The Evolution of the Cognitive Map

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Abstract

The hippocampal formation of mammals and birds mediates spatial orientation behaviors consistent with a map-like representation, which allows the navigator to construct a new route across unfamiliar terrain. This cognitive map thus appears to underlie long-distance navigation. Its mediation by the hippocampal formation and its presence in birds and mammals suggests that at least one function of the ancestral medial pallium was spatial navigation. Recent studies of the goldfish and certain reptile species have shown that the medial pallium homologue in these species can also play an important role in spatial orientation. It is not yet clear, however, whether one type of cognitive map is found in these groups or indeed in all vertebrates. To answer this question, we need a more precise definition of the map. The recently proposed parallel map theory of hippocampal function provides a new perspective on this question, by unpacking the mammalian cognitive map into two dissociable mapping processes, mediated by different hippocampal subfields. If the cognitive map of non-mammals is constructed in a similar manner, the parallel map theory may facilitate the analysis of homologies, both in behavior and in the function of medial pallium subareas.

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Introduction

In 1947, Edward C. Tolman addressed his colleagues at Berkeley with a bold argument for the existence of a mental representation in the rat. He proposed that rats have a cognitive map; that 'in the course of learning, something like a field map of the environment gets established in the rat's brain... And it is this tentative map, indicating routes and paths and environmental relationships, which finally determines what responses, if any, the animal will finally release.' [Tolman, 1948, p 192]. Thirty years later, John O'Keefe and Lynn Nadel made the equally bold proposal that this map was mediated by the rat's hippocampal formation [O'Keefe and Nadel, 1978]. The concept of the cognitive map is now widely used as a framework for hippocampal function [Burgess et al., 1999a, b]. The cognitive map can be operationally defined as novel route construction that cannot be explained by orienting either by pure path integration or by the use of beacons coincident with the goal [Jacobs and Schenk, 2003].

While experimental psychologists were investigating spatial representation in laboratory mammals, animal behaviorists had begun studying the mechanisms of long-distance navigation in birds [Baker, 1984]. Gustav Kramer, a pioneer in this field, first demonstrated the use of the sun as a compass in orientation [Kramer, 1952], and soon after proposed the concept that pigeons must navigate using both a compass and information organized in a

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map-like way [Kramer, 1953; reviewed in Schmidt-Koenig, 1979]. This became known as the 'map and compass concept' of long-distance navigation, where the navigator homes accurately from an unfamiliar release point. The map-and-compass concept was developed further, notably by Hans Wallraff [Wallraff, 1991, 1996], and has remained the theoretical framework for research in avian navigation, despite controversy on the exact nature of the map [Schmidt-Koenig, 1979; Baker, 1984; Berthold, 1993; Walcott, 1996]. In contrast, the concept of a mental representation in rats, such as the cognitive map, was anathema to the prevailing behaviorist climate in psychology at that time [Glickman, 1985] and did not stimulate subsequent research until the role of the hippocampus was identified [Best and White, 1999]. It is only recently, therefore, that the parallels between the cognitive map of the laboratory rat and map-and-compass navigation in the pigeon have been openly discussed [Bingman, 1990].

The question remains: is the rat's cognitive map functionally equivalent to map-and-compass navigation in pigeons? The similarities between the two systems, and their reliance on the hippocampus, certainly suggests that these types of spatial orientation could be homologous. If so, does the rat use a map and a compass? Perhaps because we assume a navigating rat does not require a compass in a small test room, theoretical models have focused on the hippocampal topographic map, which is encoded using some directional information, and how this map encodes both spatial and nonspatial information [McNaughton et al., 1996; Eichenbaum et al., 1999].

Yet test spaces of different sizes may or may not recruit different brain structures, and a maze in a room might or might not pose the same problem as a release in open territory. In both cases, the navigator is released in a new location and must find its way to a familiar goal by constructing a novel route. New studies of pigeons orienting in large indoor test rooms indeed suggest that their use of landmarks is similar to that seen in laboratory rats [Prior et al., 2002]. Homing under natural conditions has also been found in a number of mammalian species, including diurnal and nocturnal rodents [Bovet, 1992]. Finally, free-ranging fox squirrels, orienting in an outdoor maze located within their own home range, appear to use similar rules and frames of reference as do laboratory rats orienting in mazes in test rooms [Jacobs and Shiflett, 1999].

The most significant difference between experimental paradigms for the laboratory rat and the homing pigeon may not be the difference between a mammal and a bird, or the absolute distance between release point and goal, but the human experimenter's ability to perceive the cues used by the navigator. Generally the laboratory experimenter provides spatial cues that are appropriate for the human range of sensory modalities. Yet even for visual stimuli, humans and passerine birds see the world in remarkably different ways [Bennett et al., 1994]. For sensory modalities where humans have less range of sensitivity, e.g., olfactory or auditory cues [Dusenbery, 1992], we know even less of the sensory environment perceived by the navigator. The general solution is to simply remove or render unreliable as many sources of nonvisual information as possible. Yet a fundamental principle of spatial orientation is that navigators utilize multiple and redundant sources of spatial information [Keeton, 1974]. It is not clear therefore how removing sensory back-up systems affects the spatial behaviors being measured in the laboratory.

We are left with the conclusion that map-and-compass navigation in the pigeon may or may not be isomorphic to the cognitive map of the laboratory rodent, which itself is often an overused and ill-defined concept [Brown, 1992; Bennett, 1996]. Nonetheless, both behaviors are mediated by the hippocampal formation [Morris et al., 1982; Bingman et al., 1995] and in both rodents and passerine birds, hippocampal size and development are correlated with spatial behaviors in the field [Sherry et al., 1992; Clayton and Krebs, 1995; Jacobs, 1995]. To determine if these map-like behaviors are homologous, the first step is define them as precisely as possible.

Unpacking the Cognitive Map

Definitions of the cognitive map range from the general, 'a record in the central nervous system of macroscopic geometric relations among surfaces in the environment used to plan movements through the environment.' [Gallistel, 1990, p 103] to the specific, 'The essence of such a structure is the existence of a global representation of objects within some manifold or coordinate system from which their mutual spatial relationships can be derived. For example, if the distances from A to B and A to C are known, then the directed distance from B to C can be extracted from the coordinate framework and the animal might thus generate a novel trajectory from B to C, even if the features of C are not immediately perceptible. The fundamental implication of the theory of 'cognitive mapping' is the existence of an internal representation of such an absolute place existing independently of objects or sensory events, but within which such experiences can be located. Such an internal model does not depend on body
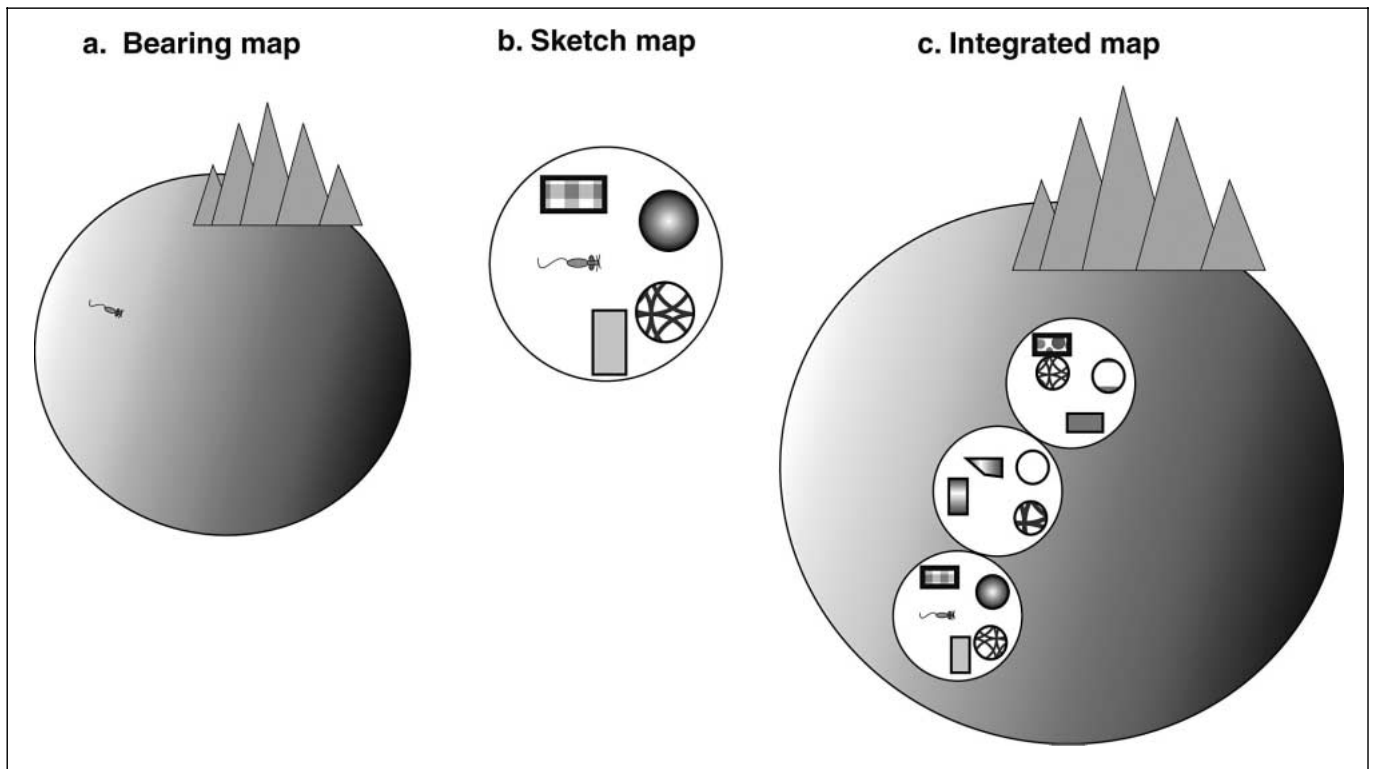
Fig. 1. A schematic of the parallel map theory. (Reprinted with permission of the American Psychological Association.) **a** Bearing map. This map is constructed from directional cues such as compass marks and gradients. Here the bearing map is formed from the transection of two gradient maps: a chemical gradient, based on odorant concentration and a visual gradient, based on a distant compass mark. Shading density represents odorant concentration. Jagged object, a compass mark. **b** Sketch map. This topographic map is constructed from the relative position of fixed positional landmarks. Solid and patterned geometric figures, positional landmarks. **c** Integrated map. This map is constructed from the integrated bearing and sketch map. By linking all sketch maps to the single bearing map, the rat can compute novel routes. Shading density represents odorant concentration. Jagged object, a compass mark. Solid and patterned geometric figures, positional landmarks.

orientation but is assumed, in some abstract way, to maintain its orientation with respect to the external world with rotation of the animal.' [Leonard and McNaughton, 1990, p 365]. Even the role of the hippocampus in mediating the cognitive map has always been controversial [Olton et al., 1980; Best and White, 1999]. More recently, treatments known to impair hippocampal function have had unpredictably mild effects on spatial orientation [Bannerman et al., 1995], which has led Eichenbaum and others to propose that spatial processing is a special example of a more abstract hippocampal function, such as relational computations [Eichenbaum et al., 1999]. This issue is also discussed by Day [2003].

One approach to this controversy is that proposed by Tinbergen in 1963 – to analyze a behavior at four conceptual levels [Tinbergen, 1963]. For the cognitive map, the questions are then: what is the physiological mechanism of the cognitive map, how does the map develop in ontogeny, what is its current adaptive significance and finally, how did such a map evolve?

The Parallel Map Theory

Recently, Françoise Schenk and I have applied this approach to the question of hippocampal function and the cognitive map. Integrating perspectives from the phylogeny, development, physiology, structure and function of the hippocampal formation of the laboratory rodent, we proposed the parallel map theory of hippocampal function [Jacobs and Schenk, 2003], which is summarized here.

The parallel map theory (PMT) is founded on the premise that there is not one map but three: the integrated (or cognitive) map and its two components, the bearing
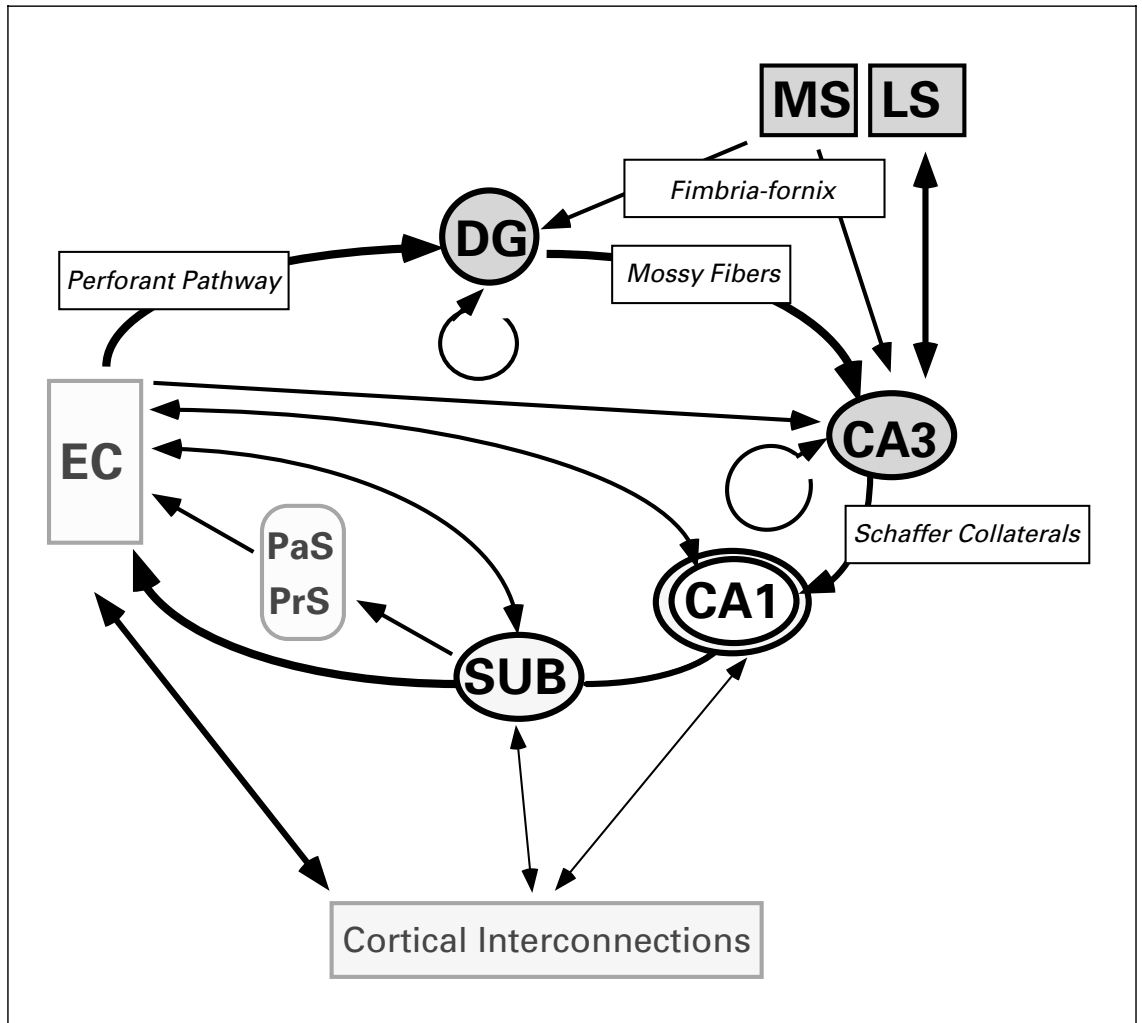
Fig. 2. Major intrinsic connections of the mammalian hippocampal formation, adapted from Amaral and Witter [1995] and reproduced with permission from the American Psychological Association. The direction of connections leads to the step-wise assembly of the integrated map. Fiber tracts are shown in italics. A unidirectional connection is indicated with a single-headed arrow, and a reciprocal connection is indicated with a double-headed arrow. Circular fields, hippocampal formation structure. Rectangular field, extrahippocampal structures. Dark shading, bearing map; white, sketch map; light shading, integrated map. EC, entorhinal cortex; DG, dentate gyrus; MS, medial septum; LS; lateral septum; CA1 and 3, fields of Ammon's horn; SUB, subiculum; PaS, parasubiculum; PrS, presubiculum.

map and the sketch map(s), which when integrated can create the novel shortcut (fig. 1). We introduce the term integrated map to distinguish it from previous definitions of the cognitive map, although it serves the same purpose. The bearing map is a multicoordinate grid map, derived from sources of distributed stimuli such as gradients. A sketch map encodes and stores fine-grained topographical data and is constructed from the memory of the positions of unique cues. The bearing and sketch maps are mediated by independent structures in the hippocampal for-

mation, with the bearing map mediated primarily by the dentate gyrus (DG) and CA3 subfield of the hippocampus proper, whereas a sketch map is mediated primarily by the CA1 subfield (fig. 2).

The bearing and the sketch maps thus represent two classes of maps. They are also constructed from two classes of cues, defined as directional and positional. Directional cues can include distributed cues such as gradients of odor, light or sound, as well as compass marks, distal visual landmarks which provide directional

but not distance cues. Positional cues are discrete and unique objects, often near the goal, that can be used to estimate distance accurately to the goal. This results in significant differences in the construction and use of the bearing and sketch maps.

The maps also differ in their stability and plasticity. The bearing map is a singular entity or representation that provides a coarse estimate of position over large distances. Once created, it serves as a scaffold for the localization of positional cues in absolute space or for global positioning. The sketch map, in contrast, is not a singular representation but a type of map. Sketch maps may coexist as a population of topographic representations of local spaces, where each sketch map encodes the navigator's position within a specific panoramic array. Such maps arise from disjoint explorations, where a navigator may experience several local areas without recognizing their directional relationship to each other (i.e., without forming an integrated map), and encodes them into separate sketch maps. Unlike the bearing map, where position can be deduced by estimating the rate of change in a gradient, a sketch map requires significant spatial memory to encode the features of individual landmarks in an array. Sketch maps may be temporary or long-lasting; they are maintained in the hippocampus as an intermediate memory store during the period of consolidation, until they are overwritten. Should the information prove to be stable, such sketch maps are consolidated relative to the bearing map. This process is mediated by the CA3 subfield of the hippocampus, which converts bearing map coordinates into discrete positional cues, that are then combined with the positional cues supplied by the CA1 subfield.

Hence in the PMT formulation, the rat hippocampus encodes position in three ways: on the grid-like bearing map, constructed from directional cues including gradients, or on a topographic sketch map, where position is defined by triangulation to discrete, local cues but divorced from the global framework, or on the integrated (or cognitive map), where multiple sketch maps are encoded relative to the single underlying bearing map (fig. 1).

Dissociating the Maps

Because the bearing map and the sketch map are mediated by different hippocampal structures, impairment of one structure should reveal residual learning by the other map. For example, if the DG is impaired, the residual sketch map phenotype (rS) will be expressed. Likewise the inactivation, impairment or lesion of a critical component of the sketch map channel (such as CA1 lesion or NMDA receptor blockade) will result in the residual bearing map phenotype (rB). These phenotypes can be behaviorally distinguished by the orientation of the navigator: the rS navigator continues to orient to remembered local cues and will even triangulate within arrays of such cues. But it cannot orient in a global framework and appears to have lost any sense of direction, other than simple stimulus-response approach or avoidance of single stimuli. The rB navigator, in contrast, is well-oriented within its coarse-grained directional map but cannot encode or recall the position of the goal relative to local cues. It can, however, orient well in a small arena, moving along transects towards directional cues (e.g., beacons, compass marks, sensory gradients).

Either of these residual map phenotypes may also appear because of the specific task environment, which is defined as the stimuli perceived by the navigator in a specific environment. Because the bearing map relies on directional cues, the loss of such cues should result in the rS phenotype, whereas the loss or randomization of positional or local cues should reveal the expression of the underlying rB phenotype. If a navigator has oriented to a space using primarily one or the other map, however, the loss of this type of cue may result in severe disorientation. This is necessarily a brief account of PMT and the interested reader is directed to the full discussion in Jacobs and Schenk [2003].

Implications of the Parallel Map Theory for Cognitive Maps in Other Taxa

In the literature on hippocampal function, the sketch map is similar to other formulations of the hippocampal map created by the CA1 subfield. The bearing map, in contrast, has few, if any, precedents in neurobiological studies of orientation in the laboratory rat [reviewed in Jacobs and Schenk, 2003]. Yet the dichotomy of maps proposed in PMT is derived from the map-and-compass concept and hence it is not surprising that the behavioral level of explanation has much in common with other models derived from this framework. For example, in Wallraff's model, the gradient or grid map is also used with extrapolation for long distance navigation and the mosaic maps are also topographic maps, constructed from remembered landmarks [Wallraff, 1991].

Such similarities suggest that similar processes may be operating in birds and mammals. Multicoordinate grid maps were first proposed in 1882 by Viguier to explain long-distance navigation in birds. This question was reopened in the mid-twentieth century by Yeagley's pro-

posal that the grid map was derived from the Coriolis force and the geomagnetic field and Matthews's proposal that birds use the gradient of the sun's movement [reviewed in Baker, 1984]. More recent proposals are the use of olfactory gradients [Papi, 1990; Wallraff, 1996]. The olfactory theory of pigeon homing, whether used as a topographic mosaic map or a gradient map, was initially greeted with skepticism [Baker, 1984] but now has arguably garnered as much or more support as its chief rival, the geomagnetic topographic map or grid map [Bingman and Able, 2002]. The use of multicoordinate grid maps, using geomagnetic gradients of inclination and intensity, has also been proposed as an explanation for homing accuracy in the green and loggerhead sea turtles [Lohmann et al., 1999].

The Constraints of Anatomy

PMT is derived from the specific anatomy of the mammalian hippocampal formation and hence it is not obvious that the same theory will apply to other vertebrates. To test the theory precisely requires studying the function of homologous subfields and their function in other groups. The bearing map function should then be subserved by the DG homologue, the sketch map by the CA1 homologue, and the integrated map should be found only when the bearing and sketch map homologues are both present and integrated, as in the mammal. The sketch map may also require significant input from extrahippocampal structures, such as isocortical areas and the subicular formation in the mammal. If so, then the sketch map may be absent in taxa that lack homologues of such multimodal association areas.

An alternate scenario, however, is that the parallel map solution is reached by different vertebrate lineages using different neural substrates. If the map is mediated by different areas in the medial pallium, such a process would not be homology but parallel homoplasy [Northcutt and Kaas, 1995]. Despite the similarities in function between the hippocampus of birds and mammals [Colombo and Broadbent, 2000], the actual subfield homologies, if any, are currently not known. Several proposals have been made based on anatomical and physiological similarities between the bird and mammal hippocampus [Szekely, 1999; Atoji et al., 2002; Hough et al., 2002; Siegel et al., 2002; Bingman et al., 2003; Kahn et al., 2003], but more research will be needed to resolve these issues. The homologues of structures such as the entorhinal cortex and subiculum are also under investigation; taxonomic differences in these presumed homologues must also have consequences for the size, resolution and encoding of the sketch

map. There may also be significant differences in the use of sketch maps – a flying animal may be able to perceive more beacons, which it could use to routinely connect multiple sketch maps into a single sketch map. Hence a bird, unlike the terrestrial, nocturnal rat, may encode a single sketch map and a single bearing map.

Assigning accurate homologies among vertebrate taxa for the DG-mediated bearing map may have a greater chance of success. Convergent evidence suggests that the small-celled area of the medial cortex in the lizard is homologous to the mammalian DG [Hoogland et al., 1998]. In the pigeon, there are arguments for [Siegel et al., 2002] and against [Atoji et al., 2002] the presence of the DG homologue. The septal nuclei, however, are homologous in reptiles, mammals and birds [Butler and Hodos, 1996]. Here, too, there are remarkable similarities and differences in the pattern of efferents and afferents among the septal nuclei, the dorsal diagonal band and the hippocampus between birds and mammals [Krayniak and Siegel, 1978a, b; Atoji et al., 2002]. If, however, there are sufficient similarities in structure and connectivity in the septohippocampal system among reptiles, birds and mammals, then we should find a homologous form of orientation that operates like a mammalian bearing map.

A caveat: the hippocampus does not mediate all spatial behavior. Rats with hippocampal lesions still have a rich battery of spatial abilities, including path integration [Alyan and McNaughton, 1999], orientation to beacons [Whishaw and Gorny, 1999] and orientation to a known goal using familiar paths [Schenk et al., 1995]. Thus a species that lacks the integrated map may also show sophisticated place learning, as has been shown in ants and bees [Collett, 1996].

Without losing sight of the limits of our knowledge of hippocampal homologies, we can still ask: if the reptile, bird, and fish medial pallium also maps space, what is the evidence that it does so in a way predicted by PMT?

The Case of the Homing Pigeon

With the exception of the laboratory rat in the laboratory maze, more research on spatial orientation has been devoted to the homing pigeon and its ability to navigate from unfamiliar release points, than any other vertebrate species [Berthold, 1991]. Hence any theory of navigation in vertebrates must address this body of work. If pigeon behavioral data are consistent with the pattern seen in the rat, this could inform the subsequent search for structural homologies or homoplasies between birds and mammals.

The question of the precise mechanism or sensory modality by which pigeons accomplish map-and-compass navigation is still a matter of debate [Able, 1996; Wallraff, 1996; Wiltschko, 1996], even if there is a general consensus on the basic principles and the phenomena involved. First, pigeons appear to be using a Kramerian map and compass [Berthold, 1993]. Second, this navigational map allows a pigeon to home from unfamiliar release points [Wallraff, 1991]. The sensory modality that leads to the establishment of navigational maps is determined by the pigeon's experience during rearing [Wiltschko et al., 1987]. The navigational map could thus be derived from different sources of gradients, depending on the developmental context. These could include large-scale atmospheric patterns of odorants [Wallraff, 1991], patterns in infrasound [Hagstrum, 2000] or geomagnetic fields [Wiltschko and Wiltschko, 1996]. In addition to the navigational map, pigeons also orient by pilotage, orienting in relationship to familiar visual landmarks that are organized into a mosaic or topographic map, an ability that does not require the navigational map [Bingman, 1990]. Such mosaic maps could be based on visual, auditory or even olfactory stimuli [Wallraff, 1991].

If this summary of a complex body of work is correct, I would then restate the case of the homing pigeon in the following parallel map terms. The homing pigeon, with its well developed olfactory centers and hippocampal formation [Casini et al., 1997], is able to return from unfamiliar release points using its integrated map. The integrated map is created from its experience during rearing. Specifically, the pigeon uses voluntary movement (i.e., free flight) to systematically sample and map gradients of odorants near the home loft. These data are used early in ontogeny, at the time of first exploration, to form a bearing map. The pigeon may also learn to use other gradients, such as geomagnetic fields or infrasound gradients. All of these sources of distributed stimuli serve as directional cues, and all may be incorporated into the permanent bearing map. Whether they are retained will depend on their reliability in space and time; unstable inputs will not be consolidated, as is true in rats for sources of spatial information [Biegler and Morris, 1993]. Thus the ontogeny of the pigeon will be paramount in determining the final components of its bearing map, as has been already established [Wiltschko et al., 1987].

During ontogeny, the pigeon also encodes topographic arrays of landmarks in the local neighborhood of the home loft. The combination of using flight to explore the terrain and the pigeon's high visual acuity should lead to rapid learning of positional landmarks. This would result in the encoding of one or more sketch maps. Such sketch map(s) are then coactivated with the bearing map to form an integrated map. Hence the pigeon, like the rat, would possess an underlying bearing map, derived from distributed cues (odorants, geomagnetic fields) and an updateable topographic sketch map, based on the array of landmarks near the home loft.

Should the pigeon now be released from an unfamiliar site, it would present the rB phenotype: its sketch map rendered useless in the face of unfamiliar landmark arrays, it would resort to the coarse-grained bearing map. Experimental manipulations that remove input to the bearing map, such as blocking olfactory inputs at the release point, would disrupt even this map and the bird would become disoriented. Other disruptions of the bearing map would include manipulations of magnetic field detection or other important directional cues, such as the sun compass. Finally, because sketch maps are combined at points of common features, sketch maps in the flying pigeon may be more integrated than those in the rat. This might lead to limited cognitive mapping ability even with lesions to the bearing map channel. However, this would only be manifest in the ability to create new shortcuts between remembered locations [i.e., between points B and C, as defined earlier in the quote from Leonard and McNaughton, 1990] not to orient homewards from a completely unfamiliar release point.

Because the sun's movement is a distributed cue, the bearing map also incorporates data from the sun compass. Thus the orientation of clock-shifted birds should represent a specific deflection or impairment of the bearing map. The systematic shifted orientation of clock-shifted birds, even from familiar sites, suggests that not only does the bearing map take precedence in unfamiliar sites where the sketch map cannot be used, but may also be the default orienting mechanism in familiar areas. Thus with the clock shift, the bearing map overrides the sketch map and hence the pigeon shows a directional shift, even when the topographic information has not changed. The same phenomenon has been observed in small-scale orientation in other contexts: despite the presence of well-learned positional cues, clock-shifted scrub jays, nutcrackers [Wiltschko and Balda, 1989], pigeons [Chappell and Guilford, 1995] and black-capped chickadees [Duff et al., 1998] persist in searching for hidden food at the predicted compass deviation.

Hippocampal Lesions
Once the integrated map is consolidated into long-term memory in the mammal, hippocampal lesions do not

affect the memory of a familiar location [Squire, 1992]. Thus the lesion of the pigeon's hippocampus should leave the previously consolidated bearing map unimpaired. It should affect only the acquisition of new data into the bearing map and any new sketch maps or their coactivation with the integrated map. Hippocampus-lesioned pigeons should not be able to learn new arrays of landmarks or new olfactory gradients but their use of the bearing map for true navigation from unfamiliar locations should be unchanged. The exception to this would occur if the only sensory input to the bearing map at the unfamiliar site was a recently acquired directional cue (e.g., new olfactory gradient). In this case, with no data from the consolidated set of directional cues, the pigeon should be amnesiac for direction.

This interpretation is consistent with lesion studies: the lesion of the hippocampus in the adult pigeon does not impair the navigational map from a familiar release point [Bingman, 1990], but such a lesion does impair the acquisition of the map in naive pigeons [Bingman et al., 1990] and in adults released in unfamiliar surroundings [Bingman and Yates, 1992]. The lesion of the piriform cortex, which mediates the olfaction-based map, impairs navigation in a similar manner, suggesting that olfactory input is critical for the pigeon's map [Gagliardo et al., 1997].

It is important to note that with extended training, a complete hippocampal lesion can be overcome in rats [Whishaw and Jarrard, 1995]. The explanation for this is the slow retraining of other neural structures for limited mapping ability. For example, the laboratory rat's parietal cortex is capable of limited mapping of an object array [Long and Kesner, 1998], and this, in combination with the pre-lesion reference memory stored in the subiculum, is probably sufficient for simple orientation tasks with sufficient training [Jacobs and Schenk, 2003]. Thus the later recovery of the pigeons with hippocampal lesions might be attributed to a similar form of plasticity in the avian brain. A hippocampal lesion in a naïve bird, however, should prevent the formation of the bearing map.

The parallels in function between the pigeon and rat hippocampus are quite consistent [Colombo and Broadbent, 2000; Bingman et al., 2003]. The present challenge is to resolve the issue of homologies of hippocampal subfields and the differences in connectivity to extrahippocampal structures, particularly the septal nuclei and the homologues of the entorhinal cortex and the subicular formation. This is no easy task, as the structure and function of mammalian hippocampal and subicular formations and parahippocampal areas are still under investigation [Amaral and Witter, 1995; Witter et al., 2000]. Yet we

must know a subfield is homologous before we can assign function (bearing or sketch map). The septal nuclei, homologous in birds and mammals [Butler and Hodos, 1996], should be critical to the bearing map in both groups, and the similarities and differences in connectivity between mammals and birds have been well-studied [Krayniak and Siegel, 1978a, b; Atoji et al., 2002]. If similar in function, a lesion or inactivation of the septal nuclei should result in a rS map phenotype. Thus, the pigeon could still use pilotage (i.e., use of previously learned sketch maps) but not the navigational map from an unfamiliar release point (i.e., use of the bearing map). In other words, this manipulation should be similar to that seen in anosmic birds. The septal-lesioned birds could continue to encode sketch maps, however, and should show little impairment for orientation to local arrays of cues, either in homing experiments or in laboratory arena experiments. Lacking a bearing map, they would not be able to link sketch maps, however, and hence could not solve cognitive mapping problems (e.g., novel routes to remembered locations in open arenas).

In conclusion, there is the potential to build substantial theoretical and empirical bridges between the results from the homing pigeon and the laboratory rat. PMT may or may not be applicable to the avian hippocampus, but it suggests testable hypotheses that could elucidate the similarities and differences among avian and mammalian hippocampal function.

The Problem of the Turtle

The green sea turtle, like the homing pigeon, has been the subject of much research on the sensory modalities used in navigation [Lohmann and Lohmann, 1996]. However, only recently have researchers succeeded in studying map-like behavior of turtles in the lab [for review see Salas, et al., 2003]. The presence of place learning in chelonians and its conspicuous absence in squamate reptiles raises the question of the function of the medial cortex in reptiles. Salas and colleagues have demonstrated true place learning in the red-eared slider turtle, where place, but not cue, learning is impaired by the lesions to the medial pallium homologue, the medial cortex [Rodriguez et al., 1994, 2002; Lopez et al., 2000, 2001]. Earlier experiments using a plus maze [Lopez et al., 2000] were less conclusive as accurate performance on a plus maze can be subserved by accurate direction, not place, learning; similar results have been found in mice with hippocampal impairments [Jacobs and

Schenk, 2003]. The more recent task, orientation to one of four visual feeders [Lopez et al., 2001], is clearly assaying spatial and place learning.

In contrast, there is as yet no positive evidence (and a wealth of negative evidence) for true place learning in a lizard [Day et al., 1999a, b, 2001]. There is therefore a significant discrepancy in the different performance by the representatives of these taxonomic groups in the laboratory mazes. There are two ways to resolve the problem: either place learning was not in fact observed in the 4-feeder study or the turtle is not a lizard. I would suggest that there is merit to each argument, which reemphasizes the importance of these studies by Salas and his colleagues [Salas et al., 2003], as well as the need for more studies.

The 4-feeder task requires the recall of the baited location on one of four visible feeders. The memory load (1 of 4, reference memory) is hence similar to the plus maze, yet here the turtle chooses its own search trajectories. Probe trials which removed, occluded or transposed positional cues in the room all resulted in significant loss of spatial accuracy in the place-trained group, but not the cue-trained group. Thus the behavior of the turtles was similar to that seen in mammals on equivalent tasks [Lopez et al., 2001].

The turtles clearly oriented to a place in relation to visual cues. But did they encode individual landmarks as directional cues in their bearing map or did they encode the array of landmarks as a sketch map? This could be tested by dissociating directional and positional cues, which should dissociate contributions by the turtle's presumed bearing and/or sketch maps. The cue transposition probe that was used in this study was a combination of some cues being rotated and some cues being transposed, and predictably impaired the place-learning group [Lopez et al., 2001]. If all cues were rotated, a turtle relying on the bearing map, i.e., taking its bearings from directional cues or orienting within a space polarized by an asymmetric array of landmarks, should show rB phenotype, characterized by long transects of the space [Jacobs and Schenk, 2003, fig. 4]. If they were relying on the sketch map, they should show accurate orientation to the goal as newly defined by the rotated position of positional cues. Removing the goal should result in a looping search pattern at the goal [Jacobs and Schenk, 2003].

The second argument to explain the discrepancy in results among reptiles, i.e., that a turtle is not a lizard, is predicated on the significant phylogenetic and physiological differences between turtles and lizards. Day [2003] has reviewed the differences between structure and function of the medial cortex in turtles and lizards elsewhere in this issue. An important difference is that turtles receive a direct visual sensory input from thalamus to the dorsal cortex which is lacking in lizards [Hall and Ebner, 1970; Bruce and Butler, 1984] that could supply a nascent sketch map with sufficient visual input to encode the array.

A more fundamental consideration, however, is the phylogenetic relationship of the lizard and turtle species studied. The taxonomic status of chelonians is currently uncertain. Mitochondrial DNA evidence suggests that the living sister group to turtles are the archosaurs (birds and crocodiles), whereas phylogenetic trees derived from morphological analyses suggest that the sister group is the lepidosaurs (lizards, snakes) [Zardoya and Meyer, 2001]. It is conceivable that new studies of spatial learning in turtles may help to resolve this debate. If turtles show evidence of place learning that is more similar to birds, then it may be because they are more closely related to this group. And if such phlyogenetic distance can be used to predict similarities of cognitive function, then a further prediction is that spatial mapping by crocodilians should be more similar to that seen in birds and turtles (i.e., presence of all three maps: bearing, sketch map and integrated map) than that seen in lizards and snakes (i.e., rB phenotype).

Clearly, there is much work to be done. An important consideration is that studies of spatial learning in reptiles by Day [1999a, b, 2001], Lopez et al. [2000, 2001] and Holtzmann et al. [1999] have been necessarily restricted to one or two species and a limited number of tasks. Even within passerine birds, spatial encoding strategy and capacity varies predictably with hippocampal size, with food-storing species relying more heavily on a global frame of reference, at least as defined in these task environments [Brodbeck, 1994; Clayton and Krebs, 1994]. Spatial encoding can also vary within family and genus in corvids [Kamil et al., 1994]. To tease apart the effects of ecological selective pressures and phylogenetic distance, the design of future studies must use a wider range of species and tasks that are chosen to dissociate specific hypotheses.

Implications for Other Taxa

Rodriguez, Salas and colleagues have also recently demonstrated place learning in the goldfish, using the plus maze and the 4-feeder task [Rodriguez et al., 2002]. The question of the cognitive map in the goldfish is clearly important to our understanding of medial pallium func-

tion. What is the structure and function of the goldfish hippocampal homologue, the lateral pallium? Given the differences in structure and connectivity between the mammalian and the actinopterygian brain, what homologies exist? Can they create a cognitive map? If so, do they use two independent circuits to create a cognitive map? This may be a difficult question to answer. Once again, medial septal impairments and the use of behavioral cue dissociation studies could determine if a two-map hierarchy exists. If so, then such tasks could be used to characterize the function of different areas in the lateral pallium of other teleost fish species, as well as other classes of fish. Correlations of subfield volume with life history traits would be another means of testing the parallel map theory. For example, the size of the neural elements coding the bearing map components should be greater in species that rely more heavily on directional than positional cues in navigation. Given that the medial pallium of amphibians also appears to be involved in learning [Bilbo et al., 2000], investigations of ecological correlates of medial pallium subfield size might also be applied to this group.

Finally, spatial learning has been extensively studied in certain invertebrate taxa, particularly hymenopteran insects such as the honey bee [Menzel, 1985; Zhang et al., 1996; Giurfa and Capaldi, 1999], several ant species [Wehner et al., 1996] as well as cockroaches [Mizunami et al., 1998; Durier and Rivault, 2001] and cephalopod molluscs, such as the octopus [Boal et al., 2000] and the squid [Boal et al., 2003]. What is the range and diversity of spatial maps in taxa with such a diversity of nervous systems? What are the common solutions? Dual processing systems are a common solution when there are functional incompatibilities [Sherry and Schacter, 1987]. Hence, as in vertebrates, parallel mapping processes may be found in species where this function is mediated by structures other than the medial pallium.

Conclusion

'Finally, I, personally, would hold further that it is also important to discover in how far these maps are relatively narrow and strip-like or relatively broad and comprehensive... The differences between such strip maps and such comprehensive maps will appear only when the rat is later presented with some change within the given environment. Then, the narrower and more strip-like the original map, the less will it carry over successfully to the new problem; whereas, the wider and more comprehensive it

was, the more adequately it will serve in the new set-up.' [Tolman, 1948, p 193].

As I see it, the challenge for the future is to identify the building blocks of spatial navigation, whether strip- or broad-maps, mosaic or grid maps, sketch or bearing maps, integrated, cognitive or navigational maps – and to determine how these are encoded by different nervous systems. Perhaps map-and-compass navigation in the pigeon, long-distance navigation in sea turtles, and the cognitive map in the laboratory rat are the same behavior, subserved by the hippocampal formation or its homologue. If so, the parallel map theory may serve as a theoretical framework for exploring the nature of spatial navigation, not only in mammals but in other vertebrate taxa as well. But even if we discover that the behaviors are not parallel maps but parallel solutions that have evolved independently in different lineages, even in invertebrates, we will have the beginning of an integrated understanding of the nature of the spatial navigation.

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