code that could be read by CA1. For example, the navigator's location could be recoded as a new object in a topographic map (i.e., on the current sketch map). This allows CA1 to calculate the new topology of the relationship among the navigator and the surrounding objects.

To create an integrated map, however, CA1 also needs directional information from the bearing map, and, hence, CA3 must transmit the location on the bearing map as well. We suggest that CA3 could do this by segregating its output to CA1 into gradient and topographic information projections. The area in CA3 that is the most likely locus for the projection of gradient map data to CA1 is the locus of heaviest projection from DG to CA (i.e., the proximal third of CA3; also the more septal area). This proximal third has also been called the projection zone (Ishizuka, Weber, & Amaral, 1990) because the axons project directly to distal CA1 with few signs of synaptic contacts enroute. We speculate that the locus for the projection of topographic data to CA1 could take place in the middle and distal areas of CA3 (midseptotemporal), which has been called the association zone on the basis of the density of within-field projections and its input from the EC (Ishizuka et al., 1990).

Finally, because all CA3 cells project both to CA1 and to the lateral septum (Swanson, Sawchenko, & Cowan, 1980), projections from proximal CA3 and middle–distal CA3 might work in parallel, allowing the updated position to be supplied as an afferent copy to the bearing map channel (i.e., septal nuclei) and the sketch map channel (CA1). In such a scenario, the CA3 would project both location (for further encoding) and expected direction (for current action). If so, then the lateral septum should show place-specific activity involved in executing the next movement on the planned trajectory. There is some evidence for this. The lateral septum is considered to be the medial territory of the striatum (Swanson & Risold, 2000). Characteristics of a structure involved in place learning include LTP-like responses with fornix stimulation in the mouse (Garcia, Vouimba, & Jaffard, 1993) and place responses that have been recorded in freely moving subjects, both in rats (Bezzi, Leutgeb, Treves, & Mizumori, 2000) and primates (Ono & Nishijo, 1999). Because the subiculum also projects to the lateral septum (LS; Amaral & Witter, 1995), we speculate that movement may be driven by instructions either from the bearing map (through CA3) or from the integrated map (through the subiculum). Hence, the parallel map structure could well be mirrored in parallel output commands to the motor system, a hypothesis that deserves more discussion than is possible here.

In summary, we propose that the bearing map is created in the DG and projected through the mossy fiber projection to CA3, which then transmits current location to CA1, in terms of both the gradient and the topographic location, and to the LS, which mediates movement along the trajectories set up in the bearing map.

Development of the Bearing Map

As Tinbergen (1963) argued, to understand a behavior, one must take into account not only its physiological mechanism but also its evolutionary history, its current ecological significance, and its development. Having discussed the history and structure of the bearing map, we now address its development and plasticity, on the basis of studies of the laboratory rat.

Structure and activity. The hippocampus is a remarkably late-maturing brain structure, with final maturation occurring at about 21 days after birth in the rat (Bayer, 1982). In some sense, HPF development does not stop but simply proceeds through different phases, in which structure, physiology, and behavior continue to change.

Not only do hippocampal subfields develop late relative to other telencephalon structures, but they also develop in a mosaic pattern. The adult cytoarchitectonic pattern in DG develops by postnatal (PN) Day 20, though mossy fibers continue to develop in adulthood (Amaral & Dent, 1981) and neurogenesis continues in the granule layer throughout life in rodents and primates (Bayer, Yackel, & Puri, 1982; Gould, Beylin, Tanapat, Reeves, & Shors, 1999). CA1 develops later, and significant dendritic arborization in the stratum lacunosum occurs in the 2nd PN month (Pokorny & Yamamoto, 1981). In female rats, CA1 dendritic arborization fluctuates naturally with levels of estrogen, as during estrus (Gould, Wooley, Frankfurt, & McEwen, 1990). Because of the close connections between HPF and the neocortex, such plasticity may result in as yet undetected structural changes that may continue throughout life (Alvarado & Bachevalier, 2000). We discuss the role of neurogenesis in a later section.

Metabolic activity also develops in a mosaic pattern. Once again, DG precedes CA1, with a marked increase in DG activity occurring around weaning and CA1 increasing a month later (Glick, Weaver, & Meibach, 1980; Meibach, Ross, Cox, & Glick, 1980). DG activity is correlated with gamma-aminobutryic acid (GABA)-ergic inhibition, which does not mature until the end of the 1st PN month in the rat (Swann, Brady, & Martin, 1989), although activity similar to LTP is found after 2 PN weeks (Battistin & Cherubini, 1994).

Behavior. Like the hippocampal subfields, spatial learning in rats develops in different stages during the 4th PN week, even in simple tasks such as spontaneous alternation (Blozovski & Hess, 1989; Douglas, Peterson, & Douglas, 1973; Egger, 1973; Waters, Klintsova, & Foster, 1997). By the time rats are weaned and have begun exploring their environment (PN Day 20–26), they are able to orient to a single goal, whether it is a water maze platform or an escape hole in an open field (Chevalley & Schenk, 1987; Rudy, Stadler-Morris, & Albert, 1987). This change in navigational strategy suggests that adult spatial behavior appears at the end of the postweaning period, around 24 days PN (Rudy et al., 1987).

However, an earlier appearance of a spatial bias toward the training position has been observed after particular types of training. When training occurs in one day with long intertrial intervals and the pups' internal temperature is carefully controlled, a significant bias toward the training quadrant appears as early as PN Day 19 (Brown & Whishaw, 2000). When training takes place in a small pool with highly salient visual cues in the immediate vicinity of the pool, a significant bias is observed at PN Day 20–22 (Carman & Mactutus, 2001).

Given juvenile rats' poor long-term memory and poor ability to thermoregulate, these special procedures may be critical in allowing the expression of a significant spatial bias toward the training position. For example, a panorama around the water maze that is particularly rich in visual cues (Carman & Mactutus, 2001) or a highly salient cue such as an illuminated hanging cup (Rudy et al., 1987) placed a short distance from the hidden platform may result in the expression of different spatial strategies and lead to a significant spatial bias. In fact, analysis of the approach trajectories of immature rats when a cue is hanging in the next quadrant reveals a progressive transformation. The juveniles start by detouring under the cue but end by making straight approaches from the start point to the platform (Chevalley & Schenk, 1987) . Moreover, juvenile rats aged 26–28 days trained on a cued-place task express a significant degree of overshadowing that is not evident in young adults (Schenk & Brandner, 1995), which suggests that they may be developing particular spatial strategies at this age.

Hence, the absolute timing of cue and place learning appears to be highly sensitive to experimental conditions. We suggest that this is because different task environments are recruiting different parallel maps. Further, the maps are developing at different rates, in tandem with underlying hippocampal structures. Hence, the bearing map should appear before the sketch map in development, and, thus, we predict that juveniles, such as the PN Day 19 juveniles in the Brown and Whishaw (2000) study, encode the place differently than do adults, relying more heavily on the bearing map until much later in development.

The Ontogeny of the Parallel Mapping System

To test this hypothesis, we need to know precisely how the hierarchy of cue use develops in the rat. There is clearly a transition from simply approaching a cue associated with the goal to a guidance system in which a distal landmark (or landmarks) can be used to determine the correct vector to the goal, whether it appears at PN Day 19 (Brown & Whishaw, 2000) or later (Rudy et al., 1987). If juvenile rats rely primarily on the bearing map, they should orient well to distributed cues, such as distant visual cues or orthogonal gradients of olfactory cues, but poorly to arrays of positional landmarks.

There is evidence that such dissociation can occur. Juvenile rats can learn the spatial position of an escape hole (homing table; Schenk, 1989) in controlled cue conditions in a warm, dry, open arena in which there is no risk of hypothermia. Using this task, Schenk found that there was a marked interaction between age and use of cues by type. During training, immature (PN Day 26–28) and adult rats were given either discrete visual or distributed olfactory information. Olfactory information was provided in a radial pattern of scented strips, none of which was close to the goal. The visual cues were an asymmetric configuration of three discrete lights, as in a previous study (Rossier, Grobety, & Schenk, 2000). Only the adults could discriminate places purely on the basis of such visual cues, despite normal visual acuity in the immature rats (Salazar, Rossier, & Schenk, 2000). The immature rats performed well only when odor cues were present (Schenk, Jacobs, Rossier, & Kiraly, 2001).

We suggest that the immature rats relied on their relatively mature bearing map and hence were more attentive to salient distributed cues, such as odor gradients emanating from the scented strips. As the sketch map matured, the rats began to rely preferentially on the visual cues. This suggests that the sketch map is slowly calibrated by the bearing map during the 2nd PN month and may not become autonomous until the 3rd month, coinciding with hippocampal maturation. The integrated map should then develop after natal dispersal and mature further during adolescence (Schenk et al., 2001). This hypothesis is confirmed by the observation that PN Day 48 rats can rely on the visual cues to solve the task only if they have experienced the conjunction of the olfactory and visual cues, as though the presence of both is necessary for such a dual coding phase (Schenk et al., 2001).

Hippocampal Sex Differences

The sex differences in navigation strategy described earlier in the laboratory rat develop during the period of DG maturation. These differences between females and males are not fixed genetically but rather appear as a consequence of exposure to gonadal hormones during the PN period (Williams et al., 1990). Thus, the differential reliance by females and males on the bearing map appears to be the result of differential exposure to hormones; the differences are eliminated or reversed with a perinatal treatment of estrogen or its metabolite, testosterone (Isgor & Sengelaub, 1998; Roof & Havens, 1992; Williams et al., 1990).

This sex difference should be reflected in the structure of male and female HPF; we predict greater development of bearing map components in males. Sexual dimorphism in the entire hippocampus (HPF volume relative to telencephalon volume) has been found both in wild rodents (Jacobs, 1995, 1996) and in wild birds (Reboreda, Clayton, & Kacelnik, 1996; Sherry et al., 1993). In both groups, the sex that relies more heavily on spatial exploration during the breeding season has a relatively larger hippocampus.

Because both laboratory rats (*Rattus norvegicus*) and mice (*Mus musculus*) are derived from species in which males roam more widely than females, we predict that the hippocampus should also be sexually differentiated in these species. This is confirmed by several measures: Male mice have more DG granule cells (Wimer & Wimer, 1985); male rats have a thicker DG granule layer (Roof & Havens, 1990), which is associated with a greater cell density (Loy, 1986), and more dendritic branching points in the DG (Juraska, 1984; Juraska, Fitch, Henderson, & Rivers, 1985). Male rats also have more mossy fibers projecting from DG to CA3 and more synapses in this projection than do females (Madeira & Paula-Barbosa, 1993; Madeira, Sousa, & Paula-Barbosa, 1991). Thus, in all sexual dimorphisms that have been described for DG or CA3 in laboratory rats and mice, there is greater structural development in males than in females. Because this correlates with the male rat's reliance on directional cues, this supports the hypothesis that the bearing map is mediated by DG and CA3.

Hippocampal Neurogenesis

A unique property of the bearing map is its role as the permanent frame or scaffold for the integrated map. Further, we propose that the bearing map is both consolidated and stored in the DG. As the map itself becomes larger and more complex with new spatial exploration, however, it needs a mechanism to add more information. In addition, if the bearing map is a permanent reference system, then it should have a high threshold for synaptic change,

in contrast to the ephemeral sketch map, which should rapidly acquire new data, overwriting the old. For the hippocampus, unlike the visual system, in which the rules of the visual environment must be organized early in development (Shatz, 1992), the spatial environment that is experienced by a navigator changes throughout life. Incorporating new spatial data in the bearing map thus may require different levels of neural plasticity—not only synaptic plasticity but the addition of new structural elements to increase storage and computational capacity.

One mechanism that serves this end is adult neurogenesis, which both increases storage and acts as a primitive form of memory consolidation. Adult neurogenesis is common in all vertebrates but mammals (Perez-Canellas, Font, & Garcia-Verdugo, 1997). It is found throughout the brain in fish (Birse, Leonard, & Coggeshall, 1980), amphibians (Polenov & Chetverukhin, 1993), and reptiles (Garcia-Verdugo, Llahi, Ferrer, & Lopez-Garcia, 1989; Lopez-Garcia, Martinez-Guijarro, Berbel, & Garcia-Verdugo, 1988; Portolés, Doménech, Martin Pérez, & Garcia Verdugo, 1988). In mammals, adult neurogenesis occurs primarily in the olfactory bulb and the granule layer of the DG (Bayer, 1985). Why neurogenesis is more locally restricted in mammals than other vertebrates is an interesting question in itself (Perez-Canellas et al., 1997). Another question is why the local restriction involves the hippocampus. One explanation may be the importance of significant structural plasticity for encoding and consolidation of the bearing map.

The recruitment of new granule cells to the DG occurs throughout life, resulting in an ever greater number of granule cells, which appear in organized growth rings (Bayer, 1982; Kaplan & Hill, 1985). This orderly process could be the result of new exploration, requiring new structure in the form of such growth rings. If so, then the rate of growth should be proportionate to the amount of new exploration that requires an updating of the bearing map.

Indeed, recent studies have found a relationship between new exploration and the rate of neurogenesis and neuron recruitment. Mice that engaged in hippocampal-dependent tasks such as water maze navigation or trace conditioning showed a significant increase in the recruitment and survival of new neurons in the DG, relative to mice performing versions of these tasks that did not require the hippocampus (Gould et al., 1999). Mice that ran on exercise wheels also showed increased recruitment of new neurons to the DG (van Praag, Kempermann, & Gage, 1999). Wheel-running experience not only predicted increased neurogenesis but was also correlated with improved performance in the water maze and enhanced LTP in the DG. In contrast, LTP in CA1 was unaffected by the wheel-running experience (van Praag, Christie, Sejnowski, & Gage, 1999).

We suggest that these patterns of neurogenesis could be interpreted as the selective activation of the bearing map and, hence, of plasticity in the DG during this activity. Wheel-running behavior produces movement of apparent linear progress. It occurs under the unusual circumstance, in the evolutionary history of the mouse, of linear movement in the absence of concurrent change in the appearance of positional landmarks. The bearing map channel, constructed from the calibration of self-movement data to sensory input, should be highly stimulated by wheel running. Because all positional landmarks remain fixed in their aspect during wheel running, however, the navigator must assume that such landmarks are directional, not positional. As the mouse continues to move forward, it should therefore continue to interpret the sensory input as a constantly expanding bearing map. These conditions should increase the activation, expansion, and neural plasticity of the bearing map channel. Therefore, wheel-running behavior should result in an increased rate of neurogenesis in the DG, enhanced navigation ability using the bearing map, and enhanced synaptic plasticity in the DG—predictions consistent with the published results of van Praag, Christie, et al. (1999; van Praag, Kempermann, & Gage, 1999). These hypotheses need be tested further with explicit manipulation of the sensory environment during running.

Testing the Theory

To test PMT, we need to isolate the parallel maps. This can be done in two ways: restrict the task environment to one class of cues (directional or positional) and observe the change in behavior of the animal or patterns of neural activity, or impair the channel for one map but not the other. Despite tens of thousands of publications on the physiology and function of the hippocampus (see reviews in O'Keefe & Nadel, 1978; Redish, 1999), few studies have provided these types of tests in enough detail to test PMT. Either the lesions are not specific to subfield, or the task environment contains both types of cues, or the assay of spatial learning is not precise enough to detect the presence and nature of residual spatial learning. Therefore, although the studies we discuss may appear to be a highly selected subset of the literature, in fact there are very few studies that meet our criteria.

Once the maps have been isolated by task environment or through the use of specific lesions or receptor blockades, residual learning must be quantified. Figure 4 illustrates the predictions of PMT for one task, the Morris water maze. The four possible experimental conditions (rB, rS, both intact, both impaired) result in different search algorithms. The analysis of these algorithms requires new image processing techniques to analyze the shape of swim paths, as standard measures (latency to platform, length of search path) do not reveal map phenotype. A recipe, therefore, for testing the predictions of PMT is to apply the methods proposed in Tables 2 and 3 to dissociate the maps and then measure the outcome of such manipulations in the water maze, as illustrated in Figure 4.

Experimental Impairment of the Bearing Map

The impairment of the bearing map should produce an rS map phenotype. These subjects should be highly dependent on unique positional landmarks. We discuss the evidence for impairment for each component of the bearing map, following the assembly line order outlined in Table 4.

Medial Septum

On the basis of his studies of working memory, Numan (2000) recently postulated a dichotomy between the hippocampus–cortical connections that encode "external stimuli" while the septohippocampal system "encode[s] and maintain[s] the self-motion cues" (p. 316). This interpretation is consistent with our dichotomy of the bearing and sketch maps; it suggests that septal lesions should impair a sense of direction and lead to an rS phenotype.

This is confirmed by lesion studies in which MS-lesioned rats have a specific deficit in sense of direction (Kelsey & Landry, 1988). In a study by Brandner and Schenk (1998), MS-lesioned rats were highly dependent on the use of a beacon to orient, presumably because they could no longer maintain an internal sense of direction. Finally, temporary inactivation of the MS with lidocaine produces a specific loss of spatial specificity to CA3, not CA1 (Mizumori et al., 1989). This is a precise characterization of the rS phenotype, in which the loss of encoding is specific to the bearing map channel and the sketch map channel is spared.

Fimbria Fornix

The fimbria fornix (FF) projection carries the major subcortical input to the HPF and hippocampal output to various areas, including the projection from MS to DG (Amaral & Witter, 1995). A high proportion of fibers afferent to the CA1 travel through the cingular bundle and thus remain unaffected by FF transection (Amaral & Witter, 1995). Therefore, FF transection should selectively impair the bearing map.

This prediction has been borne out in a series of experiments by Whishaw and colleagues (1995). Here, the FF transection appeared to eliminate the rat's directional orientation, but without impairing its recognition of the goal location. Whishaw described this as the dissociation of a sense of direction and of place. We interpret this as an rS phenotype, in which the rat's orientation is based on the residual ability to encode unique positional landmarks.

Whishaw and Jarrard's (1995) interpretation of these results as a dissociation between knowing the place and being able to organize a trajectory to the place is entirely consistent with PMT. The bearing map system provides a link for efficient approach trajectories, which also allows immediate reversal learning. This capacity is irrevocably lost following the FF transection (Whishaw & Tomie, 1997).

Rats with FF transection also exhibit a change in response to cues. Place units in such rats appeared no longer to distinguish directional landmarks but relied heavily on positional landmarks in a radial maze. The spatial correlates of hippocampal units were severely disrupted by rotation of the maze and maintained some significant firing in a particular arm, most likely on the basis of olfactory cues (Miller & Best, 1980; Shapiro et al., 1989). This, too, we interpret as an rS phenotype, characterized by overreliance on unique positional (i.e., local, not distal) cues.

Dentate Gyrus

Several early studies suggested that the role of the DG in spatial navigation could be dissociated from that of the HP. For example, the colchicine-induced lesion of the granule layer in rats was found to impair spatial learning, as expected, but it did not affect the spatial selectivity of pyramidal cells (McNaughton et al., 1989). The authors interpreted this as evidence that spatial information can be conveyed to the pyramidal cells in the absence of granule cells, a controversial conclusion at that time but a result that is consistent with PMT. Another intriguing result from this study is a trend toward a decrease in directional bias in lesioned animals, a result that is expected in an rS phenotype.

Gilbert et al. (2001) recently effected the double dissociation of DG and CA1 function. With selective DG lesions, rats could not orient accurately to a cued location in an open arena when a second, decoy cue was placed a close distance from the original target. The impairment disappeared at greater separations between target and decoy. Moreover, this impairment was not seen in CA1-lesioned rats (Gilbert et al., 2001).

One interpretation of this impairment is that the DG is needed to disambiguate panoramic views associated with certain positional landmarks. If the DG lesion produces an rS map phenotype, then rats are limited to the use of sketch maps. Hence, they are forced to encode the location of objects using local cues only. In an open arena in which local cues are situated at some distance from the goal, these cues provide only a coarse map for mapping the test objects. Such a coarse map should suffice when the objects are far apart, as they can be associated with unique local landmarks. But without the bearing map, objects that are close together cannot be disambiguated by their position on vectors to distal objects. Therefore, the rS phenotype rats should be impaired at small but not large separation of objects.

CA3

To date, there have been no clear behavioral dissociations of CA3 function. In an early study by Jarrard, there was no effect of CA3 lesion on a place-learning task (Jarrard, 1983). As in most studies, however, this lack of effect could have been masked by residual spatial learning (i.e., rS phenotype).

As described earlier, one of the most intriguing findings is that CA3 place units lose spatial specificity with MS inactivation, whereas CA1 units are unimpaired (Mizumori et al., 1989). This finding has been used as evidence for understanding the hippocampus as a series of independent channels (Amaral & Witter, 1995).

The Sketch Maps

Under natural conditions, the physical space in which mammals navigate is not a carpentered test room but a complex world, in which new panoramic views are learned piecemeal, in linked fragments (Bovet, 1992; Huxter, Thorpe, Martin, & Harley, 2001; Jacobs & Shiflett, 1999; Schenk, Grobety, & Gafner, 1997). These fragments are obtained in discrete exploratory episodes (Eilam & Golani, 1988). Thus, encoding of space must link exploratory bouts within the same region of space. We propose that the sketch map evolved to code such a series of topographic maps, whereas the spatial relation among sketch maps was obtained from the directional bearing map (e.g., information combining direction of movement relative to the start of the journey and orientation relative to a given compass mark). Like a theatrical stage, if the bearing map is the bare stage, which serves as the framework for a changing display, the sketch maps are the rapidly changing sets, each defining a new location. With new exploration, a new version of the sketch map is rapidly formed and is indexed in similar coordinates (as the previous sketch map) to the bearing map.

Hence, the sketch map is not a cognitive map, nor is it a single, permanent topographic map. It is, in fact, a sketch of a new locale. It can be thought of as a minimap of a subspace rather than as the map of all space. It encodes the chains or chunks of disconnected local views from a particular point in space and is based on the locations of unique positional landmarks. As the navigator moves through the environment and comes to new vantage points with

new panoramic views, a new sketch map is formed. Thus, under natural conditions, as a mammal explores new terrain, it creates multiple, disconnected sketch maps. Some maps may be linked to each other by common positional landmarks. Yet even with links through common landmarks, this representation alone (i.e., multiple sketch maps) cannot pass the test of the cognitive map: constructing a novel route between previously disconnected sketch maps.

As a caveat, we note that the spatial experience of the laboratory rat may be qualitatively different from that of the wild rodent. A lab rat exploring a single open arena possesses at most two or three sketch maps (i.e., at least two panoramic views of the task environment, differing by 180° in direction). In contrast, a wild rodent may encode tens or hundreds of sketch maps over a period of weeks or months. In fact, wild gray squirrels show an increase in brain and hippocampal volume during the fall harvest of nuts (Lavenex, Steele, & Jacobs, 2000), a strategy that may require the spatial encoding of many thousands of spatial locations (Jacobs & Liman, 1991). The frame of reference used by wild squirrels to orient to a goal in their home territory, however, does appear to be similar to that used by the laboratory rat in a test room: an extramaze, allothetic frame of reference (Jacobs & Shiflett, 1999).

Once the sketch map is encoded, the next step is to encode the orientation of the sketch maps within the bearing map and to each other, creating the integrated map (see Table 4). Whether or not a particular sketch map is integrated, however, it continues to remain active and independent until it is no longer accurate. If there is a change in the location or identity of landmarks in the topographic array, then the sketch map is overwritten by a new sketch map. If there are no changes in the array, then the map is maintained in memory and could serve some function in long-term storage. Under natural conditions, a rodent navigator should have a single, permanent but expanding bearing map, whereas the coding of positional landmarks and sketch maps may be ephemeral. We suspect that most sketch maps have a short life in the HPF. They may be stored elsewhere as spatial objects, possibly chunked to one another.

Although sketch maps are independent and dissociable from each other and from the bearing map, it is possible that they can be linked to each other by associations between common positional landmarks during an exploration. In this way, chains of sketch maps may be formed, creating a route. In our view, creating a route is radically different from the simple route learning due to the systematic repetition of the same trajectory. Normal rodents may spontaneously generate and learn efficient routes, whereas subjects with selective hippocampal lesions have to be specially trained to follow and learn these routes, as in the experiments cited earlier by Whishaw et al. (1995) in the discussion of the FF.

How Spatial Is the Sketch Map?

The function of a sketch map is to represent the identity and location of a group of landmarks, the positions of which are coded relative to each other. This group is defined by the animal's exploratory strategy. It is also determined by the proximity among salient features. It even can be defined as a spatial object or configuration. Our conception of the sketch map differs from a single visual local view, however, because it integrates different viewpoints and is based on multiple sensory modalities. Poucet and Benhamou (1997) have proposed a mechanism for processing the fragments of a map. The resulting supramodal panoramic local view can thus be activated by priming from any one of these sensory modalities. This is similar to our concept of the sketch map.

Because the aspect and appearance of a positional landmark change with the position and movement of the observer, the processing of a sketch map must integrate the ongoing body position of the observer. Thus, information about head direction is critical to the formation of a sketch map. Path integration, however, although it is a main source of direction for the bearing map, is not necessary. As a consequence, sketch maps are spatial objects, because the relational coding within a sketch is purely allocentric. The observer's head orientation only allows it to code the relations among the sketch map components and is not stored as such. In this way, within-sketch map relations are spatial (allocentric), whereas between-sketches map relations are secondary either to their link with a common bearing map or to a simple sketch-to-sketch relation based on locomotion.

Thus, in spite of their spatial construction, sketch maps are disconnected from absolute locations in space, unless they are linked to all other sketch maps through the bearing map. In the absence of the latter, sketch maps can also be linked to one another in specific routes, particularly if subjects are repeatedly trained to follow systematic approach routes. This is why we suggest that the special training procedure used by Whishaw et al. (1995) can lead to apparently normal place memory. This also emphasizes the role played by the bearing map during exploration in ordering sketch maps within the spatial integrated map.

Because a sketch map is based on positional landmarks and because positional landmarks have both spatial and nonspatial properties, a sketch map may encode both spatial and nonspatial properties of an array. These properties of the sketch map—encoding nonspatial data in unique spatial arrays and linking sketch maps in a unique temporal sequence—set the stage for encoding of unique temporal events or episodes.

Overall, our concept of a sketch map has much in common with other models of hippocampal function. It may function as a temporary memory store, as postulated by Rawlins (1985); it may create maps through the "automatic encoding of attended events," as proposed by Morris and Frey (1997, p. 1489), and sketch maps may be linked to each other by the fragment fitting process outlined by Worden (1992); they also have some qualities of the scenes proposed by Gaffan (1991). Moreover, sketch maps must code the nonspatial properties of the objects or positional landmarks from which they are composed, as in Eichenbaum et al.'s (1999) hypothesis of memory space.

Finally, we predict that a given sketch will be recognized as such in spite of changes in size, although this might induce a generalized activity response (see Poucet & Benhamou, 1997). On the other hand, changes in the configuration of the components should trigger reexploration of the modified component (novelty or change reaction).

Structure and Plasticity of the Sketch Map

The structure that mediates the sketch map, CA1, is the hippocampal component that has been studied in the most detail in electrophysiological recording. Thus, it is no surprise that our

description is similar to other models in which CA1 encodes a topographic allocentric representation. Our model differs in that a CA1-mediated representation is not necessarily the cognitive map; it may be a temporary sketch map that is later incorporated into the integrated map.

Because the sketch maps are temporary representations, they should be served by a more rapid form of plasticity than that in the bearing map. For example, rapid updating of the sketch map should occur when an animal attends to a change in positional landmarks. This can occur when a new area is explored or when positional landmarks have been shifted or replaced in a familiar area.

Another implication of the sketch map is for the role of the hippocampus in reducing interference (Shapiro & Olton, 1994). The precise remapping of sketch maps to unique positional landmarks should be correlated with a reduction in interference. We suggest that this is because it is difficult to differentiate (and, hence, not overwrite) sketch maps without knowing their relative position on the bearing map.

There is currently a general agreement that the major form of synaptic plasticity for CA1 function is NMDA-mediated LTP (Morris, 1990). This form of plasticity is appropriate for the rapid encoding and reconfiguration required for constructing and updating a sketch map. In fact, a rat's spatial exploration of new terrain has been shown to reverse NMDA-mediated LTP in the rat (Xu, Anwyl, & Rowan, 1998). CA1 is also sensitive to changes in positional landmarks. With *c-fos* response as an assay, CA1 was selectively activated after a rat viewed familiar objects in a novel scene. After it viewed the novel scenes, *c-fos* response increased in postrhinal areas and CA1 but decreased in DG and the subiculum (Wan, Aggleton, & Brown, 1999). This differential activation of DG and CA1 supplies additional evidence for the independent but complementary nature of these two structures, which is appropriate for the major components of the parallel maps.

There are predictable sex differences in CA1 plasticity. Males appear to rely preferentially on the bearing map, whereas females rely preferentially on the sketch map, and females should be more sensitive to changes in the topology of positional cues. Females do express an immediate reaction to the change of positional landmarks in spite of the fact that the directional information contribution to the bearing map has not changed (Williams & Meck, 1993). Hence, we expect that plasticity in the sketch map might be a hallmark of the female hippocampus. Circulating levels of estrogen have a significant effect on CA1 structure and function in adult female rats. Naturally occurring levels of estrogen cause significant dendritic branching in the estrus female (Gould et al., 1990). This is accompanied by increased levels of LTP in the presence of natural peaks in estrogen concentration (Warren, Humphreys, Juraska, & Greenough, 1995).

Experimental Impairment of the Sketch Map

Many studies have examined the role of CA1 function and the NMDA receptor in spatial learning. Few studies have attempted to isolate the specific function of CA1, however. PMT predicts that CA1 lesion or the blockade of NMDA-mediated LTP should not abolish spatial learning but instead should reveal the residual learning capabilities of the bearing map (i.e., an rB phenotype).

CA1

The behavioral dissociation of DG function by Gilbert et al. (2001) was one half of a double dissociation between DG and CA1. The task that created an impairment in CA1-lesioned rats was quite different: It was the temporal ordering of visits to arms of the radial arm maze, a task that Chiba, Kesner, and Reynolds (1994) had previously shown to be impaired in hippocampal-lesioned rats. Yet even though CA1-lesioned and hippocampal-lesioned rats were impaired on this task, the DG-lesioned rats were not (Gilbert et al., 2001). This result is consistent with an rB phenotype—a selective loss of the ability to link different panoramic views or sketch maps. The loss of temporal order is also predicted from the lesion of the sketch map channel, because one operation possible with sketch maps is to link and sequentially activate them.

The Role of the NMDA Receptor

The dissociation of NMDA-mediated LTP and spatial learning has posed a serious challenge to the theory of the hippocampus as a cognitive map (Bannerman et al., 1995; Saucier & Cain, 1995). As we interpret these results, because this receptor is found in high concentration in CA1, the loss or blockade of these receptors should produce the rB phenotype. In contrast, techniques that are selective for the receptors of transmitters found in greater abundance in the DG should produce the rS phenotype. Such paradoxical dissociations of LTP and spatial learning thus may be the outcome of residual learning by the unaffected channel.

If the NMDA blockade selectively impairs CA1, it should produce the rB phenotype (see Table 2). Therefore, rats experiencing the NMDA blockade should be able to navigate using directional cues. The water maze is a task that requires both bearing and sketch maps and particularly requires a high-resolution sketch map for high spatial accuracy, as accurate approach trajectories must be computed to hit the platform or to correct misses. Therefore, NMDA blockade and, hence, impairment of the sketch map should produce a greater deficit in the water maze than in the radial arm maze, which relies more heavily on directional cues. If the rat knows how to solve the water maze using its bearing map, an accurate performance later under NMDA blockade should be possible because of the residual bearing map.

We suggest that this accounts for the effect of pretraining on NMDA blockade (Bannerman et al., 1995; Saucier & Cain, 1995). Our interpretation is as follows: Intact rats with prior training had had experience solving the task using the full complement of spatial representation (bearing, sketch, and integrated maps). In addition, the rats were male and, hence, were likely to have relied on the bearing map. When the NMDA-blockade selectively impaired the sketch map, these pretrained rats were able to recall their strategy of using a bearing map. This change in swim behavior (illustrated in Figure 4) should be detectable with quantitative analyses of swim path shape but also can be seen in the raw data published by Bannerman et al. (1995). Finally, although the rats showed the rB phenotype, this representation had only a low resolution and was inadequate for unimpaired performance in the water maze, and, hence, the rats' performance rose only to an intermediate level.

The pretraining effect was abolished, however, when the pretraining occurred in a curtained maze. Here, NMDA blockade

during the second maze abolished accurate orientation (Bannerman et al., 1995). Our interpretation is that the curtained maze eliminated directional cues during pretraining and, hence, prevented the rats from learning to solve the water maze using the bearing map. Therefore, these rats were prevented from learning during NMDA blockade.

Our prediction that the NMDA blockade after pretraining should produce a lesser impairment in the radial arm maze is supported by two studies (Caramanos & Shapiro, 1994; Shapiro & O'Connor, 1992). We would interpret these results as the rat's successful reliance on a residual bearing map to solve the highly directional radial arm maze.

Genetic engineering techniques can also be used to selectively lesion neurotransmitter receptors in hippocampal subfields. Results from two such studies are consistent with PMT predictions of residual learning and plasticity in the remaining channel. Knockout of CA1-localized NMDA-mediated LTP impaired the spatial selectivity of place cells (McHugh, Blum, Tsien, Tonegawa, & Wilson, 1996). This could be interpreted as need for the NMDA-mediated tuning in the high-resolution sketch map. Even though these mice should have shown the rB phenotype, the place specificity of the sketch map would be impaired.

Residual learning was also observed when the knockout of a neuronal glycoprotein eliminated LTP in the DG but did not eliminate CA1 LTP (Nosten-Bertrand et al., 1996). We suggest that in this study, the rS phenotype produced by the knockout procedure allowed the animals to recover to normal performance levels. In contrast, in the study by McHugh et al. (1996), the rB phenotype would not allow recovery of place specificity in dorsal CA1 pyramidal cells.

Harking back to spatial learning by turtles, we note that mice with calcium-calmodulin-kinase II (CCKII) mutations showed difficulty orienting in an open water maze but could nonetheless solve a water-filled plus maze (Silva et al., 1992). In our view, the mice had an rB phenotype and could not locate a place, only a direction (i.e., our interpretation of the performance by turtles in a water-filled plus maze). We suggest that orientation by CCKII mice and turtles was mediated by their homologous brain structures: the small-celled area of the medial cortex in the turtles, and the DG in the mice. It would be interesting to test this proposition by combining selective lesions with precise behavioral assays of the bearing map in mice and turtles. These results point, however, to the great potential of these genetic techniques (e.g., a double dissociation of receptor types and, thus, potentially of the parallel maps).

The Integrated Map

The integrated map emerges from the coding of the sketch maps in relation to the bearing map (see Table 4). Once this occurs, novel routes and shortcuts can be calculated from the resultant integrated map. The navigator can also chunk elemental sketch maps to form larger sketch maps. Thus, the integrated map provides two important cognitive capacities. It permits the navigator to induce the length and direction of the paths needed to travel from one sketch map to another, on the basis of their relative location on the bearing map. It emerges from the interaction of the two maps and allows long-term storage of chunks of sketch maps (or, potentially, episodes) for later retrieval from long-term memory. By this means, it is possible to derive the direction of movement that is needed to move from one sketch map to another, even if this movement is discontiguous. In fact, it is the function of the integrated map to compute this vector. It allows the navigator to compute the shortest route between two sketch maps that have no positional landmarks in common.

Coactivation

The fact that discrete sketch maps (or chains of sketch maps) have been stored with an index of their situation on a bearing map allows them to be positioned relative to each other in a single integrated map. This spatial index for the sketch maps is due to the coactivation of the two maps. This facilitates the direct access (or recall) during later movements in that locale. And because sketch maps are assigned to unique locations on the single bearing map, it is possible to distinguish them unambiguously from each other.

Structural Components of the Integrated Map

Forming an integrated map requires two components: a representation of the bearings with the environment, and a representation of the relationships among discrete objects. The integrated map also requires a reference memory representation of the current or most recent integrated map of the environment. To have full integrated map capacity, all components must therefore be functional: the components of the bearing map (MS, DG, CA3), the sketch map (CA1), and the subiculum, which mediates the reference memory of the integrated map. (There are no doubt upstream structures projecting to these components, particularly subcortical areas, that are important for map integration.) The two component maps (bearing and sketch) must also have intact afferent projects, such as the FF projection from MS to DG, the mossy fiber projection from DG to CA3, and the Schaffer collaterals from CA3 to CA1 (see Figure 3).

Map Assembly

The neural architecture of the HPF is uniquely characterized by one-way connections from CA3 to CA1 to the subiculum (Amaral & Witter, 1995). We interpret this architecture as the assembly line necessary to construct the integrated map (see Table 4). We propose that 1-D maps that are initially encoded in DG are then combined there to form the 2-D bearing map. This information is then projected to CA3. CA3 projects the location as a position on the bearing map (and as a discrete object) to CA1. CA1 integrates the location on the bearing map with the current sketch map and thereby calibrates the sketch map with the bearing map.

Once the integrated map has been formed, CA1 extracts new routes from the integrated map. CA1 is a complex and topographically organized structure, with direct projections from sensory areas such as the EC, olfactory bulb, and neocortical areas as well as thalamic nuclei (Amaral and Witter, 1995). This complex architecture may reflect CA1′s role as the constructor of sketch maps and the locus of the integration of these maps with the bearing map. In this case, CA1 topology reflects two functions: its role as the encoding of new sketch maps as well as the locus of the current status of the integrated map. From the integrated map (probably dorsal CA1), the role of this area is to extract the temporal order

of positional landmarks on novel routes, calculated from the integrated map.

Consolidation of the Integrated Map

Both bearing and sketch maps must be stored in long-term memory to be retrieved later, albeit in different locations. We suggest that the storage of the bearing map is within the DG and, hence, that the DG provides the index to all allocentric encoding (see Teyler & DiScenna, 1986, for an earlier proposal of indexing by the hippocampus). In contrast, the sketch maps are most likely stored in the temporoparietal neocortex. The question of whether the integrated map is stored as such is less clear. This depends on the definition of what is a single sketch map and whether there is overlap among sketch maps encoded for a given environment. If sketch maps are coded when directional information is available, the relation among sketch components may be associated with at least one major gradient and with the vector from path integration. Such dual coding of successive sketch maps would become more frequent as the environment is intensively patrolled, leading to the long-term storage of linked sketch maps. This may be why overtrained memory for familiar places can be retrieved even after hippocampal damage (Teng & Squire, 1999). Although we do not suggest that a global integrated map is stored in long-term memory, we predict that consolidation may stabilize the relationships among sketch maps if they have been linked by locomotion. However, preoperative training in the water maze, although it facilitates acquisition, does not seem to facilitate task reacquisition and has little effect on probe trials (Morris, Schenk, Tweedie, & Jarrard, 1990). This suggests that very little of the integrated map has been transferred out of the hippocampus during consolidation.

Reference Memory Representation of the Integrated Map

After the integrated map is created by the hippocampus, it is still necessary to have a reference memory representation to make the map available for use and updating. Unlike DG and HP, the subiculum has reciprocal connections with hippocampal, thalamic, and cortical areas. We suggest, therefore, that it might store the reference memory representation of the integrated map that has been constructed by the hippocampus. If so, lesions of the subiculum would differ in subtle ways from hippocampal lesions: They would impair reference memory for the integrated map but not working memory. Place units in the subiculum should also differ from those in the hippocampus, as we discuss later.

Experimental Impairment of the Integrated Map

Damage to one channel should simultaneously impair the relevant map and the integrated map.

Subiculum

A selective lesion of the subiculum should impair the reference memory of the relationship among sketch maps (i.e., the integrated map). Hence, result of this should be an rB phenotype. The animal should show partial recovery, because it could learn to navigate with the remaining bearing map. Such qualitative differences between subiculum-and hippocampus-lesioned groups have been observed. Rats with subicular lesions (rB) appeared to swim around the entire pool. This swim pattern was quite different from the progressively adjusted loops commonly seen in rats with an rS phenotype (e.g., rats with septal lesions). Moreover, the rats with a subiculum lesion seemed to have little memory between sessions (i.e., impaired reference memory), although they were capable of expressing memory for a new platform position after four trials in a match-to-place test (i.e., intact working memory; Morris et al., 1990).

On the basis of the foregoing discussion, a pure subicular lesion (rB phenotype) should impair learning of the new location but leave residual capacities based on the bearing map intact. This should result in a residual ability to learn new positions based on the bearing map, in which new locations can be encoded. Consistent with this interpretation, subiculum-lesioned rats showed improvement in platform location within trial blocks (Morris et al., 1990). This suggests that they could find the platform by swimming transects, orienting with the bearing map (see Figure 4).

Hippocampus Lesions Sparing the Subiculum

The challenge to any spatial theory of hippocampal function is to explain residual spatial learning after a complete hippocampal lesion, defined as the absence of cell bodies and/or all neural tissue of the DG and HP. Yet learning by hippocampal-lesioned rats can occur under certain conditions, and, with additional training, a hippocampal-lesioned rat can show significant recovery. The explanation for this may lie in the nature of the training. Recovery does not occur quickly but only with special training, such as alternating trials with a visible and an invisible platform at the same position (Whishaw et al., 1995; Whishaw & Gorny, 1999; Whishaw & Jarrard, 1995). The logistical difficulty with this lesion is that hippocampal-lesioned rats cannot generate controlled trajectories (i.e., trajectories associated with predictable changes in sensory input, based on the 2-D bearing map). They therefore cannot form sketch maps of positional cues, which are scarce in a swimming pool when no salient cue is provided in the vicinity of the pool. The solution of attracting the rat to the visible platform to facilitate learning of these cues is an elegant one. Training the rats in this way allows them to link egocentric views that could then become an effective substitute for true allocentric place learning.

For example, under such prolonged training, a secondary system may be slowly brought online to compensate for the loss of hippocampal function. The parietal cortex appears to act as a spatial map, associating objects and places (Burgess, Jeffrey, & O'Keefe, 1999; Long & Kesner, 1998). Therefore, hippocampal-lesioned rats could, with special training, slowly develop a parietal map to navigate to the platform. The subiculum could also play a role in this type of learning, as it could encode a new reference map for the environment, constructed from this limited parietal input. Neither of these strategies produce intact learning ability, but, with enough training, there should be some recovery of function. If either of these components (parietal, subiculum) were missing, however, there would be no recovery.

This prediction is confirmed in a study of the locus of ibotenic lesions on spatial learning: Rats whose lesion included both the hippocampus and some part of the subiculum showed no recovery (Morris et al., 1990). This would be expected if the rat had lost not only its sense of direction (lesioned bearing map channel) and its

ability to calculate a new position (lesioned sketch map channel) but also the ability to retain any new learned spatial relations (lesioned subiculum).

Lesion placement. In addition to complete hippocampal lesions, removing tissue from either dorsal or ventral hippocampal regions produces different patterns of impairment. Dorsal lesions produce a greater impairment than do ventral lesions (E. Moser, Moser, & Andersen, 1993; M.-B. Moser & Moser, 1998; M.-B. Moser, Moser, Forrest, Andersen, & Morris, 1995). In addition, the degree of impairment is proportionate to the amount of tissue lost; small dorsal lesions impaired the probe test performance, whereas large (more than 20% of the hippocampus) lesions impaired latency to the platform (E. Moser et al., 1993). We suggest that the small dorsal lesions selectively impaired the CA1 and the sketch map and, hence, the ability to encode the local position of the platform. In other words, the dorsal lesion produced an rB phenotype, and the ventral lesion produced an rS phenotype. The dorsal lesion (rB phenotype) allows escape latencies to remain low or intermediate, as in the case of the pretraining effect (Bannerman et al., 1995). Ventral lesions (rS) should have less effect, because of the greater use of the sketch map in the water maze. With larger lesions, however, both maps are lost, and escape latencies increase. This prediction could be tested by correlating the loss of tissue for each subfield (DG, CA3, or CA1) in a dorsal or ventral lesion of different magnitudes with quantitative analyses of swim paths produced by the rat.

Hippocampal residual learning and path integration. In our view, path integration is not a hippocampus-dependent representation but instead is a source of data for the bearing map, providing it with a default direction value. PMT therefore predicts that rats with hippocampal lesions are not impaired in path integration (a 1-D representation) but instead are impaired in integrating path integration into a spatial representation (a 2-D representation). Thus, the key question is whether lesioned rats are impaired in path integration or in orienting with a vector derived from path integration. This prediction is supported by evidence that hippocampal rats are only impaired in tasks requiring a spatial representation but not in pure path integration studies (Alyan & McNaughton, 1999). In another study, hippocampal rats could only home through path integration using combined self-movement, surface, and visual cues but were unable to do so with only self-movement cues (Maaswinkel, Jarrard, & Whishaw, 1999). Such learning, depending on the training, could be residual learning by the subiculum, even in the absence of CA1. Hippocampal lesions also abolish the rB phenotype, which is indispensable for orienting in a dark region of an open field with no olfactory cues (Schenk et al., 1995).

Entorhinal Cortex

The EC occupies a special role in hippocampal function. It projects to every subfield and has reciprocal connections with CA1 (Witter et al., 2000). It is thus an active partner for both sketch and bearing maps, and lesions of the EC alone should reveal significant residual capacities, similar to lesions of the DG and HP. Indeed, like rats with hippocampal lesions (Morris et al., 1990), EC-lesioned rats show stereotyped swim loops that become progressively more likely to cross the platform location (Schenk & Morris, 1985). The actual expressed phenotype critically depends on the task and the tissue remaining in the subiculum, if in fact there is a residual capacity by the subiculum and parietal to develop sketch-like maps. In fact, EC-lesioned rats do show similar residual capacities to hippocampal-lesioned rats, in contrast to rats with a combined EC and subiculum lesion, which show no recovery (Schenk & Morris, 1985). This also raises the question of the significance of the direct EC–CA1 connection (Witter, Griffioen, Jorritsma-Byham, & Krijnen, 1988). This connection may play an important role for sketch map reorganization, as is required in the acquisition of learning a new place in a familiar environment.

Hippocampal Unit Activity

Neural activity in specific HPF areas, as measured by unit or field recordings (and functional imaging, once finer spatial resolution has been achieved), should be activated differentially depending on the map that is being constructed or accessed for a particular task.

Predictions

The parallel maps may be active individually at any time, though, under most conditions, they should be active simultaneously (see Table 4). For example, new exploration along gradients should selectively activate the bearing map channel. In contrast, exploration into arrays of new positional landmarks or the introduction of a new positional landmark should selectively activate the sketch map channel. Rearrangement of these landmarks or other mismatch detection (O'Keefe, 1976) should also activate the sketch map channel units. Activation of one component may then require an update of the integrated map, which should activate the whole assembly line (see Table 4).

An obvious test, then, is to examine the activity of place cells in different HPF subfields in reaction to specific task environment or cue manipulation conditions. However, spatial selectivity should be found in sites that encode place, which could be found in a 2-D representation in the bearing map based on directional cues, or a 2-D representation in the sketch map constructed from positional landmarks, or in the integrated map. Spatial selectivity in itself may therefore not distinguish easily between mapping systems. The critical test is instead the response of units to changes in task environment. For example, altering directional cues should activate units in the bearing map channel, and manipulating positional landmarks should primarily activate the sketch map channel, but having to navigate between two discontiguous sketch maps should activate the integrated map.

There are significant obstacles to testing these predictions with the current unit activity literature. First, as we have just discussed, it is not yet clear precisely how subfields differentiate by spatial specificity. Second, the location of the unit must be precisely defined. In addition to differences among subfields, there is also a highly organized topography of projections among subfields. Output from CA3, for example, differentiates into three zones, each of which remains segregated in CA1 (Ishizuka et al., 1990). A similar topography is seen in perforant path projections (Witter et al., 2000) and in the CA1 projection to the subiculum (Amaral & Witter, 1995). Such regular topography is likely to be involved in functional differentiation of independent channels within the hippocampus (Amaral & Witter, 1995). We suspect that this topography is related to the segregation of bearing, sketch, and inte-

grated maps in the hippocampus. Hence, unit activity may very well differ among such segregated channels.

There is also evidence that hippocampal regions vary in unit activity. For example, place fields in ventral HPF are sparser and less finely tuned than are those recorded in dorsal HPF (M. W. Jung, Wiener, & McNaughton, 1994), corresponding to the differentiation of dorsal–ventral function discussed earlier. A new focus of physiological studies has been the recording of hippocampal ensembles, with the goal of discerning topographical patterns of activity. This has met with mixed results, perhaps because of methodological differences among studies (Hampson, Simeral, & Deadwyler, 1999; Redish et al., 2001). At this point, however, there is no clear consensus on the relationship between unit location and the pattern of activity.

Task environment is also critical in the evaluation of unit activity in relation to PMT. Single-track environments (e.g., plus maze, radial arm maze), favored in some studies (McNaughton et al., 1996; Mizumori, Ragozzino, Cooper, & Leutgeb, 1999; O'Keefe & Speakman, 1987; Redish et al., 2001), provide a test environment that is clearly organized into directional vectors. Rats in such an environment, particularly male rats, might naturally rely more heavily on the bearing map. These rats might therefore recruit a different pattern of cell ensembles than might rats navigating in less directional environments, such as the round cylindrical arena with a single cue card, the task developed by Muller, Kubie, and Ranck (1987; Ranck, 1973). The card in this task environment provides a simple directional landmark and perhaps positional landmarks from the edges of the card. Because other directional cues are generally missing in this environment, however, unit recordings might biased toward activity in the sketch map in the cylindrical, cue-card arena and the bearing map channel in the radial arm maze.

Given these caveats, some unit activity studies may shed some light on the mechanism underlying the parallel mapping systems. We address two categories of unit activity, place units and head direction units.

Head Direction Units

As we discussed earlier, orienting in a sketch map requires a different type of directional information than does orienting in the bearing map. Mapping positional landmarks requires three types of information. Visual input on the size, shape, and aspect of the object contributes to its identification. Vestibular information mediates the integration of the changes in aspect with changes in egocentric movements. Finally, knowledge of the direction in which the observer is looking (i.e., head direction) facilitates the computation of relative position. Processing the relation between different positional landmarks thus involves motion parallax and the information coded by the head direction units. In comparison, path integration is related to whole body translation, and, thus, rotation should be more critical for gradient discrimination. The neural basis of head direction units in structures that project to the hippocampus is becoming well elucidated (Taube & Muller, 1998; Taube, Muller, & Ranck, 1990). We have a different interpretation of the function of these units. We propose that the head direction system, involving the anterior dorsal thalamus, postsubiculum, and CA1, furnishes directional data not to the bearing map but to the sketch map. In fact, head direction and place information converge in CA1 (Leutgeb, Ragozzino, & Mizumori, 2000), but because head direction units are related to major directional cues, the bearing map may play a critical role in updating the head direction units. This may be one way the efficacy of the bearing map affects sketch map processing.

Place Units

We summarize relevant findings from the literature by their relationship to different maps.

Evidence for the bearing map. We have already discussed the dissociation of CA3 and CA1 unit activity with MS inactivation, for which MS inactivation resulted in a loss of spatial selectivity in CA3 but not in CA1 (Mizumori et al., 1989). This is concordant with the critical role of the MS input for the bearing map and hence for CA3 spatial coding but not for the sketch map, which retains its spatial specificity.

A second observation that is consistent with activity in the bearing map is that place cells appear preconfigured: A rat introduced into a novel arena immediately shows large (i.e., low resolution) place fields at the beginning of exploration (Wilson & McNaughton, 1993). These coarse fields could be evidence for the existing bearing map. Carrying the subject among laboratory rooms would not disrupt such a map, although the map might be disrupted by vestibular disorientation. This would also explain why place cells update their location using directional information (O'Keefe & Burgess, 1996).

Evidence for the sketch map. The sketch map allows the navigator to refine the coarse resolution of the bearing map. If CA1 is the primary area encoding new sketch maps, then it should rapidly encode and tune positional landmarks to create the working memory copy of the integrated map. Several studies have demonstrated the role of the NMDA receptor, which is found in high density in CA1, in fine tuning place fields (Kentros et al., 1998). The knockout of the gene for a key subunit of the NMDA receptor in CA1 affects the spatial selectivity of CA1 place cells; mice lacking this receptor showed reduced LTP in the CA1 and had coarser resolution of place fields (McHugh et al., 1996).

Evidence for the integrated map. A noted characteristic of place unit studies is the diversity of place cell spatial specificity. For example, a study of CA1 and CA3 place units categorized three types according to their response to landmarks: those responding to distal or local landmarks, and those responding to both types (Gothard, Skaggs, Moore, & McNaughton, 1996). We speculate that these three types correspond to units engaged in three maps: bearing map units encoding distal (i.e., directional) landmarks, sketch map units encoding local (i.e., positional) landmarks, and integrated map units encoding both. If so, then there should be some segregation of function by subfield. CA3 neurons should specify place in relation to the directional cues, such as the geometry of the array, whereas CA1 units could be involved in integrated map or sketch map representations. Therefore, CA1 units could respond to both classes of cues, though we speculate that the area most distal to CA3, which receives input from the CA3 projection zone, should be more responsive to directional cues than should units in the midseptotemporal regions of CA1, which receive inputs from the CA3 associational zone.

Another finding, related to cue control, is the differential control of place units by the landmarks according to their position in the

environment. In these studies, landmarks at the edge of an arena exert greater control over unit activity compared with the same landmark placed in the center of the arena (Cressant, Muller, & Poucet, 1997, 1999; Hetherington & Shapiro, 1997). We suggest that the central placement of landmarks, in the absence of directional cues to inform the bearing map, leads objects in the center of the field to be processed as a sketch map. In contrast, the same objects in the periphery provide both directional and positional information, allowing the rat to calculate an integrated map. Furthermore, sketch maps must be encoded in unique locations on the bearing map. With centrally placed objects and, hence, no directional reference, there is a loss of control of unit response by cues. Here, rats cannot associate the objects (i.e., the sketch map relating these objects to one another) with a stable bearing map, and sketch maps are not consolidated, but, instead, different sketch maps continue to be created. This leads to the apparent low resistance to rotation of cues.

Alternatively, rats may link their sketch map to a distant object that provides some directional information. In this case, place fields would be disturbed if the configuration was rotated, because the rat expects intra-arena landmarks to maintain a certain relation to the extramaze world. Evidence for these alternatives may be provided by experiments using the round cylinder paradigm by Knierim, Kudrimoti, and McNaughton (1995, 1998). Because of the nature of the task, rats cannot link the inside of the cylinder to the outside through self-movement and path integration. They also cannot see distal cues. With this absence of directional cues, it is difficult to encode the current location (and current sketch map) in relation to the bearing map. Head direction may also be poorly coded when directional cues are absent. Under such conditions, sketch maps may not be coded accurately, and, consequently, units might be less accurately controlled by cues.

Another intriguing case is offered by place cell studies using two identical environments in which unit activity is measured as rats explore first one, then a second environment (Barnes, Suster, Shen, & McNaughton, 1997; Skaggs & McNaughton, 1998; Tanila, 1999; Wilson & McNaughton, 1993). Depending on the experimental conditions, different responses are obtained from ensemble recordings of pyramidal cells. For example, old rats are less likely to retrieve the same map for a given environment than are young rats, which is interpreted as an age-related decline in retrieving information from an intact spatial framework (Barnes et al., 1997). Perhaps this framework could be conceptualized as the bearing map. If so, then this is an age-related impairment in the binding of new sketch maps to the consolidated bearing map. Because of the sketch map's reliance on NMDA-mediated LTP, this leads to the prediction that the sketch and integrated maps should be more sensitive to the processes of normal aging than is the bearing map.

A second interesting comparison is among adult rats experiencing different experimental layouts, as in studies by Skaggs and McNaughton (1998) and Tanila (1999). In the former study, rats moved from one identical environment (A) along a connecting corridor to a second environment (B). Here, CA1 place cells showed similar patterns of activity in A and B. In the latter study, the rat moved through a door directly into the second identical arena. Here, CA3 place cells completely remapped in B, but, when the rat returned to A, the pattern of activity retained the distinction between the two environments. These two experiments differ in many ways. For example, in the latter study, the rats only saw one environment at a time, and this may have aided them in maintaining independent representations (Tanila, 1999). Yet it is intriguing that the recordings in the study by Skaggs and McNaughton (1998) were located in CA1, but the recording locations in the study by Tanila (1999) were located mostly in CA3, with some units in CA1. As Tanila pointed out, "the only ensemble . . . that showed preserved location of firing with respect to common visual cues was the CA1 ensemble" (p. 244). Thus, in both studies, CA1 neurons appeared agnostic to absolute location but instead responded to the immediate visual panorama, a behavior consistent with sketch map function. Lacking information on the relative position of each map in absolute space, CA1 could not distinguish between them. We interpret the responses of the CA3 units, in maintaining their absolute location, as consistent with CA3 access to data from the bearing map. These data would allow the CA3 ensembles to differentiate the two visually identical environments by their unique location on the bearing map. One could test this interpretation by recording CA1 and CA3 ensembles while systematically changing cues available in the task environment. Removing directional cues (both internal and external) should decrease the ability of CA3 units to encode a location and to differentiate the two environments.

Finally, we have suggested that the role played by the subiculum is to hold a reference or efferent copy of the integrated map during the period of memory consolidation by temporal and parietal cortices. In this sense, place units in the subiculum should be similar to those in CA1. There are several intriguing experiments on cue control of subiculum units that bear on this question. The surprising finding has been that subiculum units seem to encode a universal map that is oblivious to changes in geometry of the arena or visual pattern (Sharp, 1999a). This, of course, differs dramatically from units in HP, which are sensitive to both parameters (Sharp, 1997). Another difference is the response to barriers within the arena: Hippocampal place cells can encompass such barriers, but subiculum place fields are inhibited by such boundaries (Sharp, 1999b). A possible interpretation of these results, cast in the framework of PMT, is that this universal map or reference memory of the integrated map encodes a location in absolute space. In contrast to the ephemeral, working memory sketch maps of CA1, the subiculum reference map should be resilient to changes in local cues. The response of the subiculum to barriers may derive from its reliance on the continuity of sight lines, to calculate trajectories based on the bearing map. This is highly speculative, of course, and here, just as in the hippocampus literature, a very different picture could emerge with comparisons of units within different projection zones of the subiculum. The question of place specificity in EC is equally important, and we suggest that, like the other major output structure to the HPF, some units in EC should reflect the characteristics of the reference memory copy and, hence, may be impervious to local changes in arena geometry, as observed (Quirk, Muller, Kubie, & Ranck, 1992).

Summary and Conclusions

The parallel map theory postulates that the two major components of the HPF, the DG and the HP, play fundamentally different roles in spatial navigation. This duality reflects the inherently dual nature of spatial navigation, the need for both map and compass,

for both directional and positional landmarks. These two classes of landmarks are selectively attended to and processed to construct parallel spatial representations, the bearing map of DG and CA3, the sketch map of CA1. These maps are both independent and complementary, each adding their unique contribution in an assembly-line fashion to create a flexible and powerful representation, the cognitive or integrated map.

Testing the Theory

The value of a theory lies in its ability to predict unique and quantifiable results. Because each parallel map is mediated by different hippocampal channels and relies differentially on mechanisms of synaptic plasticity, the maps should be dissociable by standard methods. Damaging one component of either channel impairs both the integrated map and the map mediated by that channel; we offer recipes for testing the theory in Tables 2 and 3. The definitive test of the theory is a double dissociation of bearing map and sketch map channels, combined with a precise measure of map phenotype for each experimental group.

We think ours is a plausible and testable theory. Given the current state of knowledge of the structure and function of many components of the HPF, however, we fully expect to revise our predictions as future research reduces uncertainty about hippocampal connections, activity, and function. At present, the complexity of HPF structure far outstrips our ability to understand the logic of its design. Even with the current evidence for topographic projections (Amaral & Witter, 1995; Scharfman, Witter, & Schwarcz, 2000; Witter et al., 2000), it has been difficult, perhaps impossible, to reconcile the complex neuroanatomy of the HPF with feasible models of its function. For example, there are currently no theoretical models or experimental studies of CA2, another subfield in HP, and therefore we have not yet included this subfield in PMT. Given this current situation, we openly acknowledge that this hypothesis of map assembly may be correct in outline but must be an oversimplification of a much more complex system and, hence, often incorrect in the details.

Given the number of methods by which the predictions can be tested, we have a significant chance of detecting errors in the theory, either in detail or in the whole. To date, the empirical literature is consistent with PMT, and when subfield functions have been dissociated, the results have confirmed our predictions. In many cases (e.g., the dissociation of LTP and learning, association of wheel running with neurogenesis, sex differences in spatial strategy), PMT offers a single mechanism for a diversity of unexplained results.

Conclusion

"Science is built up with facts, as a house is with stones. But a collection of facts is no more a science than a heap of stones is a house" (Poincaré, 1913, p. 18). The unsolved question of hippocampal function remains at the forefront of cognitive neuroscience. With thousands of published studies on hippocampal function and physiology, this literature represents a prodigious heap of stones. Many structures have been built from these stones to account for the hippocampus's role in spatial navigation and human memory. We have described here another such structure, the parallel map theory. We believe that, in comparison with previous theories, our structure rests on a deeper foundation, the evolutionary history of spatial navigation and the hippocampal formation in vertebrates. By constructing a model from the simplest units of navigation, orientation to 1-D maps from distributed stimuli, we have progressed inexorably to the conclusion that the hippocampus must be encoding and integrating parallel mental representations of the external environment. If our predictions are confirmed, PMT will have profound implications for principles of spatial navigation and the function of the mammalian hippocampus.

References

Abeliovich, A., Paylor, R., Chen, C., Kim, J. J., Wehner, J. M., & Tonegawa, S. (1993). PKC-gamma mutant mice exhibit mild deficits in spatial and contextual learning. *Cell, 75,* 1263–1271.

Akesson, S. (1996). Geomagnetic map used for long-distance navigation? *Trends in Ecology & Evolution, 11,* 398–400.

Alerstam, T. (1990). *Bird migration.* Cambridge, England: Cambridge University Press.

Alvarado, M. C., & Bachevalier, J. (2000). Revisiting the maturation of medial temporal lobe memory functions in primates. *Learning & Memory, 7,* 244–256.

Alyan, S., & McNaughton, B. L. (1999). Hippocampectomized rats are capable of homing by path integration. *Behavioral Neuroscience, 113,* 19–31.

Amaral, D. G., & Dent, J. A. (1981). Development of the mossy fibers of the dentate gyrus: I. A light and electron microscopic study of the mossy fibers and their expansions. *Journal of Comparative Neurology, 195,* 51–86.

Amaral, D. G., & Witter, M. P. (1995). Hippocampal formation. In G. Paxinos (Ed.), *The rat nervous system* (2nd ed., pp. 443–493). San Diego, CA: Academic Press.

Bannerman, D. M., Good, M. A., Butcher, S. P., Ramsay, M., & Morris, R. G. M. (1995, November 9). Distinct components of spatial learning revealed by prior training and NMDA receptor blockade. *Nature, 378,* 182–186.

Barnes, C. A. (1979). Memory deficits associated with senescence: A neurophysiological and behavioral study in the rat. *Journal of Comparative and Physiological Psychology, 93,* 74–104.

Barnes, C. A., Suster, M. S., Shen, J., & McNaughton, B. L. (1997, July 17). Multistability of cognitive maps in the hippocampus of old rats. *Nature, 388,* 272–275.

Battistin, T., & Cherubini, E. (1994). Developmental shift from long-term depression to long-term potentiation at the mossy fibre synapses in the rat hippocampus. *European Journal of Neuroscience, 6,* 1750–1755.

Bayer, S. A. (1982). Changes in the total number of dentate granule cells in juvenile and adult rats: A correlated volumetric and 3H-thymidine autoradiographic study. *Experimental Brain Research, 46,* 315–323.

Bayer, S. A. (1985). Neuron production in the hippocampus and olfactory bulb of the adult rat brain: Addition or replacement? In F. Nottebohm (Ed.), *Annals of the New York Academy of Sciences: Vol. 457. Hope for a new neurology* (pp. 163–172). New York: New York Academy of Sciences.

Bayer, S. A., Yackel, J. W., & Puri, P. S. (1982, May 21). Neurons in the rat dentate gyrus granular layer substantially increase during juvenile and adult life. *Science, 216,* 890–892.

Benhamou, S., & Poucet, B. (1998). Landmark use by navigating rats (*Rattus norvegicus*): Contrasting geometric and featural information. *Journal of Comparative Psychology, 112,* 317–322.

Bennett, A. T. D. (1996). Do animals have cognitive maps? *Journal of Experimental Biology, 199,* 219–224.

Best, P. J., & White, A. M. (1999). Placing hippocampal single-unit studies in a historical context. *Hippocampus, 9,* 346–351.

Bezzi, M., Leutgeb, S., Treves, A., & Mizumori, S. J. (2000). Information analysis of location-selective cells in hippocampus and lateral septum [Abstract]. *Society for Neuroscience Abstracts, 26,* 11.

Bingman, V. P. (1990). Spatial navigation in birds. In R. P. Kesner & D. S. Olton (Eds.), *Neurobiology of comparative cognition* (1st ed., pp. 423–447). Hillsdale, NJ: Erlbaum.

Bingman, V., Bagnoli, P., Ioalé, P., & Casini, G. (1989). Behavioral and anatomical studies of the avian hippocampus. In V. Chan-Palay & C. Kohler (Eds.), *The hippocampus: New vistas. Neurology and neurobiology* (Vol. 52, pp. 379–394). New York: Liss.

Birse, S. C., Leonard, R. B., & Coggeshall, R. E. (1980). Neuronal increase in various areas of the nervous system of the guppy, Lebistes. *Journal of Comparative Neurology, 194,* 291–301.

Bliss, T. V. P., & Collingridge, G. L. (1993, January 7). A synaptic model of memory: Long-term potentiation in the hippocampus. *Nature, 361,* 31–39.

Bliss, T. V. P., & Lomo, T. (1973). Long-lasting potentiation of synaptic transmission in the dentate area of the anaesthetized rabbit following stimulation of the perforant path. *Journal of Physiology, 232,* 331–356.

Blozovski, D., & Hess, C. (1989). Hippocampal nicotinic cholinergic mechanisms mediate spontaneous alternation and fear during ontogenesis but not later in the rat. *Behavioural Brain Research, 35,* 209–220.

Bovet, J. (1992). Mammals. In F. Papi (Ed.), *Animal homing* (pp. 321–361). London: Chapman & Hall.

Brandner, C., & Schenk, F. (1998). Septal lesions impair the acquisition of a cued place navigation task: Attentional or memory deficit? *Neurobiology of Learning and Memory, 69,* 106–125.

Brown, R. W., & Whishaw, I. Q. (2000). Similarities in the development of place and cue navigation by rats in a swimming pool. *Developmental Psychobiology, 37,* 238–245.

Bruce, L. L., & Neary, T. J. (1995). The limbic system of tetrapods: A comparative analysis of cortical and amygdalar populations. *Brain, Behavior and Evolution, 46,* 224–234.

Burgess, N., Jeffery, K. J., & O'Keefe, J. (1999). Integrating hippocampal and parietal functions: A spatial point of view. In N. Burgess, K. J. Jeffery, & J. O'Keefe (Eds.), *The hippocampal and parietal foundations of spatial cognition* (pp. 3–29). Oxford, England: Oxford University Press.

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The human hippocampus and spatial and episodic memory, *Neuron, 35,* 625–641.

Butler, A. B., & Hodos, W. (1996). *Comparative vertebrate anatomy: Evolution and adaptation.* New York: Wiley-Liss.

Caramanos, Z., & Shapiro, M. L. (1994). Spatial memory and N-methyl-D-aspartate receptor antagonists APV and MK-801: Memory impairments depend on familiarity with the environment, drug dose, and training duration. *Behavioral Neuroscience, 108,* 30–43.

Carman, H. M., & Mactutus, C. F. (2001). Ontogeny of spatial navigation in rats: A role for response requirements? *Behavioral Neuroscience, 115,* 870–879.

Cheng, K. (1986). A purely geometric module in the rat's spatial representation. *Cognition, 23,* 149–178.

Cheng, K., & Gallistel, C. R. (1984). Testing the geometric power of an animal's spatial representation. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), *Animal cognition* (pp. 409–423). Hillsdale, NJ: Erlbaum.

Chevalley, A.-F., & Schenk, F. (1987). Immature processes of spatial learning in hooded rats [Abstract]. *Society for Neurosciences Abstracts, 17,* 5.

Chiba, A. A., Kesner, R. P., & Reynolds, A. M. (1994). Memory for spatial location as a function of temporal lag in rats: Role of hippocampus and medial prefrontal cortex. *Behavioral and Neural Biology, 61,* 123–131.

Cohen, N. J., & Eichenbaum, H. (1991). The theory that wouldn't die: A critical look at the spatial mapping theory of hippocampal function. *Hippocampus, 1,* 265–268.

Cohen, N. J., & Eichenbaum, H. (1993). *Memory, amnesia, and the hippocampal system.* Cambridge, MA: MIT Press.

Collett, T. S., & Baron, J. (1994, March 10). Biological compasses and the coordinate frame of landmark memories in honeybees. *Nature, 368,* 137–140.

Collett, T. S., Cartwright, B. A., & Smith, B. A. (1986). Landmark learning and visuo-spatial memories in gerbils. *Journal of Comparative Physiology: A, Sensory, Neural, and Behavioral Physiology, 158,* 835–851.

Cressant, A., Muller, R. U., & Poucet, B. (1997). Failure of centrally placed objects to control the firing fields of hippocampal place cells. *Journal of Neuroscience, 17,* 2531–2542.

Cressant, A., Muller, R. U., & Poucet, B. (1999). Further study of the control of place cell firing by intra-apparatus objects. *Hippocampus, 9,* 423–431.

Day, L. B., Crews, D., & Wilczynski, W. (1999). Spatial and reversal learning in congeneric lizards with different foraging strategies. *Animal Behaviour, 57,* 393–407.

Day, L. B., Crews, D., & Wilczynski, W. (2001). Effects of medial and dorsal cortex lesions on spatial memory in lizards. *Behavioural Brain Research, 118,* 27–42.

Deadwyler, S. A., & Hampson, R. E. (1999). Anatomic model of hippocampal encoding of spatial information. *Hippocampus, 9,* 397–412.

Dobzhansky, T. (1951). *Genetics and the origin of species.* (3rd ed.). New York: Columbia University Press.

Douglas, R. J., Peterson, J. J., & Douglas, D. P. (1973). The ontogeny of a hippocampus-dependent response in two rodent species. *Behavioral Biology, 8,* 27–37.

Dusek, J. A., & Eichenbaum, H. (1997). The hippocampus and memory for orderly stimulus relations. *Proceedings of the National Academy of Sciences, USA, 94,* 7109–7114.

Dusenbery, D. B. (1992). *Sensory ecology.* New York: Freeman.

Dyer, F. C. (1994). Spatial cognition and navigation in insects. In L. A. Real (Ed.), *Behavioral mechanisms in evolutionary ecology* (pp. 66–98). Chicago: University of Chicago Press.

Egger, G. J. (1973). Novelty induced changes in spontaneous alternation by infant and adult rats. *Developmental Psychobiology, 6,* 431–435.

Eichenbaum, H., Dudchenko, P., Wood, E., Shapiro, M., & Tanila, H. (1999). The hippocampus, memory, and place cells: Is it spatial memory or a memory space? *Neuron, 23,* 209–226.

Eilam, D., & Golani, I. (1988). The ontogeny of exploratory behavior in the house rat (Rattus rattus): The mobility gradient. *Developmental Psychobiology, 21,* 679–710.

Fernandez, A. S., Pieau, C., Reperant, J., Boncinelli, E., & Wassef, M. (1998). Expression of the Emx-1 and Dlx-1 homeobox genes define three molecularly distinct domains in the telencephalon of mouse, chick, turtle and frog embryos: Implications for the evolution of telencephalic subdivisions in amniotes. *Development, 125,* 2099–2111.

Font, C., Lanuza, E., Martinez-Marcos, A., Hoogland, P. V., & Martinez-Garcia, F. (1998). Septal complex of the telencephalon of lizards: III. Efferent connections and general discussion. *Journal of Comparative Neurology, 401,* 525–548.

Frier, H. J., Edwards, E., Smith, C., Neale, S., & Collett, T. S. (1996). Magnetic compass cues and visual pattern learning in honeybees. *Journal of Experimental Biology, 199,* 1353–1361.

Gaffan, D. (1991). Spatial organization of episodic memory. *Hippocampus, 1,* 262–264.

Gallistel, C. R. (1990). *The organization of learning.* (1st ed.). Cambridge, MA: MIT Press.

Garcia, R., Vouimba, R. M., & Jaffard, R. (1993). Spatial discrimination learning induces LTP-like changes in the lateral septum of mice. *NeuroReport, 5,* 329–332.

Garcia-Verdugo, J. M., Llahi, S., Ferrer, I., & Lopez-Garcia, C. (1989). Postnatal neurogenesis in the olfactory bulbs of a lizard. A tritiated thymidine autoradiographic study. *Neuroscience Letters, 98,* 247–252.

Gilbert, P., Kesner, R., & Lee, I. (2001). Dissociating hippocampal subregions: A double dissociation between dentate gyrus and CA1. *Hippocampus, 11,* 626–636.

Glick, S. D., Weaver, L. M., & Meibach, R. C. (1980, March 7). Lateralization of reward in rats: Differences in reinforcing thresholds. *Science, 207,* 1093–1095.

Gluck, M. A., & Myers, C. E. (2001). *Gateway to memory: An introduction to neural network modeling of the hippocampus and learning.* Cambridge, MA: MIT Press.

Gothard, K., Skaggs, W. E., Moore, K. M., & McNaughton, B. L. (1996). Binding of hippocampal CA1 neural activity to multiple reference frames in a landmark-based navigation task. *Journal of Neuroscience, 16,* 823–835.

Gould, E., Beylin, A., Tanapat, P., Reeves, A., & Shors, T. J. (1999). Learning enhances adult neurogenesis in the hippocampal formation. *Nature Neuroscience, 2,* 260–265.

Gould, E., Wooley, C. S., Frankfurt, M., & McEwen, B. S. (1990). Gonadal steroids regulate dendritic spine density in hippocampal pyramidal cells in adulthood. *Journal of Neuroscience, 10,* 1286–1291.

Granger, R., Wiebe, S. P., Taketani, M., & Lynch, G. (1996). Distinct memory circuits composing the hippocampal region. *Hippocampus, 6,* 567–578.

Greene, C. H., & Cook, R. G. (1997). Landmark geometry and identity controls spatial navigation in rats. *Animal Learning & Behavior, 25,* 312–323.

Hampson, R. E., Simeral, J. D., & Deadwyler, S. A. (1999, December 9). Distribution of spatial and nonspatial information in dorsal hippocampus. *Nature, 402,* 610–614.

Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology.* Oxford, England: Oxford University Press.

Hasselmo, M. E. (2000). Septal modulation of theta dynamics: What is the function of the theta rhythm? In R. Numan (Ed.), *The behavioral neuroscience of the septal region* (pp. 92–114). New York: Springer.

Helbig, A. J., Berthold, P., & Wiltschko, W. (1989). Migratory orientation of blackcaps (Sylvia atricapilla): Population-specific shifts of direction during the autumn. *Ethology, 82,* 307–315.

Hetherington, P. A., & Shapiro, M. L. (1997). Hippocampal place fields are altered by the removal of single visual cues in a distance-dependent manner. *Behavioral Neuroscience, 111,* 20–34.

Holmes, O. W. (1889). *The autocrat of the breakfast-table.* Boston: Houghton Mifflin. (Original work published 1885)

Holtzman, D. A. (1998). From slither to hither: Orientation and spatial learning in snakes. *Integrative Biology, 1,* 81–89.

Holtzman, D. A., Harris, T. W., Aranguren, G., & Bostock, E. (1999). Spatial learning of an escape task by young corn snakes, Elaphe guttata guttata. *Animal Behaviour, 57,* 51–60.

Hoogland, P. V., Martinez-Garcia, F., Geneser, F. A., & Vermeulen-Vanderzee, E. (1998). Convergence of thalamic and cholinergic projections in the "dentate area" of lizards. *Brain, Behavior and Evolution, 51,* 113–122.

Hoogland, P. V., & Vermeulen-Vanderzee, E. (1990). Intrinsic and extrinsic connections of the cerebral cortex of lizards. In W. K. Schwerdtfeger & W. J. A. J. Smeets (Eds.), *The forebrain of reptiles* (pp. 20–29). Basel, Switzerland: Karger.

Huang, Y.-Y., Kandel, E. R., Varshavsky, L., Brandon, E. P., Qi, M., Idzerda, R. L., et al. (1995). A genetic test of the effects of mutations in PKA on mossy fiber LTP and its relation to spatial and contextual learning. *Cell, 83,* 1211–1222.

Huxter, J. R., Thorpe, C. M., Martin, G. M., & Harley, C. W. (2001). Spatial problem solving and hippocampal place cell firing in rats: Control by an internal sense of direction carried across environments. *Behavioural Brain Research, 123,* 37–48.

Isgor, C., & Sengelaub, D. R. (1998). Prenatal gonadal steroids affect adult spatial behavior, CA1 and CA3 pyramidal cell morphology in rats. *Hormones and Behavior, 34,* 183–198.

Ishizuka, N., Weber, J., & Amaral, D. G. (1990). Organization of intrahippocampal projections originating from CA3 pyramidal cells in the rat. *Journal of Comparative Neurology, 295,* 580–623.

Jacobs, L. F. (1995). The ecology of spatial cognition: Adaptive patterns of hippocampal size and space use in wild rodents. In E. Alleva, A. Fasolo, H.-P. Lipp, & L. Nadel (Eds.), *Studies of the brain in naturalistic settings* (pp. 301–322). Dordrecht, the Netherlands: Kluwer Academic.

Jacobs, L. F. (1996). Sexual selection and the brain. *Trends in Ecology and Evolution, 11,* 82–86.

Jacobs, L. F., Gaulin, S. J. C., Sherry, D. F., & Hoffman, G. E. (1990). Evolution of spatial cognition: Sex-specific patterns of spatial behavior predict hippocampal size. *Proceedings of the National Academy of Sciences, USA, 87,* 6349–6352.

Jacobs, L. F., & Liman, E. R. (1991). Grey squirrels remember the locations of buried nuts. *Animal Behaviour, 41,* 103–110.

Jacobs, L. F., & Shiflett, M. W. (1999). Spatial orientation on a vertical maze in free-ranging fox squirrels (*Sciurus niger*). *Journal of Comparative Psychology, 113,* 116–127.

Jacobs, L. F., & Spencer, W. D. (1994). Natural space-use patterns and hippocampal size in kangaroo rats. *Brain, Behavior and Evolution, 44,* 125–132.

Jarrard, L. E. (1983). Selective hippocampal lesions and behavior: Effects of kainic acid lesions on performance of place and cue tasks. *Behavioral Neuroscience, 97,* 873–889.

Jung, C. (1964). Approaching the unconscious. In C. G. Jung, M.-L. von Franz, & J. Freeman (Eds.), *Man and his symbols* (pp. 18–103). Garden City, NY: Doubleday.

Jung, M. W., Wiener, S. I., & McNaughton, B. L. (1994). Comparison of spatial firing characteristics of units in dorsal and ventral hippocampus of the rat. *Journal of Neuroscience, 14,* 7347–7356.

Juraska, J. M. (1984). Sex differences in developmental plasticity in the visual cortex and hippocampal dentate gyrus. In G. J. de Vries (Ed.), *Progress in brain research* (Vol. 61, pp. 205–214). Amsterdam: Elsevier.

Juraska, J. M., Fitch, J. M., Henderson, C., & Rivers, N. (1985). Sex difference in the dendritic branching of dentate granule cells following differential experience. *Brain Research, 333,* 73–80.

Kali, S., & Dayan, P. (2000). The involvement of recurrent connections in area CA3 in establishing the properties of place fields: A model. *Journal of Neuroscience, 20,* 7463–7477.

Kaplan, H., & Hill, K. (1985). Hunting ability and reproductive success among male Ache foragers. *Current Anthropology, 26,* 223–246.

Kavaliers, M., Eckel, L. A., & Ossenkopp, K. P. (1993). Brief exposure to 60 Hz magnetic fields improves sexually dimorphic spatial learning performance in the meadow vole, Microtus pennsylvanicus. *Journal of Comparative Physiology: A, Sensory, Neural, and Behavioral Physiology, 173,* 241–248.

Kavaliers, M., Ossenkopp, K. P., Prato, F. S., Innes, D. G. L., Galea, L. A. M., Kinsella, D. M., & Perrot-Sinal, T. S. (1996). Spatial learning in deer mice: Sex differences and the effects of endogenous opioids and 60 Hz magnetic fields. *Journal of Comparative Physiology: A, Sensory, Neural, and Behavioral Physiology, 179,* 715–724.

Keeton, W. T. (1974). The mystery of pigeon homing. *Scientific American, 231*(6), 96–107.

Kelsey, J. E., & Landry, B. A. (1988). Medial septal lesions disrupt spatial mapping ability in rats. *Behavioral Neuroscience, 102,* 289–293.

Kentros, C., Hargreaves, E. L., Hawkins, R. D., Kandel, E. R., Shapiro, M. L., & Muller, R. V. (1998, June 26). Abolition of long-term stability of new hippocampal place cell maps by NMDA receptor blockade. *Science, 280,* 2121–2126.

Kimchi, T., & Terkel, J. (2001). Magnetic compass orientation in the blind

mole rat Spalax ehrenbergi. *Journal of Experimental Biology, 204,* 751–758.

Kimura, D. (1999). *Sex and cognition.* Cambridge, MA: MIT Press.

Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1995). Place cells, head direction cells, and the learning of landmark stability. *Journal of Neuroscience, 15,* 1648–1659.

Knierim, J. J., Kudrimoti, H. S., & McNaughton, B. L. (1998). Interactions between idiothetic cues and external landmarks in the control of place cells and head direction cells. *Journal of Neurophysiology, 80,* 425–446.

Langley, C. M. (1994). Spatial memory in the desert kangaroo rat (*Dipodomys deserti*). *Journal of Comparative Psychology, 108,* 3–14.

Lavenex, P., Steele, M. A., & Jacobs, L. F. (2000). The seasonal pattern of cell proliferation and neuron number in the dentate gyrus of wild adult eastern grey squirrels. *European Journal of Neuroscience, 12,* 643–648.

Leonard, B., & McNaughton, B. L. (1990). Spatial representation in the rat: Conceptual, behavioral, and neurophysiological perspectives. In R. P. Kesner & D. S. Olton (Eds.), *Neurobiology of comparative cognition* (pp. 363–422). Hillsdale, NJ: Erlbaum.

Leutgeb, S., Ragozzino, K. E., & Mizumori, S. J. Y. (2000). Convergence of head direction and place information in the CA1 region of hippocampus. *Neuroscience, 100,* 11–19.

Levine, R. L., & Bluni, T. D. (1994). Magnetic field effects on spatial discrimination learning in mice. *Physiology & Behavior, 55,* 465–467.

Light, P., Salmon, M., & Lohmann, K. J. (1993). Geomagnetic orientation of loggerhead sea turtles: Evidence for an inclination compass. *Journal of Experimental Biology, 182,* 1–9.

Lohmann, K. J., Hester, J. T., & Lohmann, C. M. F. (1999). Long-distance navigation in sea turtles. *Ethology Ecology & Evolution, 11,* 1–23.

Lohmann, K. J., & Johnsen, S. (2000). The neurobiology of magnetoreception in vertebrate animals. *Trends in Neurosciences, 23,* 153–159.

Lohmann, K. J., & Lohmann, C. M. F. (1996a, March 7). Detection of magnetic field intensity by sea turtles. *Nature, 380,* 59–61.

Lohmann, K. J., & Lohmann, C. M. F. (1996b). Orientation and open-sea navigation in sea turtles. *Journal of Experimental Biology, 199,* 73–81.

Long, J. M., & Kesner, R. P. (1998). Effects of hippocampal and parietal cortex lesions on memory for egocentric distance and spatial location information in rats. *Behavioral Neuroscience, 112,* 480–495.

Lopez, J. C., Rodriguez, F., Gomez, Y., Vargas, J. P., Broglio, C., & Salas, C. (2000). Place and cue learning in turtles. *Animal Learning & Behavior, 28,* 360–372.

Lopez-Garcia, C., Martinez-Guijarro, F. J., Berbel, P., & Garcia-Verdugo, J. M. (1988). Long-spined polymorphic neurons of the medial cortex of lizards: A Golgi, Timm, and electron-microscopic study. *Journal of Comparative Neurology, 272,* 409–423.

Loy, R. (1986). Sexual dimorphism in the septohippocampal system. In R. L. Isaacson & K. H. Pribram (Eds.), *The hippocampus* (Vol. 3, pp. 301–315). New York: Plenum.

Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R., & Papi, F. (1998). The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proceedings of the Royal Society of London, Series B, 265,* 2279–2284.

Maaswinkel, H., Jarrard, L. E., & Whishaw, I. Q. (1999). Hippocampectomized rats are impaired in homing by path integration. *Hippocampus, 9,* 553–561.

Maaswinkel, H., & Whishaw, I. Q. (1999). Homing with locale, taxon, and dead reckoning strategies by foraging rats: Sensory hierarchy in spatial navigation. *Behavioural Brain Research, 99,* 143–152.

Madeira, M. D., & Paula-Barbosa, M. M. (1993). Reorganization of mossy fiber synapses in male and female hypothyroid rats: A stereological study. *Journal of Comparative Neurology, 337,* 334–352.

Madeira, M. D., Sousa, N., & Paula-Barbosa, M. M. (1991). Sexual dimorphism in the mossy fiber synapses of the rat hippocampus. *Experimental Brain Research, 87,* 537–545.

Marr, D. (1971). Simple memory: A theory for archicortex. *Philosophical Transactions of the Royal Society of London, Series B, 262,* 24–81.

Martinez-Garcia, F., & Olucha, F. E. (1990). Afferent projections to the Timm-positive cortical areas of the telencephalon of lizards. In W. K. Schwerdtfeger & W. J. A. J. Smeets (Eds.), *The forebrain of reptiles* (pp. 30–40). Basel, Switzerland: Karger.

McHugh, T. J., Blum, K. I., Tsien, J. Z., Tonegawa, S., & Wilson, M. A. (1996). Impaired hippocampal representation of space in CA1-specific NMDAR1 knockout mice. *Cell, 87,* 1339–1349.

McNaughton, B. (1996, May 30). Cognitive cartography. *Nature, 381,* 368–369.

McNaughton, B. L., Barnes, C. A., Gerrard, J. L., Gothard, K., Jung, M. W., Knierim, J. J., et al. (1996). Deciphering the hippocampal polyglot: The hippocampus as a path integration system. *Journal of Experimental Biology, 199,* 173–185.

McNaughton, B. L., Barnes, C. A., Meltzer, J., & Sutherland, R. J. (1989). Hippocampal granule cells are necessary for normal spatial learning but not for spatially-selective pyramidal cell discharge. *Experimental Brain Research, 76,* 485–496.

McNaughton, B. L., & Morris, R. G. M. (1987). Hippocampal synaptic enhancement and information storage within a distributed memory system. *Trends in Neuroscience, 10,* 408–415.

Medina, L., & Reiner, A. (2000). Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends in Neurosciences, 23,* 1–12.

Meibach, R. C., Ross, D. A., Cox, R. D., & Glick, S. D. (1980). The ontogeny of hippocampal energy metabolism. *Brain Research, 204,* 431–435.

Miller, V. M., & Best, P. J. (1980). Spatial correlates of hippocampal unit activity are altered by lesions of the fornix and entorhinal cortex. *Brain Research, 194,* 311–323.

Mizumori, S. J. Y., McNaughton, B. L., Barnes, C. A., & Fox, K. B. (1989). Preserved spatial coding in hippocampal CA1 pyramidal cells during reversible suppression of CA3c output: Evidence for pattern completion in hippocampus. *Journal of Neuroscience, 9,* 3915–3928.

Mizumori, S. J. Y., Ragozzino, K. E., Cooper, B. G., & Leutgeb, S. (1999). Hippocampal representational organization and spatial context. *Hippocampus, 9,* 444–451.

Moffat, S. D., Hampson, E., & Hatzipantelis, M. (1998). Navigation in a "virtual" maze: Sex differences and correlation with psychometric measures of spatial ability in humans. *Evolution and Human Behavior, 19,* 73–87.

Morris, R. G. M. (1984). Development of a water-maze procedure for studying spatial learning in the rat. *Journal of Neuroscience Methods, 11,* 47–60.

Morris, R. G. M. (1990). Synaptic plasticity, neural architecture, and forms of memory. In E. James, L. McGaugh, E. Norman, M. Weinberger, J. L. McGaugh, N. M. Weinberger, & G. Lynch (Eds.), *Brain organization and memory: Cells, systems, and circuits* (pp. 52–77): New York: Oxford University Press.

Morris, R. G. M., & Frey, U. (1997). Hippocampal synaptic plasticity: Role in spatial learning or the automatic recording of attended experience? *Philosophical Transactions of the Royal Society of London, Series B, 352,* 1489–1503.

Morris, R. G. M., & Hagen, J. J. (1983). Hippocampal electrical activity and ballistic movement. In W. Seifert (Ed.), *Neurobiology of the hippocampus* (pp. 321–331). New York: Academic Press.

Morris, R. G., Hagan, J. J., & Rawlins, J. N. (1986). Allocentric spatial learning by hippocampectomised rats: A further test of the "spatial mapping" and "working memory" theories of hippocampal function. *Quarterly Journal of Experimental Psychology: Comparative and Physiological Psychology, 38*(B), 365–395.

Morris, R. G. M., Schenk, F., Tweedie, F., & Jarrard, L. (1990). Ibotenic lesions of the hippocampus and/or subiculum: Dissociating components

of allocentric spatial learning. *European Journal of Neuroscience, 2,* 1016–1029.

Moser, E., Moser, M. B., & Andersen, P. (1993). Spatial learning impairment parallels the magnitude of dorsal hippocampal lesions but is hardly present following ventral lesions. *Journal of Neuroscience, 13,* 3916–3925.

Moser, M.-B., & Moser, E. I. (1998). Functional differentiation in the hippocampus. *Hippocampus, 8,* 608–619.

Moser, M.-B., Moser, E. I., Forrest, E., Andersen, P., & Morris, R. G. M. (1995). Spatial learning with a minislab in the dorsal hippocampus. *Proceedings of the National Academy of Sciences, USA, 92,* 9697–9701.

Muller, R. U., Kubie, J. L., & Ranck, J. B. (1987). Spatial firing patterns of hippocampal complex-spike cells in a fixed environment. *Journal of Neuroscience, 7,* 1935–1950.

Nadel, L., O'Keefe, J., Shapiro, M., McNaughton, B. L., & Disterhoft, J. (1998). Symposium: Hippocampal neurons: Place cells or more [Abstract]? *Society for Neuroscience Abstracts, 24,* 503.

Neisser, U. (1976). *Cognition and reality: Principles and implications of cognitive psychology.* New York: Freeman.

Northcutt, R. G. (1995). The forebrain of gnathostomes: In search of a morphotype. *Brain, Behavior and Evolution, 46,* 275–318.

Northcutt, R. G. (1996). The agnathan ark: The origin of craniate brains. *Brain, Behavior and Evolution, 48,* 237–247.

Nosten-Bertrand, N., Errington, M. L., Murphy, K. P. S. J., Tokugawa, Y., Barboni, E., Koslova, E., et al. (1996, February 29). Normal spatial learning despite regional inhibition of LTP in mice lacking Thy-1. *Nature, 379,* 826–829.

Numan, R. (2000). Septal modulation of the working memory for voluntary behavior. In R. Numan (Ed.), *The behavioral neuroscience of the septal region* (pp. 298–326). New York: Springer.

O'Keefe, J. (1976). Place units in the hippocampus of the freely moving rat. *Experimental Neurology, 51,* 78–109.

O'Keefe, J. (1993). Hippocampus, theta and spatial memory. *Current Opinion in Neurobiology, 3,* 917–924.

O'Keefe, J., & Burgess, N. (1996, May 30). Geometric determinants of the place fields of hippocampal neurons. *Nature, 381,* 425–428.

O'Keefe, J., & Conway, D. H. (1980). On the trail of the hippocampal engram. *Physiological Psychology, 8,* 229–238.

O'Keefe, J., & Dostrovsky, J. (1971). The hippocampus as a spatial map: Preliminary evidence from unit activity in the freely-moving rat. *Brain Research, 34,* 171–175.

O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* Oxford, England: Oxford University Press.

O'Keefe, J., & Speakman, A. (1987). Single unit activity in the rat hippocampus during a spatial memory task. *Experimental Brain Research, 68,* 1–27.

Olcese, J. M. (1990). The neurobiology of magnetic field detection in rodents. *Progress in Neurobiology, 35,* 325–330.

Ono, T., & Nishijo, H. (1999). Active spatial information processing in the septo-hippocampal system. *Hippocampus, 9,* 458–466.

Papi, F. (Ed.). (1992). *Animal homing.* London: Chapman & Hall.

Perez-Canellas, M. M., Font, E., & Garcia-Verdugo, J. M. (1997). Postnatal neurogenesis in the telencephalon of turtles: Evidence for nonradial migration of new neurons from distant proliferative ventricular zones to the olfactory bulbs. *Developmental Brain Research, 101,* 125–137.

Phillips, J. B., & Borland, C. (1994). Use of a specialized magnetoreception system for homing by the eastern red-spotted newt Notophthalmus viridescens. *Journal of Experimental Biology, 188,* 275–291.

Poincaré, H. (1913). *Science and method* (F. Maitland, Trans.). London: Thomas Nelson and Sons.

Pokorny, J., & Yamamoto, T. (1981). Postnatal ontogenesis of hippocampal CA1 area in rats. I. Development of dendritic arborisation in pyramidal neurons. *Brain Research Bulletin, 7,* 113–120.

Polenov, A. L., & Chetverukhin, V. K. (1993). Ultrastructural radioautographic analysis of neurogenesis in the hypothalamus of the adult frog, Rana temporaria, with special reference to physiological regeneration of the preoptic nucleus: II. Types of neuronal cells produced. *Cell & Tissue Research, 271,* 351–362.

Portolés, M., Doménech, J. M., Martin Pérez, V., & Garcia Verdugo, J. M. (1988). A Golgi and electron microscope study of the ventral septum in the reptile, Podarcis hispánica. *Anatomischer Anzeiger, 165,* 311–326.

Poucet, B. (1989). Object exploration, habituation, and response to a spatial change in rats following septal or medial frontal cortical damage. *Behavioral Neuroscience, 103,* 1009–1016.

Poucet, B., & Benhamou, S. (1997). The neuropsychology of spatial cognition in the rat. *Critical Reviews in Neurobiology, 11,* 101–120.

Poucet, B., Chapuis, N., Durup, M., & Thinus-Blanc, C. (1986). A study of exploratory behavior as an index of spatial knowledge in hamsters. *Animal Learning & Behavior, 14,* 93–100.

Quirk, G. J., Muller, R. U., Kubie, J. L., & Ranck, J. B., Jr. (1992). The positional firing properties of medial entorhinal neurons: Description and comparison with hippocampal place cells. *Journal of Neuroscience, 12,* 1945–1963.

Ranck, J. B. (1973). Studies on single neurons in dorsal hippocampal formation and septum in unrestrained rats: I. Behavioral correlates and firing repertoires. *Experimental Neurology, 41,* 462–531.

Rawlins, J. N. (1985). Associations across time: The hippocampus as a temporary memory store. *Behavioral and Brain Sciences, 8,* 479–528.

Reboreda, J. C., Clayton, N. S., & Kacelnik, A. (1996). Species and sex differences in hippocampus size in parasitic and non-parasitic cowbirds. *NeuroReport, 7,* 505–508.

Redish, A. D. (1999). *Beyond the cognitive map: From place cells to episodic memory.* Cambridge, MA: MIT Press.

Redish, A. D., Battaglia, F. P., Chawla, M. K., Ekstrom, A. D., Gerrard, J. L., Lipa, P., et al. (2001). Independence of firing correlates of anatomically proximate hippocampal pyramidal cells. *Journal of Neuroscience, 21,* 1–6.

Redish, A. D., & Touretzky, D. S. (1997). Cognitive maps beyond the hippocampus. *Hippocampus, 7,* 15–35.

Richter-Levin, G., Thomas, K. L., Hunt, S. P., & Bliss, T. V. P. (1998). Dissociation between genes activated in long-term potentiation and in spatial learning in the rat. *Neuroscience Letters, 251,* 41–44.

Rolls, E. T. (1996). A theory of hippocampal function in memory. *Hippocampus, 6,* 601–620.

Romer, A. S. (1977). *The vertebrate body* (5th ed.). Philadelphia: Saunders.

Roof, R. L., & Havens, M. D. (1990). A testosterone related sexual dimorphism in the dentate gyrus of the rat [Abstract]. *Society for Neuroscience Abstracts, 20,* 328.

Roof, R. L., & Havens, M. D. (1992). Testosterone improves maze performance and induces development of a male hippocampus in females. *Brain Research, 572,* 310–313.

Rossier, J., Grobety, M.-C., & Schenk, F. (2000). Spatial learning by rats across visually disconnected environments. *Animal Learning & Behavior, 28,* 16–27.

Rossier, J., Haeberli, C., & Schenk, F. (2000). Auditory cues support place navigation in rats when associated with a visual cue. *Behavioural Brain Research, 117,* 209–214.

Rudy, J. W., Stadler-Morris, S., & Albert, P. (1987). Ontogeny of spatial navigation behaviors in the rat: Dissociation of "proximal"-and "distal"-cue-based behaviors. *Behavioral Neuroscience, 101,* 62–73.

Salazar, R., Rossier, J., & Schenk, F. (2000). Delayed maturation of spatial mapping: Eight-week old rats are unable to integrate discrete controlled visual cues in a configuration. *European Journal of Neuroscience, 12*(Suppl. 11), 86d.

Samsonovich, A., & McNaughton, B. L. (1997). Path integration and cognitive mapping in a continuous attractor neural network model. *Journal of Neuroscience, 17,* 5900–5920.

Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females

use different distal cues in a virtual environment navigation task. *Cognitive Brain Research, 6,* 351–360.

Saucier, D., & Cain, D. P. (1995, November 9). Spatial learning without NMDA receptor-dependent long-term potentiation. *Nature, 378,* 186–189.

Scharfman, H. E., Witter, M. P., & Schwarcz, R. (2000). *The parahippocampal region: Implications for neurological and psychiatric diseases.* New York: New York Academy of Sciences.

Schenk, F. (1989). A homing procedure for studying spatial memory in immature and adult rodents. *Journal of Neuroscience Methods, 26,* 249–258.

Schenk, F., & Brandner, C. (1995). Enhanced visuspatial memory following pre and postnatal choline treatment. *Psychobiology, 23,* 302–312.

Schenk, F., Grobety, M. C., Lavenex, P., & Lipp, H.-P. (1995). Dissociation between basic components of spatial memory in rats. In E. Alleva, A. Fasolo, H.-P. Lipp, & L. Nadel (Eds.), *Behavioural brain research in naturalistic and semi-naturalistic settings* (Vol. 82, pp. 207–223). Dordrecht, the Netherlands: Kluwer Academic.

Schenk, F., Jacobs, L. F., Rossier, J., & Kiraly, M. (2001). Steps in the development of spatial cognition in rats: Evidence for a dual mapping system [Abstract]. *Society for Neuroscience Abstracts, 27,* 1436.

Schenk, F., & Morris, R. G. M. (1985). Dissociation between components of spatial memory in rats after recovery from the effects of retrohippocampal lesions. *Experimental Brain Research, 58,* 11–28.

Schöne, H. (1984). *Spatial orientation: The spatial control of behavior in animals and man.* Princeton, NJ: Princeton University Press.

Schwerdtfeger, W. K. (1984). *Structure and fiber connections of the hippocampus.* Berlin: Springer-Verlag.

Shapiro, M. L., & O'Connor, C. (1992). N-methyl-D-aspartate receptor antagonist MK-801 and spatial memory representation: Working memory is impaired in an unfamiliar environment but not in a familiar environment. *Behavioral Neuroscience, 106,* 604–612.

Shapiro, M. L., & Olton, D. S. (1994). Hippocampal function and interference. In D. L. Schacter & E. Tulving (Eds.), *Memory systems 1994* (pp. 87–117). Cambridge, MA: MIT Press.

Shapiro, M. L., Simon, D. K., Olton, D. S., Gage, F. H. D., Nilsson, O., & Björklund, A. (1989). Intrahippocampal grafts of fetal basal forebrain tissue alter place fields in the hippocampus of rats with fimbria-fornix lesions. *Neuroscience, 32,* 1–18.

Sharp, P. E. (1997). Subicular cells generate similar spatial firing patterns in two geometrically and visually distinctive environments: Comparison with hippocampal place cells. *Behavioural Brain Research, 85,* 71–92.

Sharp, P. E. (1999a). Complimentary roles for hippocampal versus subicular/entorhinal place cells in coding place, context, and events. *Hippocampus, 9,* 432–443.

Sharp, P. E. (1999b). Subicular place cells expand or contract their spatial firing pattern to fit the size of the environment in an open field but not in the presence of barriers: Comparison with hippocampal place cells. *Behavioral Neuroscience, 113,* 643–662.

Shatz, C. J. (1992). The developing brain. *Scientific American, 267,* 61–67.

Shepherd, G. M. (1994). *Neurobiology* (3rd ed.). New York: Oxford University Press.

Sherry, D. F., Forbes, M. R. L., Khurgel, M., & Ivy, G. O. (1993). Greater hippocampal size in females of the brood parasitic brown-headed cowbird. *Proceedings of the National Academy of Sciences, USA, 90,* 7839–7843.

Sherry, D. F., & Hampson, E. (1997). Evolution and the hormonal control of sexually-dimorphic spatial abilities in humans. *Trends in Cognitive Science, 1,* 50–56.

Sherry, D. F., Jacobs, L. F., & Gaulin, S. J. C. (1992). Adaptive specialization of the hippocampus. *Trends in Neurosciences, 15,* 298–303.

Sherry, D. F., & Vaccarino, A. L. (1989). Hippocampus and memory for food caches in black-capped chickadees. *Behavioral Neuroscience, 103,* 308–318.

Sherry, D. F., Vaccarino, A. L., Buckenham, K., & Herz, R. S. (1989). The hippocampal complex of food-storing birds. *Brain, Behavior and Evolution, 34,* 308–317.

Silva, A. J., Paylor, R., Wehner, J. M., & Tonegawa, S. (1992, July 10). Impaired spatial learning in alpha-calcium-calmodulin kinase II mutant mice. *Science, 257,* 206–211.

Skaggs, W. E., & McNaughton, B. L. (1998). Spatial firing properties of hippocampal CA1 populations in an environment containing two visually identical regions. *Journal of Neuroscience, 18,* 8455–8466.

Squire, L. R. (1992). Memory and the hippocampus: A synthesis from findings with rats, monkeys, and humans. *Psychological Review, 99,* 195–231.

Squire, L. R., & Zola-Morgan, S. (1991, September 20). The medial temporal lobe memory system. *Science, 253,* 1380–1386.

Strasser, R., & Bingman, V. P. (1997). Goal recognition and hippocampal formation in the homing pigeon (Columba livia). *Behavioral Neuroscience, 111,* 1245–1256.

Striedter, G. F. (1997). The telencephalon of tetrapods in evolution. *Brain, Behavior and Evolution, 49,* 179–213.

Suzuki, S., Augerinos, G., & Black, A. H. (1980). Stimulus control of spatial behavior on the eight-arm maze in rats. *Learning and Motivation, 11,* 1–18.

Swann, J. W., Brady, R. J., & Martin, D. L. (1989). Postnatal development of GABA-mediated synaptic inhibition in rat hippocampus. *Neuroscience, 28,* 551–561.

Swanson, L. W., Köhler, C., & Björklund, A. (1987). The limbic region. I: The septohippocampal system. In A. Björklund, T. Hökfelt, & L. W. Swanson (Eds.), *Handbook of chemical neuroanatomy, integrated systems of the CNS, Part I* (Vol. 5, pp. 125–136). Amsterdam: Elsevier.

Swanson, L. W., & Risold, P.-Y. (2000). On the basic architecture of the septal region. In R. Numan (Ed.), *The behavioral neuroscience of the septal region* (pp. 1–14). New York: Springer.

Swanson, L. W., Sawchenko, P. E., & Cowan, W. M. (1980). Evidence that the commissural, associational and septal projections of the region inferior of the hippocampus arise from the same neurons. *Brain Research, 197,* 207–212.

Szekely, A. D. (1999). The avian hippocampal formation: Subdivisions and connectivity. *Behavioural Brain Research, 98,* 219–225.

Tanila, H. (1999). Hippocampal place cells can develop distinct representations of two visually identical environments. *Hippocampus, 9,* 235–246.

Taube, J. S., & Muller, R. U. (1998). Comparisons of head direction cell activity in the postsubiculum and anterior thalamus of freely moving rats. *Hippocampus, 8,* 87–108.

Taube, J. S., Muller, R. U., & Ranck, J. B. (1990). Head-direction cells recorded from the postsubiculum in freely-moving rats. *Journal of Neuroscience, 10,* 420–435.

Teng, E., & Squire, L. R. (1999, August 12). Memory for places learned long ago is intact after hippocampal damage. *Nature (London), 400,* 675–677.

Teyler, T. J., & DiScenna, P. (1986). The hippocampal memory indexing theory. *Behavioral Neuroscience, 100,* 147–154.

Tinbergen, N. (1963). On the aims and methods of ethology. *Zeitschrift fur Tierpsychologie, 20,* 410–433.

Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological Review, 55,* 189–208.

Vander Wall, S. B. (1982). An experimental analysis of cache recovery in Clark's nutcracker. *Animal Behaviour, 30,* 84–94.

Vanderwolf, C. H. (1969). Hippocampal electrical activity and voluntary movement in the rat. *Electroencephalography and Clinical Neurophysiology, 26,* 407–418.

van Praag, H., Christie, B. R., Sejnowski, T. J., & Gage, F. H. (1999). Running enhances neurogenesis, learning, and long-term potentiation in

mice. *Proceedings of the National Academy of Sciences, USA, 96,* 13427–13431.

van Praag, H., Kempermann, G., & Gage, F. H. (1999). Running increases cell proliferation and neurogenesis in the adult mouse dentate gyrus. *Nature Neuroscience, 2,* 266–270.

Vargha-Khadem, F., Gadian, D. G., Watkins, K. E., Connelly, A., Van Paesschen, W., & Mishkin, M. (1997, July 18). Differential effects of early hippocampal pathology on episodic and semantic memory. *Science, 277,* 376–380.

Walker, M. M., Diebel, C. E., Haugh, C. V., Pankhurst, P. M., Montgomery, J. C., & Green, C. R. (1997, November 27). Structure and function of the vertebrate magnetic sense. *Nature, 390,* 371–376.

Wallraff, H. G. (1996). Seven theses on pigeon homing deduced from empirical findings. *Journal of Experimental Biology, 199,* 105–111.

Wan, H., Aggleton, J. P., & Brown, M. W. (1999). Different contributions of the hippocampus and perirhinal cortex to recognition memory. *Journal of Neuroscience, 19,* 1142–1148.

Warren, S. G., Humphreys, A. G., Juraska, J. M., & Greenough, W. T. (1995). LTP varies across the estrous cycle: Enhanced synaptic plasticity in proestrus rats. *Brain Research, 703,* 26–30.

Waters, N. S., Klintsova, A. Y., & Foster, T. C. (1997). Insensitivity of the hippocampus to environmental stimulation during postnatal development. *Journal of Neuroscience, 17,* 7967–7973.

Wehner, R., Michel, B., & Antonsen, P. (1996). Visual navigation in insects: coupling of egocentric and geocentric information. *Journal of Experimental Biology, 199,* 129–140.

West, M. J. (1990). Stereological studies of the hippocampus: A comparison of the hippocampal subdivisions of diverse species including hedgehogs, laboratory rodents, wild mice and men. In J. Storm-Mathisen, J. Zimmer, & O. P. Ottersen (Eds.), *Progress in brain research* (Vol. 83, pp. 13–36). Amsterdam: Elsevier.

West, M. J., & Schwerdtfeger, W. K. (1985). An allometric study of hippocampal components: A comparative study of the brains of the European hedgehog, the tree shrew, and the marmoset monkey. *Brain Behavior and Evolution, 27,* 93–105.

Whishaw, I. Q. (2000). The septohippocampal system and path integration. In R. Nunan (Ed.), *The behavioral neuroscience of the septal region* (pp. 270–297). New York: Springer.

Whishaw, I. Q., Cassel, J.-C., & Jarrard, L. E. (1995). Rats with fimbria-fornix lesions display a place response in a swimming pool: A dissociation between getting there and knowing where. *Journal of Neuroscience, 15,* 5779–5788.

Whishaw, I. Q., & Gorny, B. (1999). Path integration absent in scent-tracking fimbria-fornix rats: Evidence for hippocampal involvement in "sense of direction" and "sense of distance" using self-movement cues. *Journal of Neuroscience, 19,* 4662–4673.

Whishaw, I. Q., & Jarrard, L. E. (1995). Similarities vs. differences in place learning and circadian activity in rats after fimbria-fornix section or ibotenate removal of hippocampal cells. *Hippocampus, 5,* 595–604.

Whishaw, I. Q., & Tomie, J. A. (1997). Perseveration on place reversals in spatial swimming pool tasks: Further evidence for place learning in hippocampal rats. *Hippocampus, 7,* 361–370.

Whishaw, I. Q., & Vanderwolf, C. H. (1973). Hippocampal EEG and behavior: Changes in amplitude and frequency of RSA (theta rhythm) associated with spontaneous and learned movement patterns in rats and cats. *Behavioral Biology, 8,* 461–484.

Williams, C. L., Barnett, A. M., & Meck, W. H. (1990). Organizational effects of early gonadal secretions on sexual differentiation in spatial memory. *Behavioral Neuroscience, 104,* 84–97.

Williams, C. L., & Meck, W. H. (1991). The organizational effects of gonadal steroids on sexually dimorphic spatial ability. *Psychoneuroendocrinology, 16,* 155–176.

Williams, C. L., & Meck, W. H. (1993). Organizational effects of gonadal hormones induce qualitative differences in visuospatial navigation. In M. Haug, R. E. Whalen, C. Aron, & K. L. Olsen (Eds.), *The development of sex differences and similarities in behavior* (pp. 179–185). Dordrecht, the Netherlands: Kluwer Academic.

Wilson, M. A., & McNaughton, B. L. (1993, August 20). Dynamics of the hippocampal ensemble code for space. *Science, 261,* 1055–1058.

Wiltschko, W., & Wiltschko, R. (1996). Magnetic orientation in birds. *Journal of Experimental Biology, 199,* 29–38.

Wimer, R. E., & Wimer, C. (1985). Three sex dimorphisms in the granule cell layer of the hippocampus in house mice. *Brain Research, 328,* 105–109.

Witter, M. P., Griffioen, A. W., Jorritsma-Byham, B., & Krijnen, J. L. M. (1988). Entorhinal projections to the hippocampal CA1 region in the rat: An underestimated pathway. *Neuroscience Letters, 85,* 193–198.

Witter, M. P., Wouterlood, F. G., Naber, P. A., & van Haeften, T. (2000). Anatomical organization of the parahippocampal-hippocampal network. In H. E. Scharfman, M. Witter, & R. Schwarcz (Eds.), *The parahippocampal region: Implications for neurological and psychiatric diseases* (Vol. 911, pp. 1–24). New York: New York Academy of Sciences.

Wood, E. R., Dudchenko, P. A., & Eichenbaum, H. (1997). Nonspatial correlates of hippocampal cellular activity in rats performing an olfactory continuous nonmatching to sample task on an open field [Abstract]. *Society for Neuroscience Abstracts, 23,* 502.

Worden, R. (1992). Navigation by fragment fitting: A theory of hippocampal function. *Hippocampus, 2,* 165–188.

Xu, L., Anwyl, R., & Rowan, M. J. (1998, August 27). Spatial exploration induces a persistent reversal of long-term potentiation in rat hippocampus. *Nature, 394,* 891–894.

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