# Evolution of Forebrain and Spatial Cognition in Vertebrates: Conservation across Diversity

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## Abstract

Historically the dominant trend in comparative brain and behavior research has emphasized the differences in cognition and its neural basis among species. In fact, the vertebrate forebrain shows a remarkable range of diversity and specialized adaptations. Probably the major morphological variation is that observed in the telencephalon of the actinopterygian fish, which undergoes a process of eversion during embryonic development, relative to the telencephalon of non-actinopterygians (for instance, amniotes), which develops by a process of evagination. These different developmental processes produce notable variation, mainly two solid telencephalic hemispheres separated by a unique ventricle in the actinopterygian radiation that contrasts with the hemispheres with internal ventricles in other groups. However, an increasing amount of evidence reveals that the forebrain of vertebrates, whether everted or evaginated, presents a common pattern of basic organization that supports highly conserved cognitive functions. We analyze here recent data indicating a close functional similarity between spatial cognition mechanisms in different groups of vertebrates, mammals, birds, reptiles, and teleost fish, and we show in addition that they rely on homologous neural mechanisms. Thus, recent functional and behavioral comparative evidence is added to the developmental and neuroanatomical data suggesting that the evolution of cognitive capabilities and their neural basis in vertebrates could have been more conservative than previously realized.

## Introduction

Comparative research on brain and behavior has been historically biased by the deeply rooted idea that vertebrate evolution follows a linear progression from 'inferior' to 'superior' forms [i.e., fishes, amphibians, reptiles, birds, mammals, primates, and in the pinnacle, humans; Hodos and Campbell, 1969, 1990; Deacon, 1990]. The vertebrate 'scale' is characterized by increasing complexity and advancement in brain organization, intelligence, and cognitive capabilities, providing at each 'stage' the evolutionary step towards the 'following' and 'superior' level and culminating, necessarily, in the characteris-

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tics of humans. According to this view, the 'primitive' or 'less evolved' vertebrate groups (e.g., fishes or amphibians) are supposed to have developed relatively simple neural circuits that underlie elemental forms of behavior. In contrast, 'more recent' groups (e.g., mammals) are thought to have evolved additionally more complex and advanced brain circuitry, sustaining more sophisticated behavioral adjustments and cognitive capabilities. Unfortunately, although misleading and anachronistic, this common sense conception of vertebrate evolution is widespread in different fields of neurosciences and psychology, even today.

Modern evolutionary biology provides a very different picture of vertebrate evolution. Rather than representing a linear series of increasing complexity, vertebrates comprise a highly diverse group in terms of morphological and functional specializations, which includes several distinct, parallel radiations derived from a common ancestral stock of fishes that have evolved separately for at least 400 million years [Carroll, 1988]. The vertebrate brain shows a remarkable range of diversity and specialized adaptations, as is apparent even in its external morphology. The degree of variation, also evident in behavioral specializations, has been fulfilled across a long history of phyletic branching and diversification. Not all behavioral and neural features have necessarily changed during the course of evolution, however. Because these radiations share a common evolutionary ancestor, from which all these groups have inherited some common features of brain and behavior organization, the brains of extant vertebrates are likely a mosaic of both primitive and derived characteristics [Wiley, 1981; Northcutt, 1981, 1995; Nieuwenhuys et al., 1998]. Much genetic, neuroanatomical, neurochemical, developmental, neurophysiological, and behavioral evidence indicates that a considerable degree of phyletic invariance of structure and function exists in the brains of vertebrates [Northcutt, 1995; Butler and Hodos, 1996; Nieuwenhuys et al., 1998].

In the present review we will examine recent evidence suggesting that spatial cognition capabilities and their neural basis could have been more conservative than previously realized. Spatial cognition has proven to be a fertile field for comparative neurobiological research. Significant empirical data have been collected over the past few years concerning spatial cognition capabilities and their neural foundations in different groups of vertebrates. In addition, considerable efforts have been made to develop coherent theoretical frameworks to interpret these results.

## Space and Cognition in Vertebrates

The ability to orient and navigate in space depends on a variety of brain mechanisms that encode the environmental information in multiple reference frameworks, centered in the receptive surfaces, in the head, the body, the objects of the exterior world, or in some more abstract directional or spatial characteristics of the environment. For example, substantial evidence shows that some brainstem (e.g., the optic tectum) and telencephalic (e.g., the frontal motor cortical areas or the parietal cortex) centers and neural circuits, are involved in the perception and action based in 'egocentric' frames of reference [Stein and Meredith, 1993; Burgess et al., 1999]. In contrast, other neural centers, such as the hippocampal pallium, seem to be essential for navigation abilities based on 'allocentric' spatial representations [i.e., representations of the 'objective' space that, by including the metrical and geometrical relationships among different features of the spatial environment, are independent of the subject's own position; O'Keefe and Nadel, 1978]. Spatial orientation and navigation require brain mechanisms for sensorimotor integration and for transforming the spatial information from some coordinate systems or reference frameworks into others. Spatial orientation implies a series of translations of the incoming multisensory information (i.e., visual, vestibular, proprioceptive, etc.) from receptive surface coordinates to head-centered coordinates to body-centered coordinates and finally to some stable allocentric or world-centered coordinate framework. Thus, different brain systems and circuits 'capture' different aspects of spatial reality and contribute to spatial cognition. This specialization is evident also in the plasticity phenomena and in the nature of the spatial learning and memory processes subserved by these spatial cognition mechanisms [Nadel, 1994].

Some basic spatial orientation mechanisms and their neural basis appear to be notably well conserved in vertebrates. For example, the degree of similarity in the vestibular mechanisms and reflexes is impressive, from fish to monkeys, including the receptor design and the vestibular neural circuits [Simpson and Graf, 1985; Fritzsch et al., 2000]. The role of the vestibular system is essential in perceptual and motor stabilization by providing an egocentric reference frame [Berthoz, 1999]. In addition, the vestibular system likely provides a 'geocentric' reference frame for orientation, anchored to the invariant direction of gravity forces [Paillard, 1991] and probably also has a role in navigation based in inertial information [Mittelstaedt and Glasauer, 1991].

The tectal mechanisms for sensorimotor integration and orientation in space also appear to be well conserved in vertebrates. The optic tectum (superior colliculus in mammals) is characterized by a specialized cytoarchitecture and microcircuitry and by profuse connectivity with other sensory and motor centers [Vanegas, 1984]. This structure provides a common body-centered frame of reference for multisensory integration and for sensory-motor transformations [Stein and Meredith, 1993] and is a crucial center for the generation of egocentrically referenced actions in space [Sparks, 2002]. Despite a number of differences (for example, in the cellular types and in the lamination pattern, as well as in some neurophysiological mechanisms), it seems that the general organization and functions of the optic tectum have been conserved across phylogeny, even in minute details (see fig. 1). The stability of tectal organization in vertebrates can be observed, for example, in the multisensory integration characteristics [Stein and Meredith, 1993]; in the presence of a spatially ordered motor map in the deep tectal layers in correspondence with the retinotopic visual map in the superficial layers [Salas et al., 1997; Sparks, 2002]; in the neurophysiological mechanisms for generating coordinated eye, head, and body movements; and in the mechanisms for coding the metrics and kinetics of these movements [Du Lac and Knudsen, 1990; Salas et al., 1997; Herrero et al., 1998; Sparks, 2002]. The optic tectum is also conservative in complex neuroanatomical features, such as the pattern of intrinsic and extrinsic connectivity and the organization of the tectoreticular projections, probably serving as a neural interface for transforming the tectal information, coded in spatial coordinates, into a temporal signal in separate brainstem generators in the reticular premotor centers [Torres et al., 2002; Isa and Sasaki, 2002]. Hence, the stability of the morphological and functional organization of the tectal system in vertebrates is really striking. Although, of course, a range of variation exists, which probably reflects the outcome of adaptive processes on an ancestral basic plan of organization inherited from the common vertebrate ancestor, these differences appear to have a minor functional significance.

The evidence showing that brainstem spatial orientation mechanisms remain well conserved in vertebrates does not raise too much controversy, probably because it fits well with traditional conceptions about brain and behavior evolution. However, the situation is quite different with respect to views on the conservation of other spatial cognition capabilities, especially those that require the participation of the forebrain (and in particular the pallium or cerebral cortex). Thus, still today, the dominant trend is that the 'more complex' cognitive capabilities – for instance, those based on the operation of the association multisensory pallium, in the motor cortex or in the hippocampal formation – are present only in a few, 'more evolved' vertebrate groups, such as mammals or birds. This belief is indeed consistent with the old idea that the vertebrate forebrain evolved in successive and sequential steps or phases, according to which the pallium of fishes consists of an olfactory-dominated paleocortex (olfactory pallium), with the subsequent emergence of the archicortex (hippocampal pallium) and, finally, the neocortex (isocortex) in more 'recent' or more 'evolved' vertebrate groups.

Indeed, the forebrain of vertebrates shows a remarkable range of morphological variation and specialized adaptations. For example, a notable developmental divergence in the telencephalon of actinopterygian fishes (for instance teleosts), the eversion or outward bend of the prosencephalic alar plate (instead of evagination), leads to solid cerebral hemispheres separated by a unique ventricle, which contrast with the internal ventricles in the telencephalic hemispheres of non-actinopterygians (for instance, amniotes). Nonetheless, an increasing amount of anatomical, developmental, and functional evidence indicates that the telencephalon presents a comparable basic pattern of organization in every vertebrate group [Northcutt, 1995; Butler and Hodos, 1996; Nieuwenhuys et al., 1998]. Moreover, despite conspicuous morphological and cytoarchitectural differences, equivalent pallial and subpallial zones can be identified, and out-group analysis indicates the homology of the three main pallial subdivisions (medial, dorsal and lateral) in vertebrates [Northcutt, 1981, 1995; Northcutt and Kaas, 1995; Butler and Hodos, 1996; Karten, 1997; Nieuwenhuys et al., 1998; Medina and Reiner, 2000]. Recent gene-expression data

**Fig. 1.** The optic tectum is a crucial neural center for the generation of egocentrically referenced actions in the space. Focal electrical stimulation in the tectum elicits coordinated eye and body movements, postural adjustment, and other motor patterns in teleost fish. **A** Characteristic vectors of evoked saccades depending on the stimulation site in the right tectum of the goldfish *(Carassius auratus)*. In goldfish, as in other vertebrates, orienting-eye movement characteristics depend on the tectal active site, thus revealing a topographically ordered motor map within the optic tectum in alignment with the retinotopic visual map. **B** The amplitude and direction of eye movements depend on the stimulation site within the tectum. The variation of the stimulation site in the rostro-caudal axis produced a systematic change in the amplitude of the horizontal component of
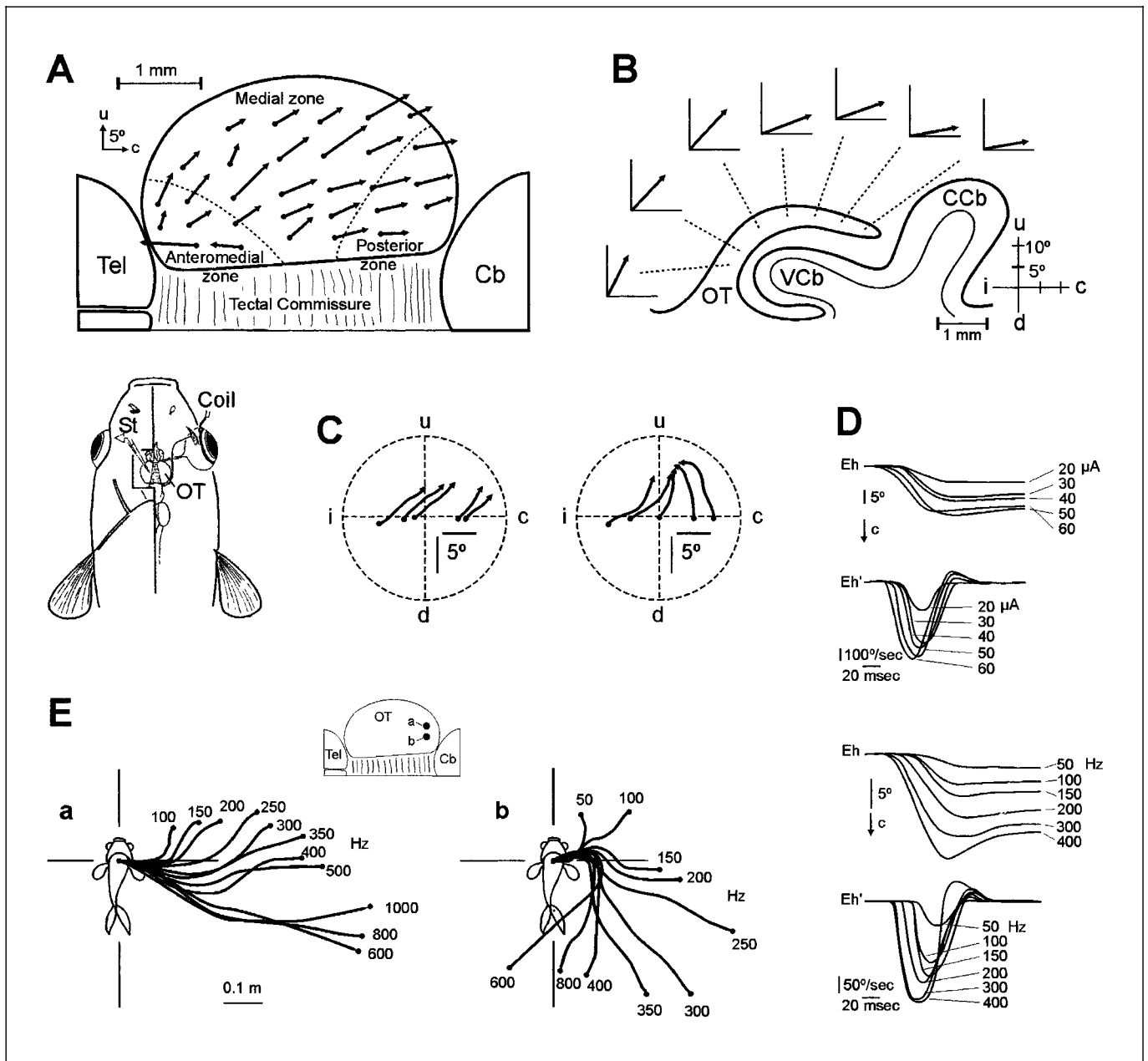
the saccade, whereas the variation of the stimulation site in the medial-lateral axis produced an increase in the vertical component of the eye movements (not shown). **C** The stimulation of anatomically separated tectal areas (as defined in A) evoked different types of eye movements. Left: Fixed vector movements, independent of the initial eye position, indicating that probably eye movements are coded retinotopically (Medial zone). Right: Goal directed movements, whose direction depends on the initial eye position, indicating probably a craneotopic codification of the eye movement direction (Antero-medial zone). **D** The direction and amplitude of the orienting responses depended not only on the tectal stimulation site, but also on the stimulus parameters. The variation of the stimulation parameters (intensity and frequency) produces systematic changes in the metric and kinetic of the evoked orientation responses. **E** Body movements evoked by the electrical microstimulation of the optic tectum in free-swimming fish. Evoked movements consisted of complete orientation responses including coordinated movements of the axial musculature, fins, and eyes, which closely resemble the natural responses. The direction and amplitude of the orienting responses depended on the tectal stimulation site and also on the stimulus parameters. The location of the two stimulation points (**a, b**) is shown on the dorsal view of the tectum. Cb, cerebellum; CCb, corpus cerebelli; Eh, horizontal component of eye position; Eh′, eye velocity trace; OT, optic tectum; St, electrode for microstimulation; Tel, telencephalon; VCb, valvula cerebelli; d, u, i, c, downward, upward, ipsiversive and contraversive direction of evoked eye saccade, respectively. [Modified from Salas et al., 1997 and Herrero et al., 1998.]

strongly support these conclusions about homology. Homeotic genes and other regulatory genes that play an important role in the regional specification of restricted telencephalic zones appear to be highly conserved throughout phylogeny. Thus, some regulatory genes typically expressed in the early amniote subpallium (i.e., *Dlx-1/2*), pallium (i.e., *Emx-1/2*), or pallial-subpallial boundary (i.e., *Pax6*) also conform to a similar pattern in teleost fish [see Wulliman and Rink, 2002].

In mammals, several cortical areas contribute, like the optic tectum, to egocentrically referenced orienting responses, by carrying sensory cross-modal integration and sensory-motor transformations. For example, several areas of the parietal and frontal cortex play a major role in encoding the location of sensory stimuli in different modalities and in coordinating orienting responses within eye-, head-, appendages-, or body-centered egocentric spatial frameworks [Graziano and Gross, 1998]. The neocortex, i.e., those cortical regions lying between the olfactory cortex, laterally, and the hippocampal cortex medially, characterized by hexalaminated structure and specific visual, auditory, somatosensory and motor regions, has long been considered unique to mammals. However, recent comparative evidence calls such 'uniqueness' into question, by indicating that the Wulst of birds, the dorsal cortex of reptiles, and the neocortex of mammals are comparable, and, therefore, might have been inherited from the ancestral pattern of pallial organization present in the stem amniotes [Northcutt, 1995; Karten, 1997; Medina and Reiner, 2000]. In addition, recent evidence shows that the dorsal telencephalic pallium of teleost fish, like the mammalian cortex, presents several separate sensory [i.e., visual, auditory, somatosensory, etc.; Prechtl et al., 1998; Saidel et al., 2001] and motor areas [Jiménez-Moya, 2003], placed in a topological position compatible with the general pallium or isocortex [Northcutt, 1995; Wulliman and Rink, 2002]. Moreover, the motor areas identified in the teleost telencephalon include several somatomotor maps of body movements, topographically ordered, as well as separate eye field areas [Jiménez-Moya, 2003]. This recent experimental evidence indicates that the pallium of teleost fish is organized in separate sensory and motor areas and that the pattern of functional organization could be strikingly similar to those described in mammals.
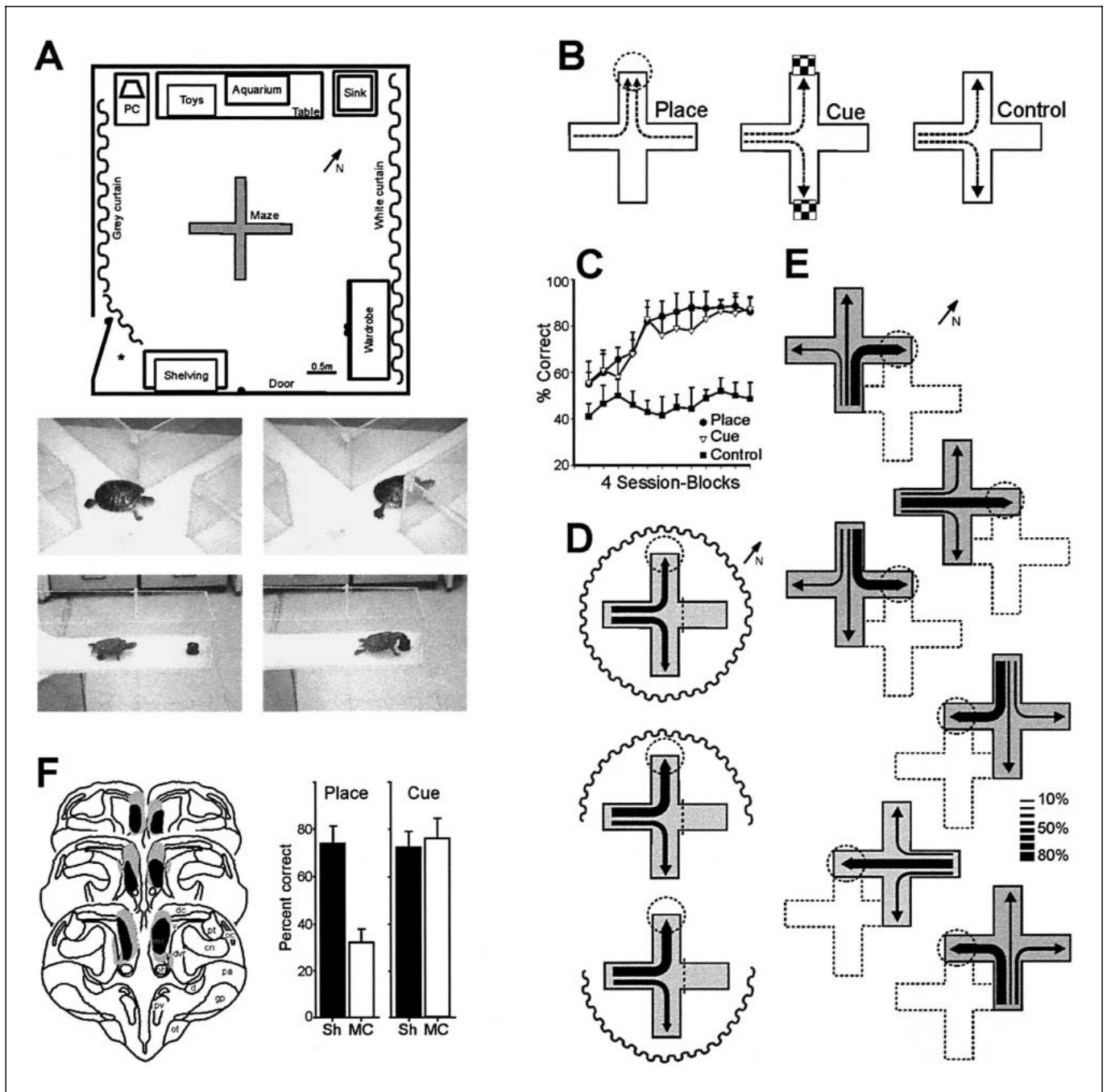
The available data on spatial cognition and its neural basis provide additional evidence consistent with the conservation of a basic pattern of forebrain organization. Thus, a considerable number of studies demonstrate that mammals and birds, in addition to using a variety of ego-

centrically referenced mechanisms for orienting, can use representations of the spatial relationships within an allocentric framework that is independent of the position of the subject [O'Keefe and Nadel, 1978; Nadel, 1991; Bingman, 1992]. Recent experimental evidence indicates that place memory capabilities based on map-like or relational memory representations of the allocentric space, supposedly an exclusive attribute of mammals and birds, are present also in reptiles and fishes (see below). Furthermore, as we will discuss in the following paragraphs, these shared spatial cognition capabilities appear to be based in homologous neural mechanisms: like the hippocampus of mammals and birds, the reptilian medial cortex is critical for cognitive mapping abilities, and similarly, the teleost lateral telencephalic pallium, the presumed homologue to the amniote hippocampus, is selectively involved in spatial cognition.

## Map-like Memory Representations of Allocentric Space in Vertebrates

Substantial evidence obtained over several decades of behavioral and neurobiological research has demonstrated that mammals and birds can use allocentric repre-

**Fig. 2.** Demonstration of place learning in turtles *(Pseudemys scripta)* trained in plus-maze tasks. In addition, recent evidence indicates that the turtle medial cortex, homologous to the hippocampus of mammals and birds, is involved in this spatial cognition capability. **A** Schematic view of the experimental setting, showing the plus-maze and the arrangement of the distal visual cues. The maze is represented in the position used for training trials. **B** Three training conditions were used. Place procedure: the goal (dotted circle) was maintained in the same place of the room throughout the experiment, but two start positions were used randomly (50% each); Cue procedure: A conspicuous intramaze visual cue (checked panel) signaled directly the location of the goal, but the position of the cue (goal) varied in a pseudorandom order from trial to trial; in addition, two start positions were used randomly (50% each); Control procedure: The location of the goal varied in a pseudorandom order from trial to trial; in addition, two start positions were used randomly (50% each). **C** Percentage of correct responses for each group during the training sessions. Place and cue trained turtles both learned their respective tasks accurately. Control animals remained at random level, ruling out the possibility of direct detection of the correct arm by uncontrolled strategies. **D** Schematic representation of the trajectories chosen by the turtles in the place group during probe tests when the distal visual cues were partial or totally occluded. The relative thickness of the arrows indicates the percentage of times that each trajectory was chosen. Turtles' navigation was based on the array of distal landmarks, as demonstrated by the failure to reach the goal when the visual land-

marks were totally occluded, but none of the cues is essential by itself, as demonstrated by the accurate performance during partial occlusion tests. **E** Trajectories chosen by the turtles in the place group in the test trials in which the maze was displaced within the room in such a way that novel start locations, never used during training, were used. The dotted circle shows the location of the goal during training trials. Note that during these test trials the end of one maze-arm always coincided with the goal place. The position of the maze during training is shown in dotted lines. Animals are able to navigate towards the goal spontaneously using novel routes from different directions, demonstrating mapping abilities. **F** Spatial cognition defi-

cits after medial cortex lesions in turtles. In this experiment, the room, the maze and the procedure were the same described above, except that, prior to training, the turtles were randomly subjected to Medial cortex lesions (MC) or sham operation (Sh). Left: Representation of the largest (grey shading) and the smallest (black shading) medial cortex lesions. Right: MC turtles trained in the place procedure showed a dramatic impairment during test trials using new start locations relative to Sh animals, indicating that MC turtles were unable to use place strategies. In contrast, medial cortex lesions did not produce deficits in cue learning. [Modified from López et al., 2001 and Rodríguez et al., 2002b.]

sentations of space for navigation and goal location [i.e., cognitive maps; O'Keefe and Nadel, 1978; Nadel, 1991; Bingman, 1992]. A cognitive map is defined as a map-like, 'world-centered' representation of absolute space that allows the subject to place itself within a stable framework and navigate accurately and flexibly within it. It is interesting to note that these map-like spatial representations, which are true relational memories, can be considered the clearest animal equivalent of human declarative or episodic memory [Clayton and Dickinson, 1998; Eichenbaum, 2000].

Contrary to the traditional view that cognitive mapping capabilities are an exclusive attribute of vertebrate groups that supposedly have evolved more complex associational structures (i.e., mammals and birds), a number of recent, thorough behavioral studies provide strong evidence indicating that reptiles and teleost fish are also able to use cognitive mapping strategies. These studies demonstrate that, like mammals and birds, turtles and goldfish can navigate accurately and flexibly to a goal on the basis of information provided by an array of landmarks, by means of encoding their spatial relationships in a map-like representation that provides a stable frame of reference [Rodríguez et al., 1994; Holtzman et al., 1999; López et al., 1999, 2000c] (fig. 2, 3). One important property of cognitive mapping-based navigation is that, as cognitive maps store redundant environmental information, when a subset of spatial cues become unavailable, accurate navigation is still possible on the basis of those that remain [O'Keefe and Nadel, 1978]. The performance of turtles and goldfish trained in place tasks agrees with this requirement: it is not impaired by the removal or occlusion of any one of the component elements of the landmark array, indicating that none of those cues is essential by itself to locate the goal [Rodríguez et al., 1994; López et al., 1999, 2000c, 2001; Stone et al., 2000] (fig. 2D).

Another distinguishing property of cognitive mapping is the ability to choose the appropriate trajectory towards the goal from novel start locations in the absence of local cues [O'Keefe and Nadel, 1978; Nadel, 1991]. Like mammals and birds, turtles and goldfish spontaneously adopt the most direct routes to the goal from previously unvisited start locations, although the new routes imply navigating in different or even opposite directions and using shortcuts or detours [Rodríguez et al., 1994; López et al., 2001] (figs. 2E, 3C). It is important to note that these results allow us to rule out the possibility that the performance of turtles and goldfish could be based on directional cues, guidance or other egocentric referenced orientation mechanisms, for example, approaching or avoiding a

particular cue, using auditory, odor, or polarized-light gradients, or relying on a 'direction sense' (e.g., a geomagnetic sense). Moreover, the ability of these animals to spontaneously choose the appropriate trajectory without a history of previous training demonstrates their capacity to represent spatial relationships in the environment independently of a body-centered reference system, because the new trajectories imply new (never experienced before) egocentric relations to landmarks.

These data, revealing spatial mapping capabilities in reptiles and teleost fish that closely parallel those described in mammals and birds, suggest the possibility that this cognition trait could have already been present in the last common ancestor of teleosts and land vertebrates and have been retained throughout phylogenesis. If this were the case, these similar behavioral and cognitive capabilities should be based on homologous neural mechanisms. Because the hippocampus is critical for cognitive mapping strategies in mammals and birds, it is important to investigate whether the cognitive mapping capabilities of reptiles and teleost fish are similarly based on the function of the pallial structures considered homologous to the hippocampus of mammals and birds.

## Conservation of Spatial Memory Function of the Hippocampus in Amniotes

In mammals and birds, damage to the hippocampal formation causes selective deficits in solving spatial problems when locating a place requires encoding its reciprocal relationships with an array of environmental features (place learning), but not when approaching a single landmark (cue learning) or when non-spatial discriminations enable the animal to reach the goal [Morris et al., 1982; Good, 1987; Sherry and Vaccarino, 1989; Bingman and Mench, 1990; Fremouw et al., 1997; Pearce et al., 1998].

The medial cortex of reptiles is considered homologous to the hippocampal formation of mammals and birds on the basis of embryological, cytoarchitectural, neurohistochemical, physiological, and connectivity evidence [Northcutt, 1981; Ulinski, 1990; Nieuwenhuys et al., 1998]. Recent experimental evidence indicates also that the medial cortex of reptiles shares a central role in spatial cognition. For example, the relative volume of the medial cortex is larger in a lizard species that forages actively for prey compared to species with a sit-and-wait strategy [Day et al., 1999]. Medial cortex lesions produce a severe and selective place memory deficit in turtles trained in a dry-maze analogue, as indicated by the post-surgery fail-
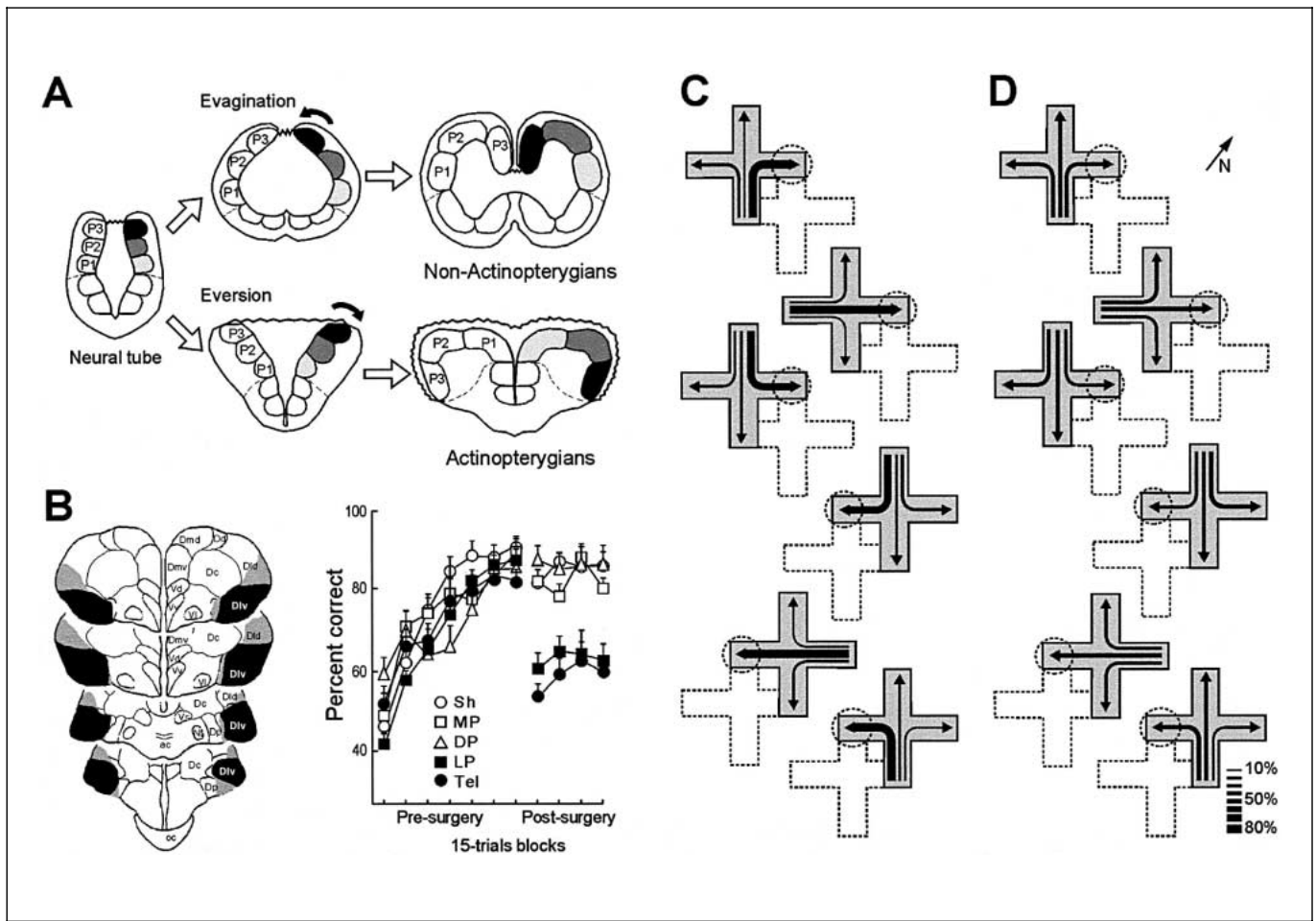
**Fig. 3. A** Schematic representation of the process of evagination and inversion that occurs in the telencephalon of non-actinopterygian vertebrates during embryonic development compared with the eversion or outward bend that occurs in actinopterygians. **B** Spatial memory deficits after lateral pallium lesions in goldfish *(Carassius auratus)*. The experimental room, the apparatus, and the procedure were the same as described in figure 2 with turtles. Left: The largest (grey shading) and the smallest (black shading) lateral pallium lesions. Right: Percentage of correct responses during pre- and post-surgery training for the lateral pallium (LP), medial pallium (MP), dorsal pallium (DP), complete telencephalic ablation (Tel), and sham opera-

tion (Sh) groups. The LP lesioned goldfish showed a dramatic place learning deficit compared with their own pre-surgery performance and relative to Sh, MP or DP lesioned animals. **C** Performance of the Sh goldfish during post-surgery test trials in which novel start locations were used. Sh operated goldfish were able to navigate accurately towards the goal place independently of start position, using novel routes and from different directions, demonstrating mapping abilities. **D** Performance of the LP lesioned goldfish after surgery. The LP goldfish were impaired in performing place responses. [Modified from Rodríguez et al., 2002b.]

ure to navigate to the goal [Rodríguez et al., 2002a]. In addition, medial cortex lesioned turtles trained in standard plus-maze place tasks fail to reach the goal during test trials, indicating that they suffer a severe place-learning impairment. In fact, these animals failed to navigate to the goal when the visual environmental cues in the proximity of the goal were excluded or when novel start positions were used [Rodríguez et al., 2002b] (fig. 2F).

These results indicate that medial cortex lesioned turtles lack the capacity to encode goal location relative to the environmental features in a unique, map-like representation (place learning). Moreover, similar to hippocampus lesions, medial cortex lesions in turtles do not impair, or even facilitate, the use of guidance and other non-relational, egocentric strategies to reach the goal [Powers, 1990; Rodríguez et al., 2002a, b]. That is, the effects of damage

in the medial cortex of turtles and in the hippocampus of mammals and birds are strikingly similar not only in relation to those functions that are impaired, but also in relation to the processes that are not affected or even facilitated.

Amniotes appear to be a monophyletic group that evolved from a single stock of primitive tetrapods during the early Carboniferous [Gaffney, 1980; Carroll, 1988]. Hence, the presence of medial cortex-dependent allocentric spatial learning and memory capabilities in reptiles, birds, and mammals suggest that this trait could be a primitive character in amniotes. That is, it could have been already present in the common reptilian ancestor of modern amniotes that inhabited the earth in the Mesozoic era and have been retained through the evolution of each independent lineage. Indeed, recent experimental evidence showing that the lateral pallium of the actinopterygian fish is similarly involved in place learning suggests the possibility that this spatial cognition-related trait may have appeared even earlier during vertebrate phylogenesis.

## Spatial Memory and Telencephalic Pallium in Actinopterygian Fish

The capability of teleost fish to navigate using map-like or relational memory strategies depends on the forebrain, as indicated by lesion studies. Thus, telencephalon ablations in goldfish severely and selectively disrupt place learning, but not cue learning or egocentric-based strategies [Overmier and Hollis, 1983; Salas et al., 1996a, b; López et al., 2000a, b; Rodríguez et al., 2002b]. Given that the eversion process that takes place during the development of the forebrain in the ray-finned fishes implies the reversal of the pallial medial-to-lateral topography observed in the evaginated telencephalons, the actinopterygian pallial area considered homologous to the amniote medial pallium or hippocampus is the lateral pallium [Northcutt and Braford, 1980; Northcutt, 1995; Nieuwenhuys et al., 1998] (fig. 3A). Recent functional studies agree with this anatomical hypothesis. For example, a study aimed at evaluating possible spatial learning-related changes in the neuronal activity of protein synthesis provided evidence for the selective involvement of the lateral pallium of teleost fish in allocentric navigation [Vargas et al., 2000]. This study investigated the transcriptional activity in different pallial areas in goldfish trained in spatial or cue learning tasks, by means of a silver stain (Ag-NOR) with high affinity for the argyrophilic proteins asso-

ciated with the nucleolar organizing region (NOR) of the neurons. The analysis showed a significant and selective increase in the NOR area of the neurons of the lateral pallium in the animals trained in the spatial learning tasks, relative to the animals trained in cue learning or control procedures.

Additional evidence implicating the teleost lateral pallium in cognitive mapping was provided by selective lesion studies. Thus, lateral pallium lesions produced a dramatic impairment in place learning and memory in goldfish trained in a plus-maze located in a room with an array of extramaze visual cues [Rodríguez et al., 2002b] (fig. 3B). A deficit in finding a familiar place is observed whenever the animals are required to navigate from novel start locations, and also when well trained start locations and routes are used (see fig. 3C–D). In fact, the place memory deficit observed after lateral pallium lesions in goldfish is as severe as that produced by the complete ablation of both telencephalic hemispheres [Salas et al., 1996a, b; López et al., 2000a; Rodríguez et al., 2002a, b]. In contrast, medial or dorsal pallium lesions do not produce any observable impairment in place learning [Rodríguez et al., 2002b] (fig. 3B). Interestingly, the involvement of the lateral pallium of goldfish in spatial cognition seems to be selective to place learning, as damage to this area does not impair cue learning or other egocentric strategies [Salas et al., 1996a, b; López et al., 2000a; Rodríguez et al., 2002b]. In summary, these results demonstrate a striking functional similarity between the hippocampal pallium of amniotes and the lateral pallium of the telencephalon of the teleost fish. The close functional similarity between spatial cognition mechanisms in different groups of vertebrates, which likely rely on homologous neural mechanisms, suggests that the forebrain of vertebrates, whether everted or evaginated, contains a common, conserved basic pattern of organization, probably inherited from an ancestral fish group that gave rise to the extant vertebrate radiations.

## Concluding Remarks

Historically, the dominant trend in comparative brain and behavior research has emphasized the differences in cognition and its neural basis among different species. In neuroscience and comparative psychology, most of this work has been conducted and interpreted within an aristotelian scala naturae framework of evolution and intelligence or, more recently, has focused on the specialized adaptations of the organisms to their natural habitats.

However, recent neurophysiological and behavioral data add support to comparative neuroanatomical evidence indicating that the evolution of some features of brain and behavior organization may have been more conservative than previously thought.

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