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Does a Vertebrate Morphotype of Pallial Subdivisions Really Exist?

Kei Yamamoto^a Pierre Estienne^a Solal Bloch^b

^aParis-Saclay Institute of Neuroscience (Neuro-PSI), Université Paris-Saclay, CNRS UMR 9197, Saclay, France;

^bUniversité de Tours, INSERM, Imaging Brain & Neuropsychiatry iBrain U1253, 37032, Tours, France

Keywords

Pallium · Homology · Comparative neuroanatomy · Convergent evolution

Abstract

Background: Comparative neuroanatomists have long sought to determine which part of the pallium in non-mammals is homologous to the mammalian neocortex. A number of similar connectivity patterns across species have led to the idea that the basic organization of the vertebrate brain is relatively conserved; thus, efforts of the last decades have been focused on determining a vertebrate “morphotype” – a model comprising the characteristics believed to have been present in the last common ancestor of all vertebrates. **Summary:** The endeavor to determine the vertebrate morphotype has been riddled with controversies due to the extensive morphological diversity of the pallium among vertebrate taxa. Nonetheless, most proposed scenarios of pallial homology are variants of a common theme where the vertebrate pallium is subdivided into subdivisions homologous to the hippocampus, neocortex, piriform cortex, and amygdala, in a one-to-one manner. We review the rationales of major propositions of pallial homology and identify the source of the discrepancies behind different hypotheses. We consider that a source of discrepancies is the prevailing assumption that there is a single “morphotype of the pallial subdivisions” throughout vertebrates. Instead, pallial subdivisions

present in different taxa probably evolved independently in each lineage. **Key Messages:** We encounter discrepancies when we search for a single morphotype of subdivisions across vertebrates. These discrepancies can be resolved by considering that several subdivisions within the pallium were established after the divergence of the different lineages. The differences of pallial organization are especially remarkable between actinopterygians (including teleost fishes) and other vertebrates. Thus, the prevailing notion of a simple one-to-one homology between the mammalian and teleost pallia needs to be reconsidered.

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Introduction

Human cognitive skills are mainly thought to rely on the architecture and computing capabilities of the neocortex. The six-layered neocortex is much more expanded in primates, notably in great apes, than in rodents. For this reason, the size and complexity of the neocortex have often been considered to reflect the cognitive capacity in mammalian species.

There is no such cortical structure in the telencephalon in nonmammals. In the classical perspective, which was influenced by *scala naturae*, a telencephalon devoid of a neocortex was interpreted as being “less evolved” than one with a layered neocortex. In this view, brain complexity

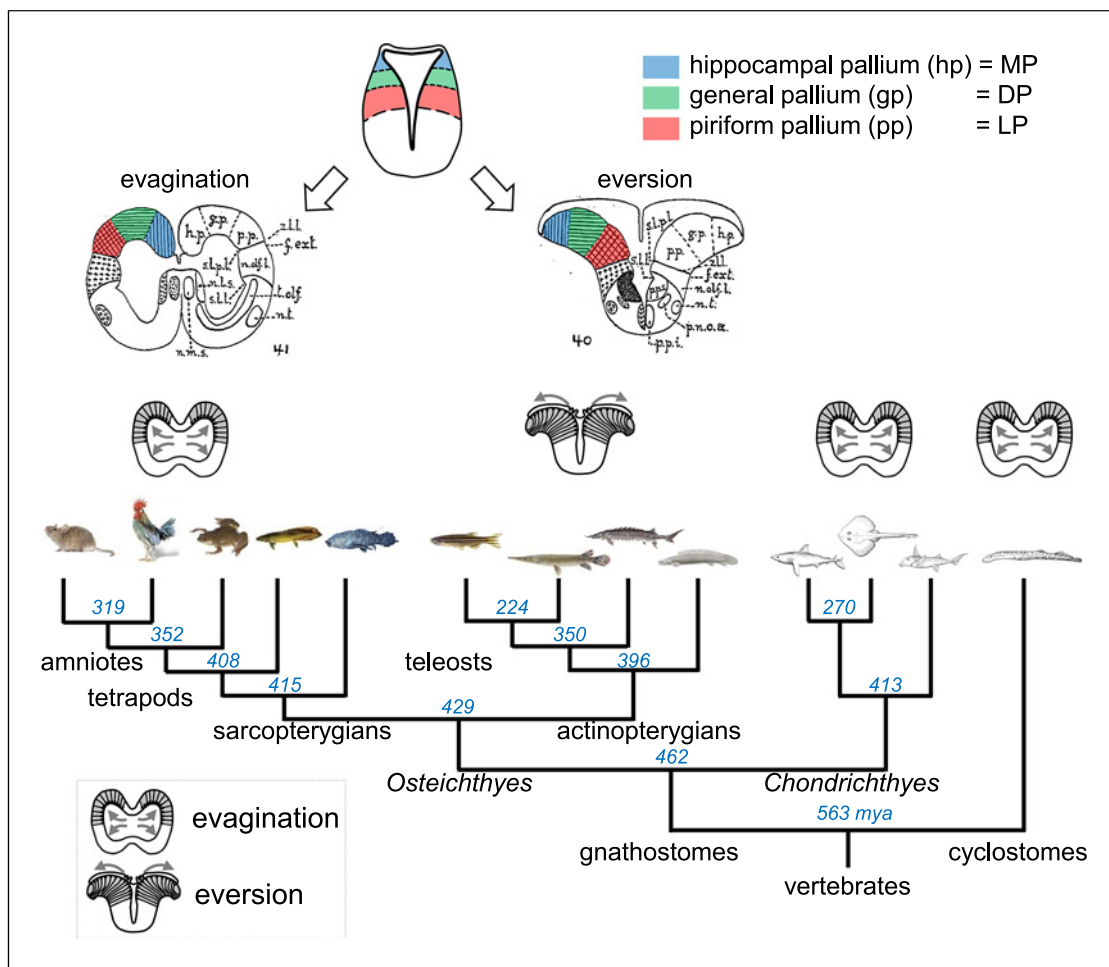


Fig. 1. Classical view of evagination and eversion. The top schematic drawings show the comparison of pallial development in eversion (actinopterygians) and evagination (all other vertebrates) proposed by Holmgren (1925). The bottom shows a simplified phylogenetic tree of vertebrates. The italic blue numbers indicate

divergence dates (million years ago [mya]) of each clade calculated using <http://www.timetree.org/> [7]. Based on cladistics analysis, it is concluded that evagination is the ancestral form, and that the everted pallium specifically evolved in actinopterygians including teleost fishes.

increased linearly with the phylogenetic “modernity” of vertebrate species, and the “neo” cortex was thought to be added on top of the “ancient” brain structures inherited from the common ancestor [1, 2]. Such a notion is now considered outdated [3]. Currently, it is considered that the basic organization of the vertebrate brain is relatively conserved, and that the mammalian neocortex develops as a part of the pallium, whose homolog is present throughout vertebrates. Note that “pallium” refers to the dorsal part of the telencephalon (where the neocortex is located in the case of mammals). In contrast, “subpallium” refers to the ventral part of the telencephalon where the striatum is located.

Having reached a consensus that brain structures are comparable among vertebrates, a main question of

comparative neuroanatomy has been to identify which part of the nonmammalian pallium is homologous to the mammalian neocortex. Despite a number of different hypotheses, a common assumption is that the pallium is divided into several subdivisions inherited from the common ancestor, which is referred to as a “morphotype” – a model comprising the characteristics believed to have been present in the last common ancestors of all vertebrates [4].

Holmgren proposed to divide the pallium into three subdivisions (Fig. 1): the hippocampal pallium (hp), general pallium (gp), and piriform pallium (pp) [5, 6]. In this view, the hippocampal pallium is homologous to the mammalian hippocampus, and the general pallium is homologous to the mammalian neocortex. The piriform

pallium contains a superficial cortical structure (the piriform cortex) and a deep nuclear structure (the piriform lobe) containing the claustrum/amygdala complex.

In recent literature, the hippocampal, general, and piriform pallia are more commonly called the medial pallium (MP), dorsal pallium (DP), and lateral pallium (LP), respectively, reflecting their topology in the pallium of the sarcopterygians (the group of lobe-finned fishes that contains mammals; see Fig. 1 for the phylogenetic relationship of vertebrate groups). In addition, Puelles and his colleagues have introduced the notion of a ventral pallium (VP). Originally defined by the absence or weak expression of the transcription factor *Emx1* in the ventral half of the tetrapod LP [8–10], the studies claiming the presence of VP underlined the importance of field homology, in which adult brain regions thought to be derived in different species from homologous embryonic precursors can be considered homologous as fields [11]. However, this model of field homology has been modified repeatedly, and accordingly, the definition and boundaries of LP and VP have changed extensively [9, 12–14].

A recent hypothesis by Striedter and Northcutt [15] proposes that the common ancestor of vertebrates did not have a DP homolog, and that DP-like structures evolved independently in cartilaginous fishes, teleosts, and amniotes. Amid the enduring debate over the regional homology of the pallium, particularly the DP, an emerging idea suggests that the similarities in functional/connectional properties between mammalian neocortex and nonmammalian pallia might be due to convergent evolution, rather than conservation [16].

Here we push this idea further: if DP-like functions can emerge several times during evolution, why do we assume that MP (hippocampal pallium) and LP/VP (piriform pallium) are conserved throughout vertebrates? Isn't it simply because we think that they "should" be more conserved than the neocortex? Classically, the hippocampus and the piriform cortex were called the archi- and paleocortices, considered "evolutionarily ancient" and preceding the emergence of the neocortex of mammals. In reality, based on thorough analyses of the currently available data, the presence of a morphotype of the LP/VP also proves doubtful. The area corresponding to the LP/VP is far from conserved, in terms of both developmental and functional aspects.

In this review, we summarize the historical aspects of the long-lasting controversy on pallial homology in the field of comparative neurobiology. We first review how pallial homology has been argued in sarcopterygians (mainly in tetrapods) and then discuss the pallial organization of actinopterygians (mainly teleosts), with new

developmental data. By doing so, it becomes evident that there are no conserved pallial subdivisions across vertebrates, at least not as currently proposed, and that several subdivisions arose independently in different lineages.

What Is the "General Pallium" or "Dorsal Pallium"?

The nomenclature MP/DP/LP/VP is based on the concept of field homology. Thus, it should be purely defined by the topology of embryonic brains. But in practice, the term DP (formerly called the "general" pallium) is used as a synonym for the area "homologous to the mammalian neocortex." For all nonmammalian vertebrates that do not have a six-layered cortical structure in the pallium, DP has been notoriously difficult to delineate [15].

It is even defined in a negative manner, as the non-hippocampal, nonolfactory pallium [17]. The question then becomes: how can we define the hippocampal and olfactory (piriform) pallium? If we consider the example of the olfactory (piriform) pallium, it has been principally defined as a major recipient area from the olfactory bulb, which is a connectivity (hodological) criterion. As such, historically, the original concept of pallial subdivisions was established by mixing hodological, functional, and developmental data. Importantly, developmental studies using gene expression data arose relatively recently, long after the concept of pallial subdivisions and their boundaries already existed. Since most recent literature uses the term MP for the hippocampal pallium, DP for the general pallium, and LP/VP for piriform pallium, we will apply "MP/DP/LP/VP" nomenclature in the following for the sake of simplicity. Nonetheless, our use of this nomenclature should not be interpreted to mean that field homology has been verified by developmental data.

The reason that researchers started to agree that nonmammals may have a neocortex homolog in the first place is largely based on similar connectivity patterns, such as sensory afferents to the pallium. Tract-tracing techniques developed in the late 1960s–70s have revealed that some nonmammalian vertebrates such as birds, reptiles, and teleosts possess sensory ascending projections reaching the pallium, with connectivity patterns comparable to the thalamocortical projections of mammals. Accordingly, the pallium has been considered an integration center of different sensory modalities, and DP has been defined as the area receiving sensory projections from the thalamus [18–20]. Notably, visual systems are intensively studied in various vertebrate species. Since the

seminal work by Schneider proposing the presence of “two visual systems” terminating in the mammalian cortex [21], most data in nonmammals have been interpreted based on this notion, seeking to identify which mammalian pathway their nonmammalian counterparts correspond to [22–27]. This data from visual systems fostered the concept that the basic brain organization of vertebrates is relatively conserved.

Neocortex-Like Connectivity in the Avian Pallium

This concept of “conservation” is further reinforced by the remarkable similarity of pallial connectivity between mammals and birds. Although the avian telencephalon does not have a mammal-like, layered neocortex, its functions and neural circuitry are surprisingly similar to those of mammals (Fig. 2). Similar to the mammalian neocortex, the avian pallium possesses visual, auditory, and somatosensory representations [28–32]. These major sensory areas receive ascending projections from the dorsal thalamus in a topographically discrete manner, which is similar to the primary sensory cortices in mammals [18–20]. Examples of visual and auditory pathways are shown in Figure 2. Notably, the notion of “two visual systems” [21, 23, 24] emphasized the similarity of neural connectivity in mammals and birds [33, 34]: one is the thalamofugal visual pathway (retina – thalamus – pallium; also known as the geniculate visual pathway in mammals) in which the retinal projections directly reach the thalamus, while the other is the tectofugal pathway (retina – tectum – thalamus – pallium; also known as the extrageniculate visual pathway in mammals) in which the retinal projections first reach the tectum, where tectal neurons project to the thalamus.

Similarly to the mammalian sensory cortices, the avian primary sensory pallium receiving modality-specific sensory information projects to other pallial areas located at their periphery, which are comparable to the secondary or higher order sensory cortices [35–37]. A recent publication in the pigeon pallium further demonstrated that the intra-pallial circuitry of these sensory areas shows a “cortex-like” layered organization [38].

The higher order sensory areas are further interconnected with the nidopallium caudolaterale (NCL), which is functionally comparable to the mammalian prefrontal cortex (PFC) (Fig. 2; executive). The PFC and NCL are both characterized by dopaminergic innervation from the midbrain dopaminergic neurons [39–42]. The functions of the mammalian PFC and NCL can be summarized as “executive functions” [35, 42], the core of which is context-dependent regulation: inhibition,

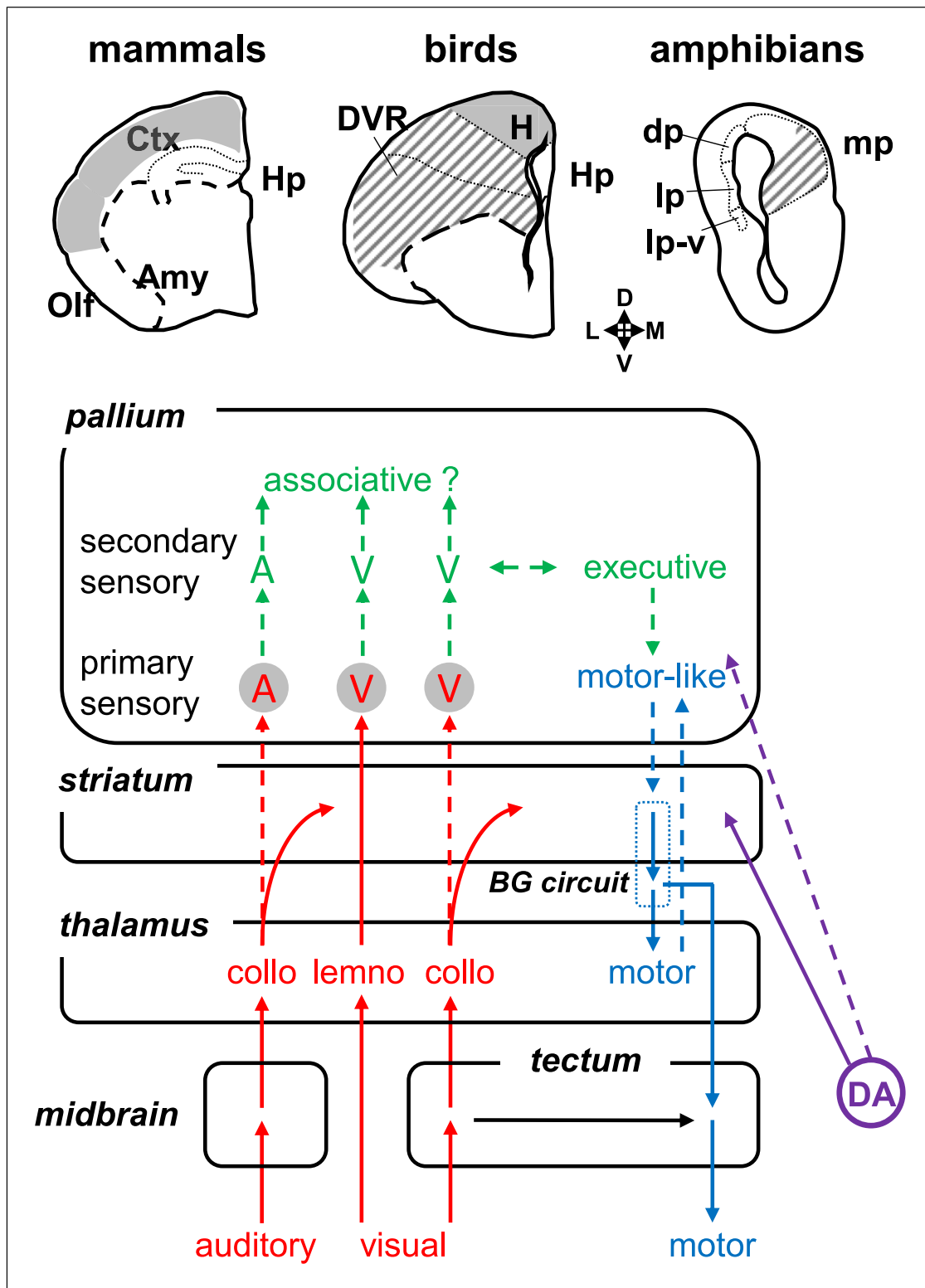
working memory, and cognitive flexibility. Expansion of the executive area is correlated with the evolution of higher order cognitive functions: a crow’s NCL is much larger compared to other birds [43], as is the case of the primate PFC compared to other mammals.

Motor-related pallial areas are not as readily identifiable as the sensory pallial areas in the avian pallium. There are two lines of studies proposing different candidates of the motor cortex-like area. In pigeons, motor cortex-like pallial areas were proposed to be located in the hyperpallium and in the dorsal arcopallium, based on the presence of descending projection neurons similar to the mammalian corticostriatal projection neurons and to pyramidal tract projection neurons [44–46]. In songbirds, neurons in the robust nucleus of the arcopallium (RA) project to the brainstem nuclei that control trachea and syrinx muscles, involved in song production. This has often been compared to the projections from the motor cortex to the nucleus ambiguus that control larynx muscles in mammalian vocal learners [47]. On the other hand, a study based on the expression of immediate early genes identified movement-related areas in the anterior nidopallium and mesopallium [48]. It is not clear whether these motor-related areas correspond to parts of the motor cortex or to the premotor cortex of mammals.

The “Dorsal” Topological Feature Is Not an Important Factor for Evolving Neocortex-Like Functions

In mammals, the neocortical areas performing sensory-motor integration develop from the dorsal portion of the telencephalic vesicle, flanked by the medially located hippocampus and the laterally located piriform (olfactory) cortex. For this reason, the major point of contention in the argument on the neocortex homolog in amniotes has been whether the thalamocortical-like sensory integration described above resides in the dorsal portion of the avian pallium or not. Based on topology, there is a consensus that the hyperpallium (also known as the Wulst, which occupies the dorsal portion of the avian pallium) of birds is homologous to the mammalian superior neocortex (the neocortical area dorsal to the lateral sulcus). However, the evolutionary origin of the dorsal ventricular ridge (DVR: the ventral portion of the avian pallium containing the nidopallium and arcopallium) has long been debated among comparative neuroanatomists.

Based on functional/hodological similarities, some authors proposed that the avian DVR is homologous to the mammalian temporal neocortex (the neocortical area



(For legend see next page.)

ventral to the lateral sulcus). Notably, the thalamorecipient pallial areas within the DVR (Fig. 2; primary sensory areas) were proposed to be homologous to the thalamorecipient cell population (layer 4) of the visual, auditory, and somatosensory cortices [18, 33, 34, 49–51] (DVR = DP hypothesis; Fig. 3a). In this hypothesis, the posterior DVR is homologous to the mammalian amygdala, and the anterior DVR is considered to be homologous to the mammalian neocortex. Contrary to this hypothesis, other authors claim that the entire DVR is homologous to the non-layered structures deep to the piriform cortex, the claustroramygdaloid region of mammals [8, 9, 17, 52, 53] (DVR = LP/VP hypothesis; Fig. 3b). Here we will not discuss each claim in detail, but in short, the best accepted argument supporting the DVR = LP/VP hypothesis was the absence or weak expression of the transcription factor *Emx1* in the DVR (notably in the nidopallium), similarly to the amygdaloid area of mammals [8, 9].

The *Emx1*-poor domain of the pallium corresponds to the ventral half of the area classically known as LP. In 2000, Puelles and his colleagues proposed the first tetrapartite model, in which he divided the classical LP into two, redefining the *Emx1*-positive dorsal portion as LP and the *Emx1*-negative (poor) ventral portion as VP (Fig. 3b), introducing a fourth subdivision [9]. Following this model, the avian DVR corresponds to the LP/VP.

However, some authors argue against the validity of this fourth pallial subdivision VP [54, 55]. First, *Emx1* is expressed in a gradient within the pallium, and its expression pattern does not delineate a clear-cut border. In mammals, *Emx1* is transiently expressed even in the area identified as VP in mice [56]. Moreover, the absence of

Emx1 expression is the only marker that can define the VP, and no other molecular/genetic marker labels the ventral portion of the pallium in both mammals and birds.

Regardless of the validity of VP, the gradient expression of *Emx1* indicates that the nidopallium (the ventral part of the DVR that is *Emx1*-negative) appears to be the most ventral part of the pallium. A histological observation of the brain of tuatara (*Sphenodon punctatus*), the closest extant relative to both snakes and lizards, also clearly shows that the DVR is derived from the most ventral part of the pallium (Fig. 4). In the avian brain, it is very difficult to tell the topological position of the DVR along the neural tube, because it is hypertrophied and completely fills in the ventricular zone (Fig. 2; birds). In contrast, in frontal sections of tuatara [57], one can observe a continuation of cell layers from the medio-DP toward the striatum (Fig. 4), clearly showing that DVR is located ventral to the piriform cortex, next to the striatum. Thus, unless the tuatara piriform cortex is misidentified, the sauropsid DVR is derived from the most ventral portion of the pallium.

These studies from sauropsids suggest that the developmental origin (topological position within the pallium) is not an important factor for generating neocortex-like connectivity patterns and functions since the DVR, being the ventral-most portion of the pallium, displays those neocortex-like connectivity and functions.

It is also noteworthy that, in amphibians, the area receiving thalamic inputs is the medial part [17, 18, 58, 59], rather than the dorsal part of the pallium (Fig. 2; amphibians). Unlike in amniotes, pallial connectivity is much less developed in amphibians and is generally

Fig. 2. Dorsal pallium (DP)-like connectivity found in mammals and birds. Simplified diagram of neural inputs and outputs related to the pallium, whose patterns are found to be similar between mammals and birds. Modality-specific sensory inputs are indicated in red arrows. Here visual and auditory pathways are shown as an example of modality-specific sensory afferents to the pallium. In the visual system, two parallel afferents are found: the tectofugal- or collo-pathway (“collo” stands for the colliculus, which is relayed via the midbrain roof), and thalamofugal- or lemno-pathway (“lemno” stands for lemniscal inputs, but the term is generally used to refer to non-collicular inputs). Motor outputs are indicated in blue (the detailed basal ganglia [BG] circuits are omitted for the sake of simplicity). Dopaminergic (DA) projections from the mesencephalon (A9/A10) to the telencephalon are indicated in purple. DA inputs to the striatum are considered to be critical for BG function throughout tetrapods, while those to the pallium (PFC in mammals and NCL in birds) are critical for executive functions. The solid arrows indicate the connectivity found in mammals, birds, and amphibians, while the dotted arrows

indicate those found only in mammals and birds. Note that many of the pallial connections are absent in amphibians. The top brain schemas (in frontal section) show the pallial area receiving thalamic projections (circled in gray in the diagram: “A” for auditory and “V” for visual areas), similarly to the primary sensory areas of the mammalian neocortex. The brain areas with filled gray indicate the agreed homology of DP due to its “dorsal” topology. The brain areas with slanted gray lines are areas receiving thalamic sensory inputs for which homology to the mammalian DP remains debated: this area is located at the ventral end of the pallium in birds, while it is at the medial end of the pallium in amphibians. A, auditory area; Amy, amygdala; BG, basal ganglia; Ctx, neocortex; DA, dopaminergic neuron; DP, dorsal pallium (amphibian structure); DVR, dorsal ventricular ridge (avian structure); H, hyperpallium (avian structure); Hp, hippocampus; LP, lateral pallium (amphibian structure); lp-v, ventral part of the lateral pallium (amphibian structure); MP, medial pallium (amphibian structure); Olf, olfactory (piriform) cortex; V, visual area. Brain orientation; D, dorsal; V, ventral; L, lateral; M, medial.

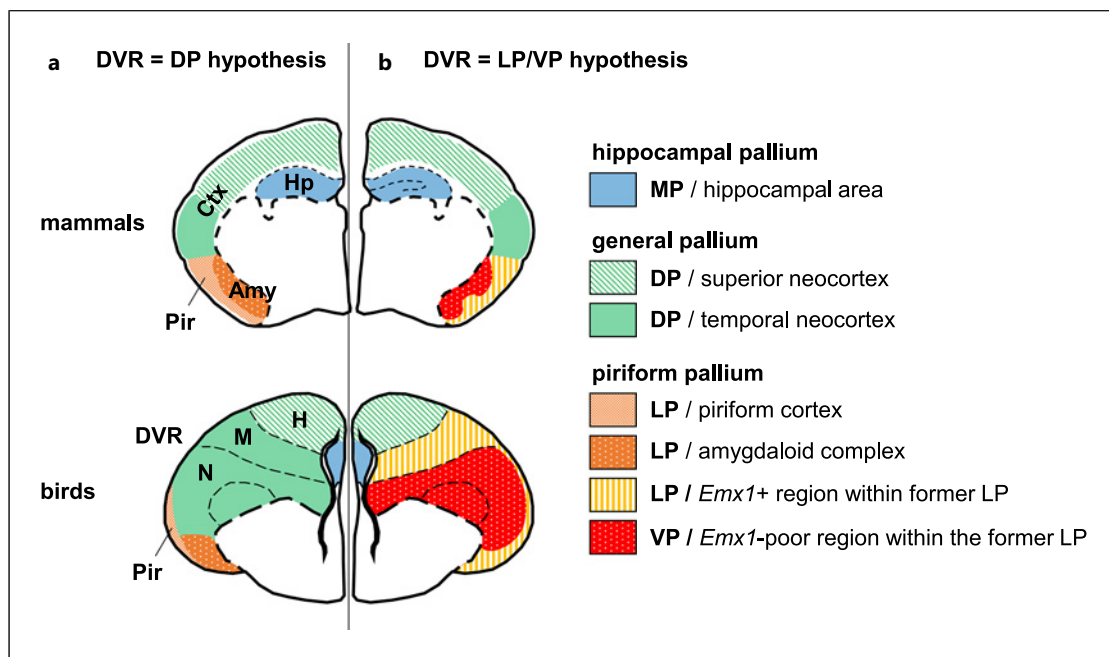


Fig. 3. Pallial homologies between mammals (top) and birds (bottom) debated during 1990s–early 2000s. The left side of the frontal section (**a**) represents “DVR = DP hypothesis,” whereas the right side of the section (**b**) represents “DVR = LP/VP hypothesis” based on the first tetrapartite model. The two different hypotheses propose different mammalian homolog of the avian

DVR. Amy, amygdaloid complex; Ctx, cerebral cortex; DP, dorsal pallium (as morphotype); DVR, dorsal ventricular ridge; h, hyperpallium; Hp, hippocampus; LP, lateral pallium (as morphotype); M, mesopallium; MP, medial pallium (as morphotype); N, nidopallium; Pir, piriform cortex; VP, ventral pallium (as morphotype).

multimodal without modality-specific sensory inputs. The majority of the sensory inputs terminate in the striatum (subpallium), thus it is possible that the sensory-motor integration is mainly performed at the level of the striatum [18, 19, 60, 61]. Nonetheless, due to some afferent/efferent projection patterns, some authors compare the MP of amphibians with the mammalian cortex or the avian DVR [17, 59].

Altogether, these studies suggest that any part of the pallium could potentially evolve neocortex-like connectivity patterns. Interestingly, Striedter and Northcutt reached a similar conclusion arguing against the prevailing notion of the “conserved pallium,” based on the cladistics analysis of olfactory projection patterns [15]. In both sarcopterygians and actinopterygians, the basal groups possess widespread olfactory projections to the pallium. Based on these observations, they hypothesize that the olfactory pallium (classical LP) may have represented a larger pallial domain in the common ancestor, and that DP (with thalamic sensory inputs) may have evolved independently in different lineages like mammals, birds, and teleosts. This idea questions the presence of DP in the morphotype of the vertebrate pallium.

Is the Limbic System Really Conserved?

Unlike DP, whose definition and presence can be debated in some species, the presence of the hippocampus, piriform cortex, and amygdala (corresponding to MP, LP/VP in the first tetrapartite model; Fig. 5b) throughout vertebrates has never been debated, with the assumption that these should be conserved pallial regions. This assumption may be related to the notion of the “limbic system” [62, 63] in which the hippocampus, piriform cortex, and amygdala were considered to be “evolutionary ancient” compared to neocortical structures.

All vertebrates possess a pallial domain with specific olfactory inputs, although their extent varies depending on the animal group. Since the pallium of the basal vertebrate lineages (cyclostomes, lungfishes, *Polypterus*) are mainly occupied by olfactory bulb inputs, it is considered that widespread olfactory projections to the pallium may be the ancestral situation in vertebrates [1], and that they have become more restricted in some lineages [15].

Lying next to the piriform cortex in mammals, the amygdala is also believed to be conserved. In mammals, the amygdala was described as a distinct structure just

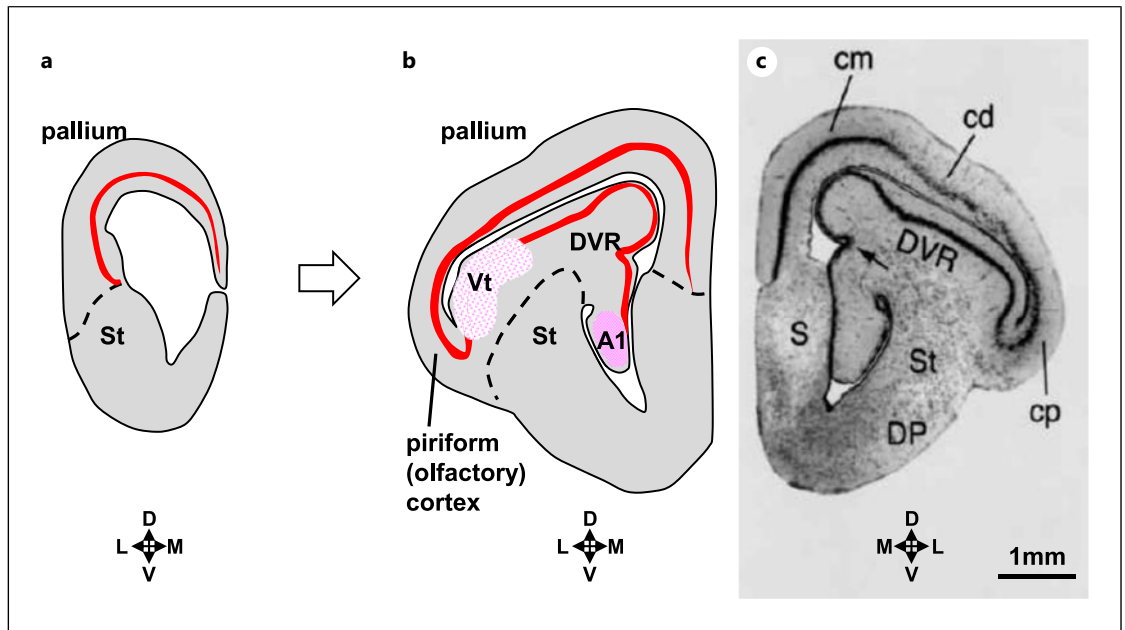


Fig. 4. Topological organization of the DVR of tuatara, *Sphenodon punctatus*. Schematic representations of the developing (**a**) and mature (**b**) telencephalic vesicle (left side of frontal sections). **c** A cresyl violet-stained section (from Reiner and Northcutt 2000) showing the mirror image of **b**. The tectofugal visual area (Vt) and the primary auditory area (A1) are situated within the DVR. The pallium of *Sphenodon* possesses a three-layered cytoarchitecture that resembles the cortical cell plate (shown as a red line in the

schema). This cell plate-like structure is continuous from the medial/DP, through the piriform cortex up to the ventral edge of the DVR. This clearly demonstrates that the DVR is topologically ventral to the piriform cortex, adjacent to the subpallium (striatum). A1, primary auditory area; cd, dorsal cortex; cm, medial cortex; cp, piriform cortex; DP, dorsal pallidum; DVR, dorsal ventricular ridge; S, septum; St, striatum; Vt, tectofugal visual area. Brain orientation: D, dorsal; V, ventral; L, lateral; M, medial.

because it appears as a distinct almond-shaped structure. Later on, it turned out that the amygdala is not a developmentally uniform entity, but is derived from pallial and subpallial parts [64]. Thus, apart from its peculiar “almond-shaped” appearance, there is no clear definition of the mammalian amygdala.

How then has the amygdala been identified in non-mammals? Here again, similarly to the case of the neocortex homolog, initial identification of the non-mammalian amygdala relied on hodological or functional properties, not on developmental data. A structure named “amygdala” in the amphibian brain appeared in the early 1900s literature in relation to the vomeronasal system [65]. Later, other amygdaloid connectivity such as with the hypothalamus was elucidated [17, 66]. Such connectivity has been crucial for identifying the amygdala in vertebrates. For instance, the currently accepted “avian pallial amygdala” consists of nuclei of the formerly named archistriatum that are highly associated with the hypothalamus (visceral-related connectivity) [67, 68] and that are involved in Pavlovian conditioning (CS-US association) [69].

Without these cytoarchitectonic/functional/hodological criteria, the identity of the “amygdala” itself collapses, as no developmental or molecular criteria exist to define this structure. Ever since Puelles’s first tetrapartite model was accepted by developmental neurobiologists in the early 2000s, molecular data were favored over functional or hodological data as criteria of regional homology. The problem of the current situation is that despite the developmental/molecular heterogeneity of the mammalian amygdala [12, 64, 70], most people stick to the notion that the amygdala should be conserved and should be found as a structural entity in nonmammalian pallia.

In reality, if we accept the DVR = LP/VP hypothesis (Fig. 3b) based on the first tetrapartite model (Fig. 5b), it goes against the concept of a “conserved amygdala.” As described in the sections above, the avian nidopallium (ventral part of DVR) is functionally more similar to the mammalian neocortex (considered DP) than to the mammalian amygdala (considered VP). If we acknowledge that the nidopallium is homologous to the amygdala (Fig. 3b), it suggests that the functions of the amygdala homolog have significantly diversified within amniotes.

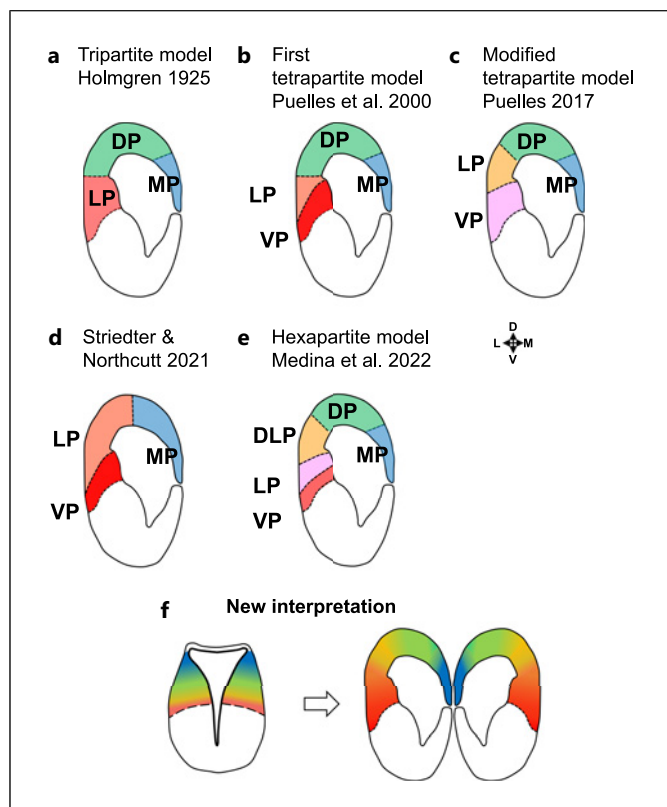


Fig. 5. Modifications of the classification of pallial subdivisions in sarcopterygians. **a–e** Frontal sections through the pallium (left side) summarizing different hypotheses of pallial subdivisions. See the text for details. The boundaries and number of pallial subdivisions keep being modified over time, depending on the criteria and species examined. Importantly, the first tetrapartite model (**b**) that was widely accepted after 2000's has been abandoned by the authors themselves (**c**), and there is no consensus proposition since then. **f** Our new interpretation. The neural tube organization is gradient and boundaries of the pallial subdivisions are not as clear as it has classically been assumed. Amy, amygdala; DLP, dorsolateral pallium; DP, dorsal pallium; LP, lateral pallium; MP, medial pallium; VP, ventral pallium. Brain orientation: D, dorsal; V, ventral; L, lateral; M, medial.

How Many Pallial Subdivisions Are There in a “Vertebrate Morphotype”?

Confusingly enough, the first tetrapartite model was later abandoned by Puelles himself, and the pallial subdivisions were completely redefined [13, 71]. Until then, the tetrapartite model was within the frame of the Holmgren tripartite model: DP was synonymous with “homologous to the mammalian neocortex,” and there was no argument regarding the boundary between DP (general pallium) and LP (piriform pallium). The only difference was whether the LP was considered to be a single sub-

division or two subdivisions, LP and VP (Fig. 5a, b). By contrast, in the new tetrapartite model proposed in 2017, Puelles repudiates the original tripartite model, modifying the border between the DP and LP (Fig. 5c). LP was redefined as the area homologous to the claustrum and the insular cortex of mammals, and VP as the area homologous to the piriform cortex, the endopiriform nucleus, and the pallial amygdala [13]. Two years later, Puelles further modified this model, considering pallial subdivisions as concentric rings, DP being situated as an “island” in a conceptually flattened forebrain [71].

As more data accumulated, the classification became even more ambiguous, with proposals from two to six subdivisions [14, 15, 72, 73]. Recent single-cell transcriptomic studies in amphibians indicated five pallial sectors showing distinct molecular profiles [72, 73]. These data were interpreted so that the five sectors would correspond to the previously proposed MP, DP, LP, VP, and an additional ventral sector that was proposed as the pallial amygdala. However, if the amygdala is a subdivision different from VP, what is VP? Note that originally, the VP was defined as the most ventral part of the pallium containing the amygdala.

Medina and her colleagues [14] also proposed a hexapartite model, in which they consider the newly defined LP by Puelles (2017) as the “dorsolateral pallium” (Fig. 5e). What is the “dorsolateral” pallium? Is it an area that shares characteristics of DP and LP? Then, why not define an area that shares characteristics of DP and MP as DMP? Although we tend to think that the neocortex (originally defined as DP) is somewhat special, the nature of the six-layered neocortex and the rest of the pallium may not be that different, to the degree that they are easily misidentified. In that sense, the organization of the pallium may be gradient (Fig. 5f).

This profusion of models raises the question: how many divisions does the vertebrate pallium actually contain? Or how many pallial divisions did the common ancestor of vertebrates possess? The foundations defining the first tetrapartite model have already collapsed, yet all the authors stick to the term MP/DP/LP/VP out of convenience.

There is no doubt that there exists a dorsoventral organization in the developing pallium along the pallial wall inherited from the common ancestor, at least within tetrapods (Fig. 5f). However, it is not clear how this organization corresponds to the subdivisions (as identified in the mature pallium) of different vertebrates in a one-to-one manner. It is possible that the pallium evolved different numbers of subdivisions in different lineages independently, and some subdivisions may not be

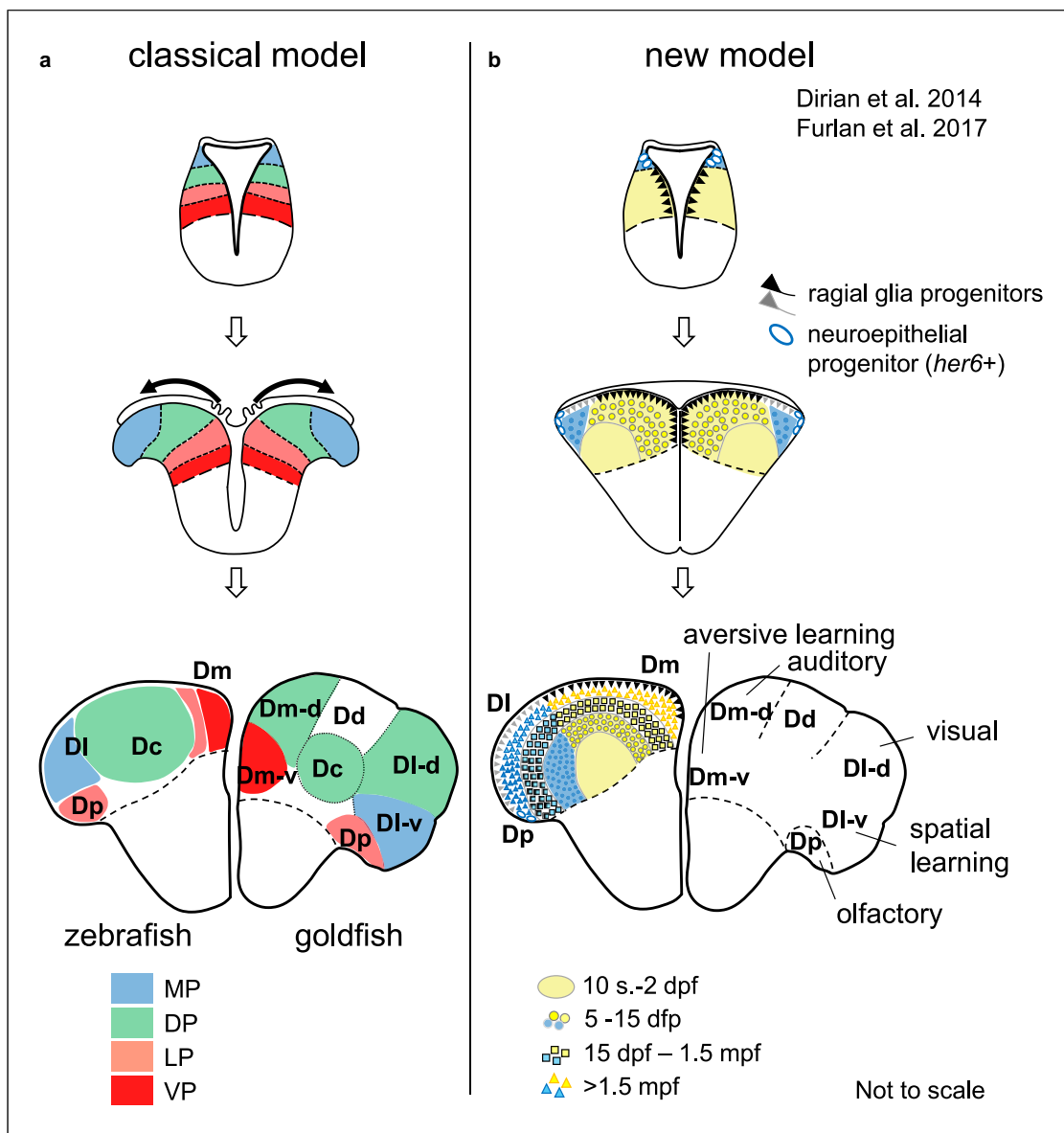


Fig. 6. New eversion theory of the teleost pallium. **a** Classical model of the pallial development of actinopterygians, color-coded with one of the prevailing pallial homology (based on the first tripartite model; Fig. 5b). The left side of the mature brain shows the zebrafish pallium, while the right side shows the goldfish pallium. Historically, pallial regions in actinopterygians have been considered as a simply reversed version of the sarcopterygian pallium (compare also with Fig. 1). **b** New model based on lineage tracing data, adapted from Dirian et al. [84] and Furlan et al. [85]. The construction of the actinopterygian pallium is not simply a reversed version of the sarcopterygian pallium. The teleost pallium does not develop by extension of the preexisting three or four

embryonic subdivisions. Instead, newly born neurons are progressively “stacking-up” on top of the old ones. All the lateral parts of the pallium containing Dl and Dp are derived from the *her6+* progenitors located at the dorsal tip of the neural tube until 2 dpf. Dc, central zone of the pallium; Dd, dorsal zone of the pallium; Dl, lateral zone of the pallium; Dl-d, dorsal part of Dl; Dl-v, ventral part of Dl; Dm, medial zone of the pallium; Dm-d, dorsal part of Dm; Dm-v, ventral part of Dm; Dp, posterior zone of the pallium; dpf, days post-fertilization; DP, dorsal pallium (as morphotype); LP, lateral pallium (as morphotype); MP, medial pallium (as morphotype); mpf, months post-fertilization; s, somites; VP, ventral pallium (as morphotype).

homologous across species. This would mean that there is not a “single morphotype” of the pallial subdivisions that can be generalized throughout vertebrates. For example,

studies on the distribution of active enhancers allowed to delineate up to eight protodomains in the developing mouse pallium [74, 75], but this may only reflect the

situation of the mammalian (or mouse) pallium, and not that of the pallia of other vertebrate groups.

It is also important to note that all the recent claims described above, except Striedter and Northcutt [15], only take into account the tetrapod pallium that is constituted by evagination. To be accepted as parts of the “morphotype,” such claims need to be validated throughout vertebrates, including those with an everted pallium.

Teleost Data Further Disprove the Current Dogma of the Pallial Subdivisions

Tetrapods, including mammals, birds, and amphibians, belong to the sarcopterygians (lobe-finned fish), while teleosts belong to the actinopterygians (ray-finned fish), the other group of bony vertebrates (*Osteichthyes*). The development of the pallium is largely different between the sarcopterygians and the actinopterygians (Fig. 1). In most vertebrates, including the sarcopterygians, the telencephalon develops via a process termed “evagination.” In this process, the central lumen of the neural tube enlarges to form two lateral ventricles (Fig. 1; left). In the pallium of actinopterygians, the lateral ventricles are not formed, since the roof of the neural tube elongates outwards to cover the pallium. This way of morphogenesis has been called “eversion” (Fig. 1; right). According to the classical eversion theory, the medial-lateral organization of the pallium of actinopterygians pallium was considered to be an inverted version of that of sarcopterygians (i.e., dorsal tip of the neural tube becomes a medial structure in sarcopterygians, while it becomes a lateral structure in actinopterygians). Since the pallium of cartilaginous vertebrates (*Chondrichthyes*) and cyclostomes develops by evagination, it is very likely that the eversion process has evolved specifically in the common ancestor of actinopterygians (Fig. 1).

Historically, the teleost pallium is abbreviated as “D” for the “dorsal telencephalic area,” and its subdivisions are named according to their topology: lateral (Dl), medial (Dm), dorsal (Dd), posterior (Dp), and central (Dc) zones of the pallium [76–78] (Fig. 6). Different authors have proposed several hypotheses regarding which part of the teleost pallium would correspond to each of the mammalian pallial subdivisions [78–83], without any consensus so far.

These hypotheses are based on the two following assumptions: (1) the teleost pallium should have one-to-one homologs of MP/DP/LP/VP of mammals (either within the frame of the tripartite or the first tetrapartite

models; Fig. 5a, b); (2) the medial-lateral organization of the pallium in actinopterygians is inverted compared to sarcopterygians (the color code represented in Fig. 1). In the following, we first introduce proposed hypotheses of pallial homology, and then, we will discuss our interpretation by assembling the current knowledge on the pallia in both sarcopterygians and actinopterygians.

Current Hypotheses of Pallial Homology in Teleosts

A set of studies in several teleost species have demonstrated that the sensory-recipient areas are distributed throughout the pallium, in a somewhat modality-specific way. For example, visual inputs terminate in the dorsal Dl, auditory inputs in the dorsal Dm, and olfactory inputs in the Dp [78, 86, 87] (Fig. 6a). The areas receiving nonolfactory inputs have been often compared to the mammalian neocortex [88].

Other sets of studies by Salas and his colleagues in goldfish have indicated that a hippocampus-like function (spatial learning) resides in the ventral Dl [89], and an amygdala-like function (active avoidance learning) resides in the ventral Dm [90]. Although there is another study showing that a medio-dorsal part of the pallium is involved in spatial learning [91], the hypothesis by Salas’s group that Dl-v and Dm-v are the hippocampal and amygdalar homologs, respectively, has been widely accepted because it fits better with the eversion theory.

Mueller and his colleagues proposed a modified version in which the goldfish data were transferred to the zebrafish pallium [83, 92]. This however poses a problem, as there are significant differences in size and complexity between the goldfish and zebrafish pallia (compare zebrafish and goldfish in Fig. 6a), and the zebrafish brain is not representative of “the teleost brain.” Nonetheless, zebrafish is becoming a popular model species in neuroscience, so the simplified zebrafish version is becoming a prevailing basis for subsequent studies [93–95]. Recent models of teleost pallium organization have adapted the first tetrapartite model. Thus, homology with tetrapods is schematized as follows: Dl = hippocampus (MP), Dc = neocortex (DP) (with nonolfactory sensory inputs); and Dp = piriform cortex (LP) (with olfactory bulb inputs), Dm = amygdala (VP).

Assumptions Constituting the Current Hypotheses of Pallial Homology between Amniotes and Teleosts Have Fallen Apart

It is important to remember that all the proposed pallial homology hypotheses between teleosts and mammals principally rely on hodological or functional

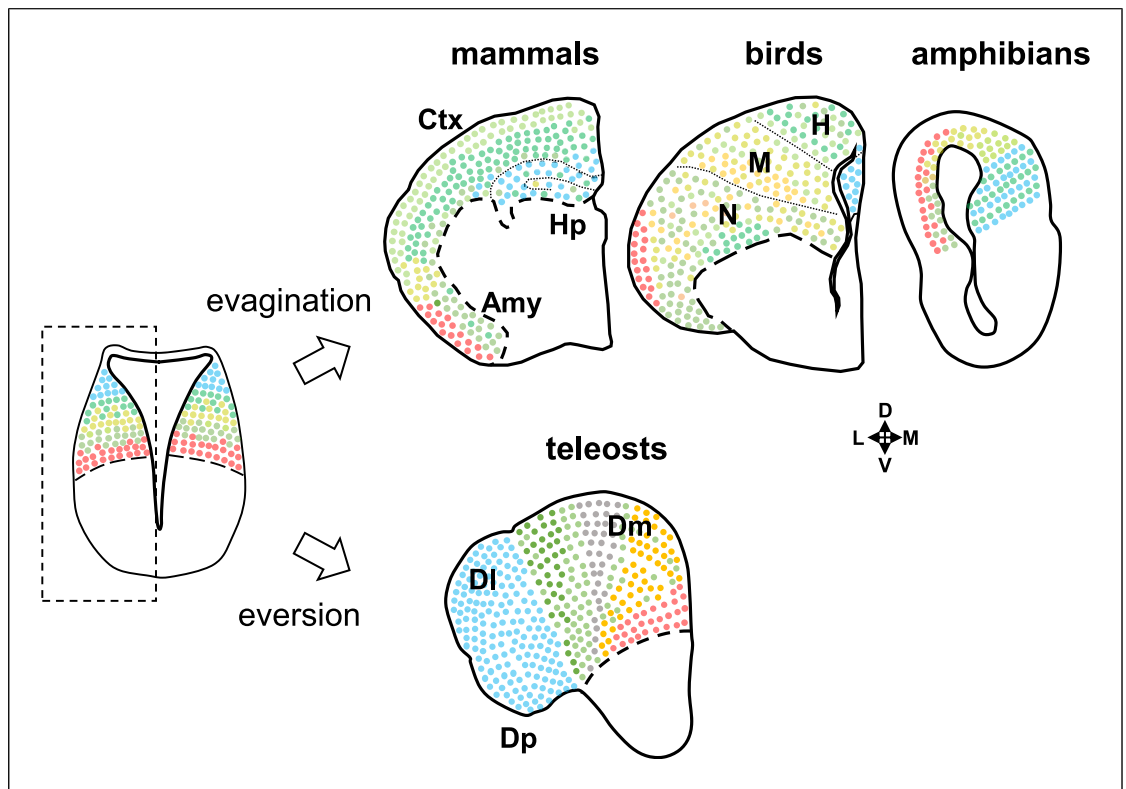


Fig. 7. Schematic representation of the new view of pallial organization in vertebrates taking into account the everted pallium. A representative embryonic neural tube (both hemispheres) is shown on the left, and adult pallia (left side of the telencephalic hemisphere) of mammals, birds, and amphibians (evaginated pallium) and of teleosts (everted pallium) are shown on the right. The gradient organization along the neural tube (Fig. 5f) is shared within the tetrapod pallium (presumably all sarcopterygians), while the dorsoventral, medial-lateral organization is very different in the teleost pallium (see Fig. 6b). None of the current models can provide a compre-

hensive morphotype across vertebrates, and homology needs to be discussed at the level of smaller cell clusters or cell types, instead of the level of cytoarchitectonically distinct subdivisions in the mature brain (e.g., neocortex, amygdala, nidopallium, Dm, Dl). Amy, amygdala (mammalian structure); Ctx, neocortex (mammalian structure); Dl, lateral part of the pallium (teleost structure); Dm, medial part of the pallium (teleost structure); Dp, posterior part of the pallium (teleost structure); H, hyperpallium (avian structure); M, mesopallium (avian structure); N, nidopallium (avian structure). Brain orientation: D, dorsal; V, ventral; L, lateral; M, medial.

(brain lesion) studies. Even though some authors aimed for molecular comparison with the mammalian and teleost pallia [92, 96], the data were interpreted with the assumption that one-to-one regional homology should exist between mammals and teleosts, and the focus was on seeking similarities while ignoring rather substantial differences.

In addition, the studies were conducted in mature brains, thus the data are not directly comparable with those conducted in developing brains in tetrapods. For example, the use of transcription factors like *Emx1* as a regional marker makes sense only at a certain stage during development, as their expression patterns largely vary in adulthood. Regarding the *Emx* genes, a zebrafish study shows that *emx3*, instead of *emx1* or

emx2, plays a critical role in pallial development [97]. The *Emx3* gene has been lost in many tetrapod species except a few species such as *Xenopus* and opossum. This indicates that the role of each *Emx* paralogous gene may be different in tetrapods and teleosts, and the importance of *Emx1* expression may be limited to the tetrapods.

Another critical point is that all these studies using molecular markers/genes have been interpreted relying on the first tetrapartite model (Fig. 5b), which has already been abandoned by many authors (Fig. 5c–e). All the data should thus be reinterpreted, integrating the newly proposed models.

Moreover, in order to support homology between mammals and teleosts based on similar phenotypes

(regardless of function, morphology, or gene expression pattern), the phenotypes shared between mammals and teleosts should also be shared in the majority of bony vertebrates. If a similarity found between teleosts and mammals is not found in birds, amphibians, or other members of actinopterygians (e.g., *Polypterus*, sturgeons, or gars), the similarity is unlikely to be a consequence of conservation, but of convergence. With careful cladistic analyses, many features that had been thought “conserved” turned out to be a consequence of convergent evolution [98–101].

Questionable Dogma of the “Conserved Amygdala”

The hypothesis of “Dm = amygdala” is the first example lacking satisfactory evidence in favor of “evolutionary continuity.” Dm is in fact not recognizable in some non-teleost actinopterygians like the *Polypterus* [102, 103]. Thus, the conservation of Dm is not at all clear even among actinopterygians.

The major arguments claiming the hypothesis of “Dm = amygdala” come from behavioral studies showing that Dm is involved in the conditioned avoidance response [90, 104]. However, using functional similarities as a claim of regional homology has been criticized by developmental neurobiologists. As discussed above in the section on the tetrapod limbic system, for instance, if the hypothesis of “avian nidopallium = VP” is true, it means that the functional properties of VP are very flexible, as the avian nidopallium is functionally rather similar to the mammalian DP.

But even more fundamentally, can we really define the amygdala by the involvement of a structure in aversive learning? Classically, the pallial amygdala (lateral and basal nuclei of amygdala) was proposed to be critical for the acquisition of Pavlovian fear conditioning (CS-US association), which led to the idea that the amygdala is a conditioned fear center [105–107]. However, this dogma on amygdala functions has been challenged by subsequent studies [108–110]. Furthermore, fMRI analyses have shown that fear learning may not be a representative function of the human amygdala, while other brain areas, such as the midcingulate cortex, anterior insula, also showed activation in response to learned threat [111]. Thus, the functional definition of the amygdala as a center for fear/aversive conditioning has become ambiguous.

Other than the involvement of Dm in the conditioned avoidance response, there are no developmental/molecular data supporting the similarity of the teleost Dm with the tetrapod amygdala. For example, *Emx1* expression, whose absence was the original definition of

VP, does not support the regional homology of the teleost Dm and the tetrapod amygdala; there are no data showing the presence of embryonic *Tbr1*-positive/*Emx1*-negative territory that gives rise to Dm in the mature pallium. Moreover, all these studies follow the first tetrapartite model of Puelles et al. (2000), so that Dm corresponds to the tetrapod VP (“Dm = amygdala = VP”) [83]. However, it is important to remember that this model is now abandoned by Puelles himself (as discussed above).

Overall, these factors weaken the justifications currently used for identifying the amygdala (or VP) in nonmammals including teleosts, making it hard to deduce its ancestral situation.

New Eversion Theory Suggests a Shared Developmental Origin of the Hippocampal-Like and Olfactory Areas in the Teleost Pallium

A large assumption of all the claims of pallial homology between teleosts and mammals is the classical “eversion theory,” in which the MP is supposed to be laterally located, and the LP to be medially located in the teleost pallium [4, 20, 83].

Nonetheless, projections from the olfactory bulb (which identify the piriform [olfactory] cortex in amniotes) terminate at the lateral end of the pallium, which is identified as Dp in teleost species [78, 112–114]. Paradoxically, the homology of Dp = piriform cortex has never been argued against, even though it is clearly not supported by the eversion theory, as the lateral end of the pallium should be hippocampal according to topology. To explain this discrepancy, Mueller et al. [83] hypothesized that the Dp is constituted by migrated cells from a part of Dm, proposing the medial and lateral edges to be the LP (Fig. 6a).

However, detailed cell lineage studies of the zebrafish pallium reject this hypothesis [84, 85]. It has been confirmed that D1 (the area proposed to be similar to the hippocampus) and Dp (the area proposed to be similar to the piriform cortex) both develop from the progenitor pools located at the dorsal tip of the early telencephalic neural tube (Fig. 6b; blue) [84, 85]. If we consider that this dorsal tip of the embryonic neural tube (Fig. 6b; blue) corresponds to MP, it means that, the teleost MP gives rise to neural populations not only playing a hippocampus-like role in spatial memory (ventral D1), but also in visual sensory (dorsal D1) and in olfactory sensory (part of Dp) processing. Thus, in teleosts, a simple “D1 = hippocampus = MP” framework is not supported by developmental data.

Indeed, contrary to the previous eversion theory, the lateral pallial area is not pushed away from the midline laterally by mechanical pressure due to neural tube growth (Fig. 6a). Instead, newly born neurons are progressively “stacking-up” on top of the old ones, like a snowball (Fig. 6b) [84, 85]. In this way, the deepest cell populations are the oldest ones, while the most superficial cells are the younger ones. The organization of the teleost pallium is thus not at all an inverted version of the tetrapod pallium. As all the hypotheses on the teleost pallium are based on this classical eversion theory, the proposed pallial homology needs to be reconsidered by taking into account this new viewpoint of eversion.

Convergent Evolution of Tectofugal Visual Pathways

The simplified hypothesis of “DI = hippocampus” [83] appears not to contradict the eversion theory, as it develops from the dorsal tip of the embryonic neural tube like the amniote hippocampus. However, this hypothesis ignores the heterogeneity of DI. Due to its sensory nature, the dorsal part of DI has also been compared to the thalamorecipient visual areas of amniotes [87, 88, 115]. With new developmental data, the diversity of this area has been underlined further.

We have recently revealed that the tectofugal visual pathway terminating in the dorsal DI is not homologous to the amniote ones but independently evolved in the teleost lineage [101]. In teleosts, different sensory modalities (visual, auditory, lateral lines, etc.) terminate in the pallium [78, 86, 87], but major sensory inputs are not from the thalamus, but from a structure called the preglomerular nuclear complex (PG) that has specifically evolved in the group of teleosts. The PG-pallium sensory projections of teleosts may be similar to the thalamocortical pathways of amniotes, but there is no continuity in the evolution of these sensory pathways [101].

As described above, the homology of tectofugal pathways in tetrapods has already been debated. In addition, prominent tectofugal visual inputs to the pallium are observed only in mammals, birds, and teleosts, and not in the intermediate taxa such as amphibians [18, 19, 60, 61, 116], sturgeons [117, 118], or *Polypterus* [119–121]. Thus, it is more probable that visual recipient areas of the pallium have emerged at least 3 times in vertebrates and were not inherited from their common ancestor. Our conclusion is consistent with the hypothesis by Striedter and Northcutt [15] that the thalamocortical-like projections would have evolved independently in different lineages.

To summarize, the teleost pallium is organized very differently from the tetrapod pallium, and although some similar functional properties are found, there are no data so far supporting the fact that similar functions reside in homologous (that is, of the same developmental origin within the neural tube) pallial subdivisions.

Conclusion

One hundred years ago, vertebrate brain evolution was believed to be unilinear, brains having evolved from a fish-type old brain toward a mammalian-type new brain with a neocortex [1–3, 122]. It turned out that the mammalian neocortex is a part of the pallium, the dorsal telencephalon that is present in all vertebrates. Since then, the hypothetical pallial subdivisions have been useful for promoting the comparative analysis of brains using nonmammalian species, leading to a large accumulation of knowledge on the vertebrate brain. However, as more data came, it turned out that the morphological divisions of the pallium are often difficult to define and not clearly conserved across all vertebrates. We have encountered serious discrepancies when we search for a single morphotype of subdivisions across vertebrates.

These discrepancies can be resolved by considering that pallium subdivisions have evolved independently; that is, several cytoarchitectonic subdivisions were established after the divergence of the different lineages. The conserved elements lie not in the cytoarchitectonic structure, but rather at the cellular or molecular level. The similar functional/hodological organization found in different taxa may be constructed using genetic “tool-kits” inherited from a common ancestor, but each tool-kit may have been recruited independently in different lineages, resulting in similar neural networks in a convergent manner. This view coincides with the idea of “cell-type homology” (Fig. 7), which is beginning to be accepted by comparative neuroanatomists investigating sauropsids [50, 55, 123, 124].

As exemplified by the independent emergence of neocortex-like functions in a relatively short time in birds (after the separation of mammals and sauropsids), the evolution of neural functions is more flexible than previously thought. This raises the possibility that brain areas that play a role in aversive or spatial learning could also evolve in a convergent manner. What makes our community cling to the idea of conservation of these

structures is the notion that the limbic brain structures should be more conserved than the neocortical structure. This is a remnant of the *scala naturae* point of view, and it is high time we fully emancipate from this dogma.

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Conflict of Interest Statement

The authors have no conflict of interests to declare.

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Author Contributions

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