

Hippocampal Pallium and Map-Like Memories through Vertebrate Evolution

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Abstract

The hippocampus in humans and other mammals is essential for episodic and relational memories. Comparative evidence indicates that a hippocampal pallium homologue is present in birds, reptiles, amphibians, ray-finned fishes, cartilaginous fishes and agnathans. Some of their characteristics, such as the topological position and the pattern of connectivity, appear remarkably well conserved. We review here substantial data showing that in all the vertebrate groups studied up to date, from fish to mammals, the hippocampus plays a fundamental role in spatial memory. In these vertebrates groups, the hippocampal pallium homologue is involved in the use of map-like, relational representations of the objective space that provide stable allocentric frames of reference, thus allowing flexible navigation. These similarities suggest a common evolutionary ancestry and indicate that the functional properties of the hippocampus appear early in the vertebrate phylogenesis and are retained through the independent evolution of the vertebrate lineages.

Keywords

Hippocampus, Spatial Memory, Amniotes, Anamniotes, Vertebrate Brain Evolution

1. Introduction

Several decades of neuroscientific and neuropsychological research put forward that the human hippocampus serves a fundamental and selective role in our capacity to recall everyday facts and events [1]-[5]. The hippocampus, the most medial division of the telencephalic pallium, is critically involved in the encoding and recollection of unique personal experiences (episodic or autobiographical memories), and in linking episodes by their

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common features into relational networks (relational memories) that support flexible memory expression. Spatial memories are also a particular form of relational memory intimately linked to the hippocampal function. Indeed, some particular forms of cognitive representations of space are considered the clearest animal equivalent to human declarative memory, and their comparative study has provided essential clues that significantly have contributed to our understanding of the hippocampal functional traits [6]-[10]. We review here data indicating that spatial cognition abilities in different groups of vertebrates are remarkably similar, and can rely on homologous neural mechanisms. Map-like spatial memories are not an exclusive attribute of mammals; these sophisticated cognitive capabilities are also present in birds, reptiles and teleost fish. In addition, neurobehavioral studies show that map-like spatial memories in these vertebrate groups depend on the hippocampal pallium.

2. Medial Pallium or Hippocampus and Map-Like Memories in Amniotes

Available data show that mammals and birds are able to use allocentric or “world centered” representations for navigation and goal location. These map-like, high order representations of the objective space (cognitive maps) provide a stable spatial frame of reference independent of the subject’s own position, thus permitting the efficient use of spatial information to navigate to a goal [10]. Cognitive mapping allows the subject to learn the location of the goal by encoding its reciprocal metrical and geometrical spatial relationships with a variety of environmental features and gives rise to distinctive behavioral features, for example, resistance to partial losses of relevant information, and flexible detouring and shortcutting [9]-[12]. In mammals and birds, allocentric, map-like spatial representations depend on the hippocampal formation. Neuropsychological and lesion studies show that damage to the hippocampus and associated structures causes selective deficits in the capacity for place learning and memory, but not when reaching the goal can be solved by alternative strategies such as approaching a single landmark (cue learning) or by non-spatial discriminations [8] [10] [13]-[18]. A number of recent thorough behavioral studies provide strong evidence indicating that also reptiles, in particular turtles, lizards and snakes, display sophisticated spatial behavior based on map-like, allocentric or relational spatial representations of the environment [19]-[26], and that these cognitive capabilities depend on the medial cortex, the reptilian pallial region considered homologous to the avian and mammalian hippocampal formation on the basis of embryological, anatomical and neurophysiological evidence [27]-[32].

The medial cortex (MC) of reptiles is organized in three layers and is composed of a medial and a dorsomedial subdivision. The medial, small-celled, and the dorsomedial, large celled subdivisions are thought to be homologous to the dentate gyrus and the hippocampus proper, respectively [33]. Moreover, the connectivity pattern of the MC subdivisions resembles that of the hippocampal formation. Like the dentate gyrus, the medial subdivision of MC of reptiles has reciprocal connections with the dorsomedial subdivision of MC and the dorsal cortex and receives inputs from the olfactory cortex. The dorsomedial subdivision of MC, like the hippocampus, is primarily connected with the medial subdivision of MC and with the contralateral dorsomedial subdivision of MC by a substantial commissural pathway. In addition, the MC of reptiles is reciprocally connected with the septal nuclei and receives inputs from the diencephalon (dorsomedial nucleus of the dorsal thalamus, mammillary nuclei and periventricular hypothalamus) and the brain stem (raphe and locus coeruleus nuclei and reticular formation) [32]-[35].

Experimental evidence indicates that the medial cortex of reptiles, like the hippocampus in mammals and birds, plays a central role in spatial cognition. In previous studies we obtained evidence indicating that MC lesions in turtles [36]-[38] produce deficits in a variety of allocentric, place learning tasks but not in cue learning and other egocentrically referenced learning tasks (**Figure 1**). For example, MC lesions produce a severe and selective place memory deficit in turtles trained in a dry-maze analogue, as indicated by the post-surgery failure to navigate to the goal [36]. In addition, MC lesioned turtles trained in a standard four-arm maze place task suffer a place-learning impairment as revealed by their failure to reach the goal during test trials. In fact, these animals lose the ability to navigate to the goal when they start from novel positions, and when the visual cues in its proximity are excluded [37]. These results indicate that MC lesioned turtles lack the capacity to encode goal location relative to the environmental features in a relational, map-like representation (place learning). MC lesions in turtles also produce deficits in the reversal learning of a spatial task, which is a characteristic effect of hippocampal lesions in mammals and birds [38]. Moreover, similar to hippocampus lesions, MC lesions in turtles do not impair, or even facilitate, the use of guidance and other non-relational, egocentric strategies to reach the goal [36] [37] [39]. That is, the effects of damage in the MC of turtles and in the hippocampus of mammals and birds

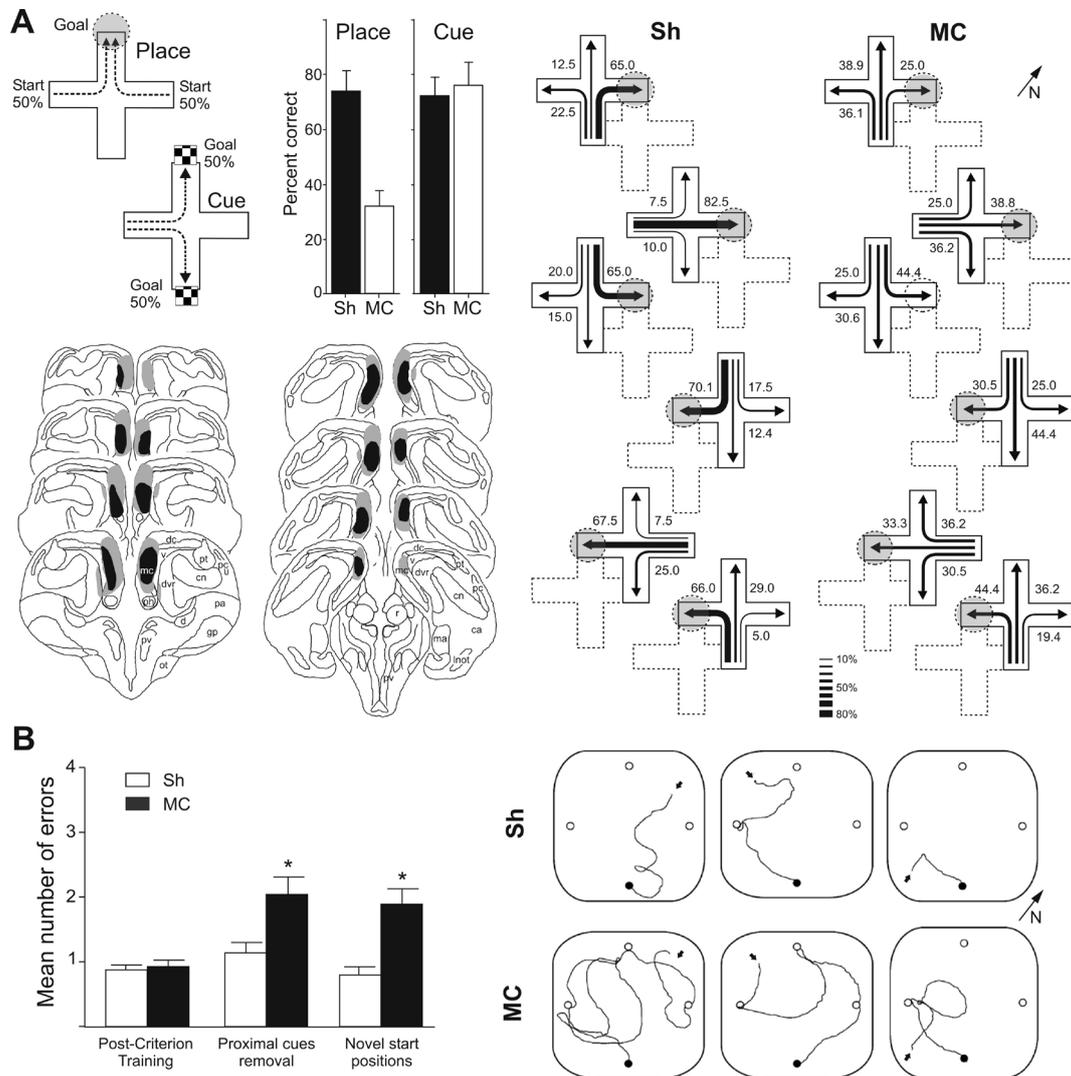


Figure 1. Spatial learning deficits in medial cortex (MC) lesioned turtles trained in allocentric spatial tasks. Lesioned animals were trained in place and cue tasks, and probe and transfer tests were conducted after the animals reached the acquisition criterion. **A** Mean percentages of correct choices for the MC and Sh turtles trained in a place or a cue task in a four-arm maze placed in the centre of a room with abundant distal visual cues. The diagrams on the left show a schematic representation of the spatial and the cue procedures. In the place task the goal (grey circle) was maintained in the same place of the room throughout the experiment, but two start positions were used randomly (50% each); in the cue task 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). MC-lesioned turtles in the place task failed to locate the goal during transfer test trials in which new start positions were used, whereas sham animals navigated directly to the goal independently of start location. In contrast, no deficit was observed in cue learning. The maze diagrams on the right show the 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 gray circles show the goal location during training. 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. The numbers and the relative thickness of the arrows denote the percentage of times that a particular choice was made. Note that the Sh animals are able to navigate towards the goal spontaneously using novel routes from different directions, demonstrating mapping abilities. Instead, MC-lesioned turtles trained in the place procedure showed a dramatic impairment during test trials in which new start positions were used. The brain drawings show a schematic representation of the largest (gray shading) and smallest (black shading) extent of the MC lesions, reconstructed in transversal sections. Abbreviations: ca, central nucleus of the amygdala; cn, core nucleus of dvr; d, area d; dc, dorsal cortex; dvr, dorsal ventricular ridge; gp, globus pallidus; ln, lateral nucleus of the olfactory tract; ma, medial nucleus of the amygdala; mc, medial cortex; ot, optic tract; pa, paleostriatum augmentatum; pc, pyriform cortex; ph, primordium hippocampi; pv, periventricular nucleus of the hypothalamus; pt, pallial thickening; r, nucleus rotundus; v, ventricle. Modified from Ref. [37]. **B** MC lesions produce a dramatic impairment in the implementation of allocentric spatial strategies in an open field maze task with four feed-

ers, where only one was baited (goal). The bars show the mean number of errors to reach the goal in the post-criterion training trials, and in the probe test in which the proximal visual cues were removed, and in the transfer test in which new start positions were used. The removal of the cues was designed to test the ability of the MC lesioned turtles to reach the goal regardless of the partial loss of relevant environmental information, a distinctive property of cognitive mapping. Note that MC-lesioned animals failed to reach the goal when the cues in its proximity were excluded or when new start positions were employed, indicating that they used a guidance strategy to solve the task. The diagrams on the right show representative searching trajectories from the start (arrow) to the goal feeder (black circle) on the transfer trials in which new start positions were employed. Note that MC-lesioned turtles, in contrast to sham operated (Sh) animals, failed to reach the goal when new start positions were employed. Asterisks denote significant statistical differences ($p < 0.05$). Modified from Ref. [36].

are strikingly similar not only in relation to the functions that are impaired, but also in relation to the processes that are not affected or even facilitated.

Neuro ecological works in Squamata (lizards and snakes) have shown that the more intensive use of space correlates positively with larger MC volume and higher neuronal plasticity. Free-ranging northern Pacific rattlesnakes (*Crotalus o. oreganus*) that return to their home area after experimental displacements have larger MC relative to the dorsal cortex, compared with hand manipulated or undisturbed snakes [40]. Interspecific comparisons in closely related species of lizards have revealed that species with higher demands on spatial abilities have increased hippocampal volume. Thus, the MC in *Acanthodactylus boskianus*, an active forager, is larger than in *A. scutellatus*, a sit-and-wait predator [41] [42]. In the snake *Agkistrodon piscivorus*, males, that have larger home ranges than females, present a larger MC as well as increased neurogenesis and cell migration relative to the dorsal cortex [43]. Territorial males of side-blotched lizards (*Uta stansburiana*) that inhabit broader areas have increased MC neurogenesis rate when compared with those living in smaller (spatially impoverished) areas [44]. Adult red-sided garter snakes (*Thamnophis sirtalis parietalis*), that present seasonal physiological and behavioral variations, have increased neurogenesis and cell migration in the MC associated with migratory rhythms [45]. In addition, although experimental data are scarce, medial pallium dependent learning and memory processes in reptiles are likely based on conserved molecular mechanisms. For example, as observed in mammals and birds, both NMDA-dependent and NMDA-independent long-term potentiation have been found in the MC of turtles [46] [47].

Hence, the presence of medial cortex-dependent allocentric spatial learning and memory capabilities in reptiles, birds, and mammals suggests that this trait could be a primitive character in amniotes. As the amniotes appear to be a monophyletic group that diverged from primitive tetrapods during the early Carboniferous, it is reasonable to assume that the hippocampus-dependent cognitive mapping memory is an ancient brain-behavior property present, at least in the stem reptilian ancestor of modern amniotes, retained through the independent evolution of each extant lineage.

3. Map-Like Memories and Hippocampal Pallium in Anamniotes

Developmental, neuroanatomical and neurophysiological evidence indicates that a pallial region homologous to the hippocampus of amniotes is also present in the forebrain of amphibians, lungfishes, ray-finned fishes, cartilaginous fishes and agnathans [27] [31], suggesting that a hippocampal pallium is a primitive feature of the vertebrate telencephalon. However, studies on spatial cognition capabilities are very scarce or even completely lacking in some anamniote groups.

Although the studies on the spatial capabilities of amphibians are clearly insufficient, recent laboratory and field experiments suggest that they possess elaborated spatial abilities [48] [49]. Also in Chondrichthyes or cartilaginous fish data concerning their spatial capabilities are really scarce, but a few experimental and field studies show that sharks (elasmobranchs) can use different strategies for navigation, and have long-term spatial memory [50]-[52]. No data are available relative to this issue in agnathans. Regrettably, there are not, to our knowledge, studies on the role of the medial pallium in spatial cognition in amphibians, cartilaginous fish and agnathans. This lack of information is particularly notable given the basal position of these groups in the vertebrate phylogenetic tree (Figure 2) and their significance for understanding the evolution of the hippocampal pallium and spatial cognition.

The greatest part of the available information on anamniotes is concentrated in ray-finned (actinopterygian) fishes. The telencephalon of these fishes constitutes a special case in vertebrates, as a result of a major divergence during the early embryogenesis [53]-[56] (Figure 3). In actinopterygians, the telencephalon develops by a

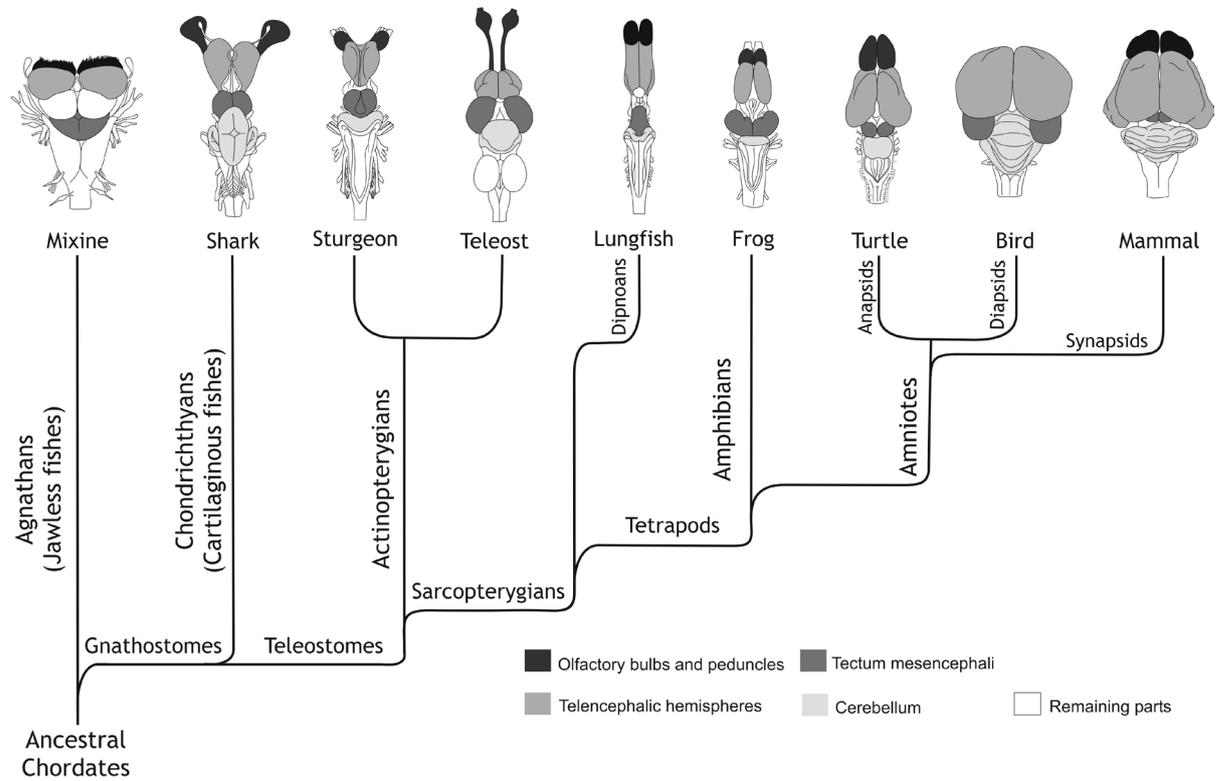


Figure 2. Cladogram illustrating the phylogenetic relationships among the main groups of extant vertebrates. The drawings show a dorsal view of the brain of representative species of each group.

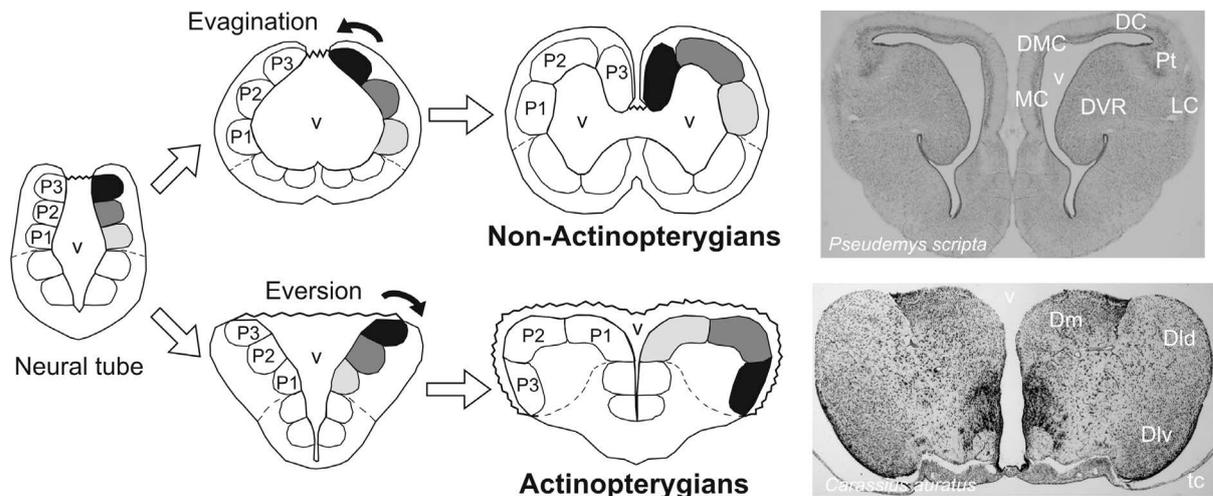


Figure 3. Schematic representation of the process of evagination and inversion that occurs in the telencephalon of non-actinopterygian vertebrates during embryonic development compared with the process of eversion or bending outward that occurs in actinopterygian fish. In tetrapods and many fishes, the evagination of the dorsolateral prosencephalic wall produces paired telencephalic hemispheres with internal ventricles. In actinopterygian fish, the dorsal portion of the embryonic prosencephalic wall curves laterally, producing two massive hemispheres flanking a single ventricular cavity. The photographs at the right show a transverse section through the telencephalon of a species representative of the evaginated forebrain (turtle, *Pseudemys scripta*) and another representative of the everted forebrain (goldfish, *Carassius auratus*). P1, P2, and P3 correspond to the three main subdivisions of the pallium. Abbreviations: DC, dorsal cortex; DMC, dorsomedial cortex; Dld, dorsal subdivision of lateral division of area dorsalis; Dlv, ventral subdivision of lateral division of area dorsalis; Dm, medial subdivision of area dorsalis; DVR, dorsal ventricular ridge; LC, lateral cortex; MC, medial cortex; Pt, pallial thickening; tc, tela choroidea; v, ventricle.

process of eversion (bending outward of the embryonic prosencephalic alar plate) instead of evagination as occurs in every other vertebrate group. As a consequence, the telencephalic hemispheres of ray-finned fishes lack internal ventricles and the medial-to-lateral topography of the pallial areas is reversed compared with that observed in every other vertebrate. Accordingly, the actinopterygian pallial area considered homologous to the hippocampus is located laterally in the telencephalon [55] [57]-[60].

Among ray-finned fishes, the teleosts are the most intensively studied group concerning the telencephalic anatomical and functional organization and the neural bases of their spatial capabilities. The topography, connections and histochemistry of the dorsolateral pallium (Dl) of teleost fish are remarkably similar to the hippocampal pallium of vertebrates with a developmentally evaginated telencephalon [27] [59] [61]. For example, Dl has widespread reciprocal connections with other pallial areas, and with the contralateral Dl. It is also reciprocally connected with the ventral nucleus of the area ventralis (Vv), considered homologous to the septal nuclei of amniotes [27], from which it receives a cholinergic input, and with the preglomerular complex of the posterior tuberculum (the possible homologue of the dorsal thalamus), from which it receives multi-sensory inputs. Dl also projects to the preoptic area and other diencephalic regions and receives inputs from the preoptic area, the locus coeruleus and the superior raphe [61]. However, within Dl, the ventral subdivision (Dlv) is the most likely candidate as the specific homologue of the tetrapod medial pallium, because of its distal topological position in the pallium, its pattern of connectivity with subcortical areas, and by the distribution pattern of several histochemical and molecular markers, for example, the dopamine receptor subtype D1B, which is characteristic of the mammalian hippocampus [62]. However, it is still under discussion whether the entire Dl, *i.e.* the dorsal subdivision (Dld) plus Dlv, or by contrast Dlv exclusively, are comparable to the hippocampal pallium. In fact, some hypotheses propose Dld as a part of the dorsal pallium or isocortex based on its topological position, its visual ascending inputs, and its visually related activity [63]-[65]. In contrast, other hypotheses, based on a topological criterion and the presumable similarity in the pattern of connections of Dld and Dlv, propose that the whole Dl should be viewed as a single primary pallial division, homologous to the mammalian hippocampus [61] [66].

Our previous studies on goldfish show that teleost fish, like land vertebrates, are able to navigate on basis of relational, map-like cognitive representations that provide world-centered, allocentric frames of spatial reference [67]-[75]. These representations, based on the encoding of multiple environmental features such as the objects and their reciprocal spatial (topological and geometrical) relationships, allow them to navigate accurately and flexibly to a goal regardless of their own actual position and local view, and use spontaneously shortcuts and detours (Figure 4). Moreover, data provided by lesion and morphofunctional studies indicate that the Dlv pallial area of teleost fishes, like the hippocampus of land vertebrates, selectively supports these spatial cognition abilities.

Dlv lesions produce dramatic learning and memory impairments in goldfish trained in tasks that require the use of allocentric spatial strategies [37] [76] [77] (Figure 4). Dlv lesions cause place-memory deficits in goldfish trained in a four-arm maze surrounded by distal visual cues [37], making the lesioned animals unable to navigate to familiar food-rewarded locations, and to implement novel routes to the goal when departing from new start positions (Figure 4A). Moreover, when goldfish with lesions in the main pallial divisions are trained in an open-field place task or in a spatial constancy task, only Dlv lesioned fish are unable to implement allocentric strategies [76] [77]. For example, Dlv lesioned fish are impaired in learning the reversal of the spatial constancy task (Figure 4B), and fail to reach the goal when the cues in its proximity are excluded (Figure 4D). By contrast damage to Dlv does not impair the use of guidance or other egocentric strategies [37] [76] [77] (Figure 4A and Figure 4B). These spatial learning and memory deficits are similar to those observed in mammals and birds following lesions in the hippocampal formation [8] [14]-[17] [78].

Studies using complementary techniques also reveal the critical role of the teleost Dlv in spatial cognition. Training goldfish in the spatial constancy task (but not in a cued version of the same task) produces an increase in the synthesis of proteins that is selective to the neurons of Dlv [76] [79] (Figure 4C), as indicated by the enlargement of the nucleolar organizing regions (the organelles associated with the synthesis of ribosomal proteins) [80]. Cytochrome oxidase histochemistry, an approach that permits to determine the brain regions undergoing long-term training-dependent metabolic changes [81]-[84], shows that training goldfish in the spatial constancy task increases the activity in Dlv but not in Dld [85]. Consistent data obtained in neuroecological studies show that increased spatial behavior demands correlate with larger Dlv in several species of teleost fishes [86] [87]. For example, in the Azorean rock-pool blennies (*Parablennius parvicornis*), the volume of the Dlv is larg-

ability to use new pathways towards a goal from unfamiliar start points, and to reorganize their spatial strategies in response to an environmental change. In contrast, the random distribution of choices by the Dlv-lesioned animals indicates a severe spatial deficit. The brain drawings in the bottom left show a schematic representation of the largest (dark gray) and smallest (light gray) extent of the Dlv and Dm lesions, reconstructed in transversal sections at the levels indicated in the lateral view of the brain. Modified from Ref. [37]. **B** Dlv lesions affect the retention (left) and the reversal learning (right) of a spatial constancy task which requires the use of allocentric or relational strategies. The insets show schematic representations of the procedure. Modified from Ref. [76]. **C** Training in the spatial constancy task produces a selective increment in the transcriptive activity of Dlv neurons, as indicated by increases in the size of the nucleolar organizing region (NOR), the nucleolar organelles associated with the synthesis of ribosomal proteins. Note that training in the cue version of the same procedure did not produce observable changes. The photograph on the right shows AgNORs (argyrophilic nucleolar organizing regions) in Dlv neurons. Dlv-d and Dlv-v correspond to the dorsal and ventral subdivisions of Dlv, respectively. Modified from Ref. [76]. **D** Dlv, but not Dm lesions, produces a dramatic impairment in the implementation of allocentric spatial strategies in a “hole-board” analogue task. In this task animals are required to find the baited feeder within a 5×5 feeder matrix surrounded by visual cues. The bars show the mean spatial accuracy index (in this index values range from 1 for the goal feeder to 0 for the most distant one) for each group during the training trials conducted after reaching the acquisition criterion and in the probe tests in which the most distal or proximal cues to the goal were removed. The diagrams on the right show representative searching trajectories from the start to the goal feeder (gray circle) on the probe trials for a representative animal of each group. Note that Dlv-lesioned goldfish failed to reach the goal when the cues in its proximity were excluded indicating that they used a guidance strategy to solve the task. Asterisks denote significant statistical differences ($p < 0.05$). Modified from Ref. [77].

er in females than in males, associated with a more demanding use of space during the breeding season [86]. In a whole, these data strongly suggest that the Dlv of the teleost telencephalic pallium is critically involved in allocentric spatial learning and memory and that, like the hippocampus of amniotes, it is an essential component of a memory system that processes and encodes environmental information in complex, high-order relational memory representations.

4. Conclusion

Comparative neuroanatomical, developmental and functional data reveal that the evolution of the vertebrate forebrain could have been more conservative than previously realized. Despite conspicuous morphological and cytoarchitectural differences, the pallium of vertebrates seems to be organized in comparable subdivisions and a hippocampal pallium homologue seems to be present in every vertebrate radiation [29] [30] [60] [63] [88]-[92]. From agnathans to mammals, the hippocampal pallium of all extant vertebrates shares a suite of developmental, neurochemical and connectivity characteristics, as well as functional properties, which can indicate a common evolutionary ancestry. Although additional studies in basal vertebrate groups are needed to understand the evolution of the allocentric navigation systems, it is reasonable to assume that some basic organizational and functional properties of the hippocampal pallium emerged early during the vertebrate phylogenesis, and that these properties are conserved during the independent evolution of the different vertebrate radiations. These conserved properties probably explain the widespread role of the hippocampal pallium in spatial cognition.

Acknowledgements

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