The Independent Evolution of Dorsal Pallia in Multiple Vertebrate Lineages

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Abstract

Comparative neurobiologists have long wondered when and how the dorsal pallium (e.g., mammalian neocortex) evolved. For the last 50 years, the most widely accepted answer has been that this structure was already present in the earliest vertebrates and, therefore, homologous between the major vertebrate lineages. One challenge for this hypothesis is that the olfactory bulbs project throughout most of the pallium in the most basal vertebrate lineages (notably lampreys, hagfishes, and lungfishes) but do not project to the putative dorsal pallia in teleosts, cartilaginous fishes, and amniotes (i.e., reptiles, birds, and mammals). To make sense of these data, one may hypothesize that a dorsal pallium existed in the earliest vertebrates and received extensive olfactory input, which was subsequently lost in several lineages. However, the dorsal pallium is notoriously difficult to delineate in many vertebrates, and its homology between the various lineages is often based on little more than its topology. Therefore, we suspect that dorsal pallia evolved independently in teleosts, cartilaginous fishes, and amniotes. We fur-

ther hypothesize that the emergence of these dorsal pallia was accompanied by the phylogenetic restriction of olfactory projections to the pallium and the expansion of inputs from other sensory modalities. We do not deny that the earliest vertebrates may have possessed nonolfactory sensory inputs to some parts of the pallium, but such projections alone do not define a dorsal pallium.

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The two of us recently wrote a book called *Brains Through Time: A Natural History of Vertebrates* [Striedter and Northcutt, 2020] in which we reviewed diverse aspects of vertebrate evolution with a focus on the nervous system. Among the evolutionary changes we discussed are major transformations of the telencephalon, especially the so-called pallium, which in mammals consists of the pallial septum, the hippocampal and parahippocampal cortices, the neocortex, the claustrinsular cortex, the olfactory cortex, and part of the amygdala. Of particular interest over the years has been the question of when and how the dorsal pallium – generally known as the neocortex in mammals – emerged during phylogeny. As we researched this topic for our book, we concluded that a dor-

sal pallium probably evolved several times independently. Specifically, we proposed that it evolved in the lineage leading to amniotes (i.e., reptiles, birds, and mammals), in the lineage leading to ray-finned fishes, and in cartilaginous fishes. Because of the general neurobiological importance of this issue, we here present a tightly focused account of the arguments that led to this conclusion. We also offer a few additional considerations, especially regarding recent findings in lampreys. We begin with a philosophical preamble and a brief history of the problem.

Similarities or Differences: Which Deserve More Attention?

Our book was explicitly focused on the “key innovations” of the major vertebrate lineages, exploring how these novelties relate to one another and contributed to each lineage’s ecological and evolutionary success. Given this focus, it was natural for us to emphasize species differences rather than conserved features. Extracting those differences from the published literature was not always easy, because many authors either eschew comparative analyses or emphasize the similarities between major taxa. Indeed, a focus on species similarities is common in many areas of biology, where the use of diverse species as “models” is a major research strategy [Bolker, 2019; Striedter, 2019]. Moreover, it seems to us that discoveries of unexpected conservation are easier to publish – especially in high-profile journals – than reports of features that are unique to specific lineages, unless the lineage includes humans. After all, conservation is relatively simple to explain as the result of “inheritance from a common ancestor.” In contrast, lineage-specific features require more complex explanations that, ideally, reference both developmental mechanisms and functional correlates.

Because we think that species similarities already receive plenty of attention in many areas of biology, including the comparative neurobiological literature, we felt justified in adopting a somewhat contrarian focus on species differences. That said, the recognition of species similarities is clearly an important exercise. As Francis Bacon wrote in 1620: “The greatest and, perhaps, radical distinction between different men’s dispositions for philosophy and the sciences is this, that some are more vigorous and active in observing the differences of things, others in observing their resemblances ... each of them readily falls into excess” [cited in Friedmann, 2004].

We wholeheartedly agree but add that science and scientists tend to go through phases in which the discovery of similarities is paramount, followed by periods where interest in differences is more useful. Generally speaking, when humans are confronted with a profusion of seemingly disparate data, it is natural for them to seek patterns, which are usually grounded in similarities. Once those patterns are identified, deviations become discernible, which then prompts another round of pattern detection. As David Bohm [1957] observed, it is this tension between order and disorder – between similarities and differences – that drives scientific advance. In short, our emphasis on species differences should not be misconstrued as advocating for chaos. Instead, we are interested in identifying species differences that stand out against a background of conserved features.

Previous Ideas about Pallial Evolution

The term *pallium* has long been used to describe the dorsocaudal part of the telencephalon in vertebrates. Some authors use *cortex* instead of pallium, but the latter term is preferable because, even in mammals, some pallial regions do not exhibit the layered organization that the cortex label generally implies. Especially in embryonic brains the pallium is recognizable at stages that exhibit no cortical layering, even in mammals.

The pallium itself has long been recognized as consisting of several divisions. The *medial pallium* is generally thought to develop into the hippocampus and some immediately adjacent structures, whereas the *lateral pallium* was traditionally regarded as olfactory cortex. In between the medial and lateral pallia, most investigators have recognized a *dorsal pallium* (aka general pallium) but, until the late 1960s, this pallial division was thought to arise relatively late in vertebrate phylogeny, specifically in the lineage leading to amniotes. This is why the principal derivative of the embryonic dorsal pallium in mammals is called the *neocortex*; it was thought to be relatively new.

Although the hippocampus in amniotes does not receive major direct projections from the olfactory bulbs (i.e., secondary olfactory projections), early comparative neuroanatomists thought that the medial pallium in amniotes (i.e., vertebrates other than amniotes) does receive at least some secondary olfactory projections. Given that the lateral pallium also receives major inputs from the olfactory bulb, as well as the aforementioned belief that amniotes lack a dorsal pallium, these early

neuroanatomists concluded that the entire pallium of anamniotes is dominated by olfactory inputs. This idea came to be known as the “smell brain hypothesis” of pallial evolution. According to this theory, it was only with the emergence of the dorsal pallium in amniotes that olfactory projections to the pallium became more limited and were displaced by inputs from other sensory modalities.

These early views were upended in the late 1960s and 1970s, when new neuroanatomical tracing techniques revealed that the secondary olfactory projections in sharks and teleost fishes (e.g., goldfish) were restricted to relatively small portions of the pallium and that some of the remaining nonolfactory regions receive inputs from other sensory modalities [Ebbesson and Heimer, 1970; Scalia and Ebbesson, 1971; Northcutt, 1981]. These observations suggested that a dorsal pallium must have evolved long before amniotes appeared. Thus emerged a general consensus that all vertebrates (or at least all jawed vertebrates) have a tripartite pallium comprising medial, dorsal, and lateral pallia [e.g., Butler and Hodos, 2005]. A few authors noted that a fourth pallial division, corresponding to pallial portions of the amygdala, might exist between the lateral pallium and the subpallium [Northcutt, 1981, 1995], but this idea for many years received relatively little attention.

This situation changed in the late 1990s, when Fernandez et al. [1998] reported that the transcription factor *Emx1* is expressed throughout most of the pallium in amphibians and amniotes but is absent from the most ventral portion of the lateral pallium. Puelles et al. [2000] recognized the importance of this finding and identified the *Emx1*-negative zone as a fourth principal division of the pallium, which they named ventral pallium. Later studies showed that this ventral pallium selectively expresses *Dbx1* [Medina et al., 2004] and, in mammals, gives rise to most of the olfactory cortex, parts of the amygdala, and the ventral endopiriform nucleus [Puelles et al., 2016]. There has been a long-running debate about the extent of this ventral pallium in reptiles and birds, where it appears to be greatly enlarged [Striedter, 1997; Puelles, 2017; Puelles et al., 2017; Wullmann, 2017b]. More important for present purposes is that this tetrapartite model of pallial organization is now widely considered to apply across all vertebrates, with the possible exception of cyclostomes (see below). If this is true, then a dorsal pallium should exist in all jawed vertebrates and be homologous between them [Northcutt, 1995; Butler and Hodos, 2005].

Chinks in the Paradigm

As we were preparing our book, we were forced to confront 2 observations that do not fit comfortably into the currently dominant view of pallial evolution. Specifically, we had to deal with the fact that: (1) the secondary olfactory projections in several anamniotes reportedly target most or all of the pallium and (2) the dorsal pallium in these anamniotes is difficult, if not impossible, to delineate with certainty. In response, we began to reconsider the smell brain hypothesis and questioned some dorsal pallium homologies.

The Smell Brain Hypothesis Revisited

Beginning in the 1980s, experimental neuroanatomical studies revealed that the secondary olfactory projections are surprisingly extensive in several anamniotes. Specifically, Northcutt and Puzdrowski [1988] showed that the olfactory bulbs in lampreys project to most of the pallium, a finding that was corroborated by Polenova and Vesselkin [1993] in a second lamprey species. Wicht and Northcutt [1993; 1998] reported analogous results for hagfishes, and Northcutt and Rink [2012] did the same for lungfishes. Given that cyclostomes (i.e., lampreys and hagfishes) as well as lungfishes are the sister groups of jawed vertebrates and tetrapods, respectively (Fig. 1), these findings suggest that widespread olfactory projections to the pallium might have been the primitive condition for vertebrates, just as the smell brain hypothesis had posited. Under this scenario, the secondary olfactory projections would have become more restricted in several vertebrate lineages, notably amniotes, ray-finned fishes, and cartilaginous fishes (Fig. 1). Alternatively, the secondary olfactory projections may have been restricted to just part of the pallium in the earliest vertebrates and later expanded in multiple lineages.

To decide between these 2 hypotheses, we considered additional data from amphibians, in which the olfactory bulb projects to the entire lateral pallial wall, including the so-called dorsal pallium, but not to most of the medial pallium [Northcutt and Royce, 1975; Neary, 1990] (Fig. 2). This pattern is intermediate between that of lungfishes (with their widely distributed olfactory projections) and the highly restricted olfactory projections in amniotes, which is interesting because amphibians are also phylogenetically intermediate between lungfishes and amniotes (Fig. 1). Comparative morphologists refer to such a pattern of orderly intermediate traits in intermediate taxa as a morphocline [Maslin, 1952]. Importantly, these data support the hypothesis that the second-

Fig. 1. Convergent restriction of secondary olfactory projections to the pallium. Shown here are the vertebrate taxa discussed in the text and their phylogenetic relationships. The circles represent the pallium, and the shaded portion represents the extent to which the olfactory bulbs project to the principal pallial zones; they are most widespread in cyclostomes and lungfishes and most restricted in elasmobranchs, teleosts, and amniotes. Also shown are the hypothesized character states at ancestral nodes and the discussed transformations (arrows).

ary olfactory projections became progressively more restricted along the lineage leading to amniotes. An analogous set of studies on ray-finned fishes [Northcutt and Davis, 1983; von Bartheld and Meyer, 1986; Northcutt, 2011] shows that the secondary olfactory projections are most extensive in the most basal lineage (i.e., *Polypterus*) and become progressively more restricted in the more derived lineages, notably teleosts (Fig. 2). Please note that we here use “basal” and “derived” to denote lineages that originated from more and less ancient nodes in the phylogenetic tree, respectively. Since our basal lineages contain few species, we evade the problems otherwise associated with identifying basal lineages [Krell and Cranston, 2004].

Based on these considerations, we endorse the hypothesis that the olfactory bulbs of early vertebrates projected throughout the pallium and that those projections became more restricted in several vertebrate lineages. In short, we think that the smell brain hypothesis was discarded prematurely and that its core idea – of the earliest vertebrates having an olfaction-dominated pallium – deserves to be resurrected. We acknowledge that some pallial neurons in the earliest vertebrates may well have received ascending inputs from other sensory modalities, but we hypothesize that these neurons *also* received olfactory inputs. One can debate whether the existence of such nonolfactory inputs to the pallium would falsify the original smell brain hypothesis entirely [Wullimann, 2017a],

or just its most extreme version, but this is not our concern here.

A Dorsal Pallium Identity Crisis

Because the dorsal pallium in amniotes is associated with nonolfactory sensory (e.g., visual and somatosensory) processing, our embrace of the smell brain hypothesis prompted us to question whether early anamniotes had a dorsal pallium. Specifically, we wondered whether they might have possessed a dorsal pallium that, in contrast to the dorsal pallium of amniotes, received secondary olfactory projections, which were subsequently lost. This hypothesis would be strengthened if extant anamniotes all had dorsal pallia that are very similar in other respects and, thus, likely to be homologous across anamniotes.

However, the existing literature on the putative dorsal pallia of anamniotes is rife with debates and uncertainties. For example, different authors have described very different boundaries for the supposed dorsal pallium of amphibians, and we currently suspect that what most researchers (including us) have previously called the dorsal pallium in amphibians is merely a transition zone between the medial and lateral pallia. It remains possible that amphibians do possess a small dorsal pallium that forms an island between the medial and lateral pallia and is apparent only at a few rostrocaudal levels [Nerea Moreno García, pers. commun.; see also Puelles, 2001], but positive evidence for this hypothesis has not been pub-

lished. Similarly, a dorsal pallium has been reported to exist in lungfishes [González and Northcutt, 2009; Northcutt, 2009], but this region is poorly differentiated from the lateral pallium and may, therefore, be a dorsal portion of the lateral pallium rather than a distinct primary pallial zone.

A dorsal pallium remains elusive also in *Polypterus*. This basal ray-finned fish does have a large pallium with several subdivisions, but a thorough analysis by Holmes and Northcutt [2003] suggested that the *Polypterus* pallium consists of only 2 large divisions, each of which contains 2 subdivisions. The medial subdivision of the dorsolateral division does not receive inputs from the olfactory bulb [von Bartheld and Meyer, 1986] (Fig. 2) and is therefore a potential homolog of the dorsal pallium in amniotes, but (in contrast to the dorsal pallium of amniotes) it does not receive thalamic input and is poorly delineated from its lateral neighbor; thus, it is a dubious dorsal pallium candidate. Other ray-finned fishes, notably teleosts, possess a more distinct structure that may be called a dorsal pallium [Mueller et al., 2011], but how this region relates to the pallial divisions of *Polypterus* remains unclear (see The Ray-Finned Fish Revolution).

The situation is even more confusing in cyclostomes. Hagfishes have a large and complex pallium that is so different from the pallium of other vertebrates that homologizing its divisions is fraught with uncertainties [Wicht and Northcutt, 1992, 1993, 1998]. The pallium of lampreys is much smaller and simpler, but whether it contains a dorsal pallium homologous to that of amniotes has long been a matter of debate (see The Lamprey Conundrum).

In short, the structures that have previously been identified as dorsal pallia in anamniotes with relatively widespread secondary olfactory projections tend to be small and poorly differentiated or (perhaps) absent entirely. This observation, in turn, suggests that dorsal pallium-like structures may well have evolved independently in the lineages in which the secondary olfactory projections became more restricted [Wullimann and Vernier, 2009]. Some of the strongest evidence in support of this hypothesis comes from ray-finned fishes.

The Ray-Finned Fish Revolution

The ray-finned fishes comprise roughly half of all vertebrates and are enormously diverse; so is their pallium. Whereas the pallium of *Polypterus* is rather simple, that of teleost fishes is complex, especially in large-brained

Fig. 2. Two similar but independent morphoclines of pallial organization. Shown here are sections through the right telencephalon of 3 ray-finned fishes (top) and 3 bony vertebrates (bottom). Axons and terminals labeled after tracer injections into the main olfactory bulb are indicated schematically. In both instances, the olfactory projections to the pallium become progressively more restricted from left to right, forming 2 independent morphoclines. Similarly, evidence for the existence of distinct dorsal pallia (Dd plus Dc in teleosts and DP in reptiles) increases from left to right. Dc, central part of area dorsalis; Dd, dorsal part of area dorsalis; DL, lateral part of area dorsalis; DL, dorsolateral pallium; Dm, medial part of area dorsalis; DM, dorsomedial pallium; Dp, posterior part of area dorsalis (replaced by Dm anteriorly); DP, dorsal pallium; LP, lateral pallium; MP, medial pallium; Sep, septum; Str, striatum; VP, ventral pallium. Adapted from Striedter and Northcutt [2000] and sources cited therein, as well as in this text.

teleosts [Braford, 2009; Harvey-Girard et al., 2012; Demski, 2013]. This complexity makes it difficult to compare the various pallial divisions of teleosts to those of other vertebrates – a problem that is compounded by the fact that the telencephalon of ray-finned fishes is everted rather than evaginated (Fig. 2) [Nieuwenhuys, 2009]. For these reasons, the various divisions of the teleostean telencephalon were wisely named according to their topological position, rather than putative homologies [Nieu-

wenhuis, 1963; Northcutt and Braford, 1980]. Undaunted, researchers have nonetheless proposed a number of hypotheses concerning the homologies of pallial divisions in teleosts. Particularly important for present purposes is that the dorsal and central parts of the dorsal telencephalon (Dd and Dc) have been identified as plausible candidates for homologs of the dorsal pallium in other vertebrates [Wullimann and Mueller, 2004; Mueller et al., 2011; Porter and Mueller, 2020].

A significant problem with this hypothesis is that Dd, which is small and indistinct in most teleosts, appears to be absent in *Polypterus* as well as sturgeons, which are another basal lineage of ray-finned fishes (Fig. 2). Sturgeons do possess a small cluster of large neurons that resembles area Dc of teleosts, but no such region is evident in the *Polypterus* pallium [Northcutt and Davis, 1983]. A large part of Dc in teleosts has strong projections to the optic tectum [Murakami et al., 1983], but numerous tracer injections into the tectum of *Polypterus* revealed no retrogradely labeled pallial cells (unpublished observations by RGN). Thus, we here observe a morphocline across the major lineages of ray-finned fishes that is consistent with Dd and Dc emerging gradually in the lineage leading to teleosts. If this is true, then Dd and Dc cannot be homologous to the dorsal pallium of other vertebrates, since the traditional definition of homology (to which we subscribe) requires that homologs share a continuous phylogenetic history since their origin in a common ancestor [Striedter and Northcutt, 1991].

In conjunction with the emergence of Dd and Dc, the pallium of ray-finned fishes became less dominated by olfactory input (Fig. 2) and, in teleosts, came to process sensory information from a variety of sensory modalities, including vision, taste, and lateral line stimuli. However, these nonolfactory sensory regions are mainly located in the lateral and medial parts of the dorsal telencephalon (Dl and Dm; see Fig. 2) [Murakami et al., 1983; Kanwal et al., 1988; Striedter, 1991; von der Emde and Prechtl, 1999; Saidel et al., 2001; Yamamoto and Ito, 2008; Demski, 2013; Ocaña et al., 2016], which are usually homologized to the medial pallium and ventral pallium of other vertebrates, respectively [Rodríguez et al., 2002; Braford, 2009; Nieuwenhuis, 2009]. Furthermore, these pallial regions in teleosts receive their sensory inputs not from the thalamus but from a complex set of structures – called the preglomerular complex – that is derived from the posterior basal diencephalon and midbrain [Bloch et al., 2020; Wullimann, 2020]. Given these data, it is most parsimonious to hypothesize that teleosts evolved a variety of novel pallial features, including Dd, long descending pro-

jections from Dc, and nonolfactory sensory regions in other pallial divisions. All of these innovations are superficially similar to features of the dorsal pallium in amniotes, but they almost certainly evolved convergently.

Those Pesky Elasmobranchs

The cartilaginous fishes comprise holocephalans (e.g., ratfishes) and a much larger lineage called elasmobranchs (i.e., sharks, skates, and rays), but experimental neurobiological data are currently available only for the latter group. Importantly, the data from elasmobranchs pose a significant challenge to our proposed model of dorsal pallial evolution, because the secondary olfactory projections in these animals are restricted to a relatively small lateral portion of the pallium [Ebbesson and Heimer, 1970; Hofmann and Northcutt, 2008; Striedter and Northcutt, 2020]. Moreover, responses to visual and electrosensory stimuli have been recorded in some of the nonolfactory pallial regions, including the medial pallium and the so-called dorsal pallium [Ebbesson and Schroeder, 1971; Bodznick and Northcutt, 1984; Bodznick, 1990]. Whether this nonolfactory sensory information is conveyed to the pallium of elasmobranchs via the thalamus or other brain regions, or both, remains debated in the literature [Luiten, 1981; Smeets and Northcutt, 1987; Hofmann and Northcutt, 2012; Wullimann and Grothe, 2013], and higher-order olfactory projections do appear to dominate the telencephalon in at least some elasmobranchs [Hofmann and Northcutt, 2008]. However, the available data are certainly consistent with the notion that cartilaginous fishes possess a region that is similar to the dorsal pallium of amniotes insofar as it lacks secondary olfactory inputs and is targeted by other ascending sensory pathways.

Since cartilaginous fishes are the sister group of bony vertebrates (including ray-finned fishes, lungfishes, and amniotes; see Fig. 1), these data weaken support for the smell brain hypothesis. However, considering the morphoclines mentioned above, it is still slightly more parsimonious to assume that widespread secondary olfactory projections are primitive for vertebrates and became restricted in elasmobranchs than to suggest that they evolved independently in cyclostomes and early bony fishes. Whether the dorsal pallium of elasmobranchs evolved independently from that in other vertebrates is similarly uncertain, but it is interesting to note that the region identified as the dorsal pallium in elasmobranchs became disproportionately large and complex in several lineages of

Fig. 3. Features of a lamprey's pallium. The top 2 transverse sections depict axons, terminals, and cell bodies labeled after tracer injections in the olfactory bulb (**a**) and dorsal thalamus (**b**). **c** Axons and cell bodies retrogradely labeled in the rostral (left) and more caudal (right) telencephalon after tracer injections in the pretectum (which likely interrupted axons projecting to the optic tectum as well). **d** Location of neurons that respond to electrical stimulation of the retina; several principal dendrites for one of these neurons are also shown. Adapted from Northcutt and Puzdrowski [1988], Northcutt and Wicht [1997], Ocaña et al. [2015], and Suryanarayana et al. [2020].

large-brained sharks and rays that emerged relatively recently during elasmobranch phylogeny [Northcutt, 1995]. All of these data make us extremely curious about pallial organization in holocephalans (the sister group of all elasmobranchs). On the basis of cytoarchitectural analysis, these animals are said to have a relatively complex dorsal pallium [Smeets et al., 2011], but in our judgement this region could be a well-developed medial pallium [Striedter and Northcutt, 2020]. Unfortunately, this idea remains speculative, as no experimental studies on the telencephalon of holocephalans have been published.

Overall, we suspect that the secondary olfactory projections became more restricted early in the evolution of cartilaginous fishes and that this restriction was associated with the origin and subsequent expansion of a dorsal pallium that is not homologous to the dorsal pallia of teleosts or amniotes. However, this hypothesis is probably the weakest link in our general model.

The Lamprey Conundrum

The pallium of lampreys has long been difficult to interpret. Part of the problem is that the secondary olfactory projections in these animals are so widespread

[Northcutt and Puzdrowski, 1988; Polenova and Vesselkin, 1993]. In addition, the telencephalon of lampreys appears to be only partially evaginated, such that the putative striatum and medial pallium remain part of an unevaginated *telencephalon impar*. Alternatively, what most observers have called the medial pallium (M? in Fig. 3) may be part of a very large prethalamic eminence [Pombal and Puelles, 1999; Pombal et al., 2009], in which case the medial pallium would be part of the evaginated pallium, which most authors call the lateral pallium. Most relevant to our present discussion is that one of us has previously identified a small dorsal pallium in lampreys [Northcutt and Puzdrowski, 1988] (D? in Fig. 3a, b), while others have doubted that lampreys possess this pallial division at all [Puelles, 2001].

Recent studies from the group of Sten Grillner (Fig. 3c, d) have shifted this debate in favor of the idea that lampreys do possess a dorsal pallium [Suryanarayana et al., 2020]. Specifically, they have shown that the dorsal part of what is traditionally called the lateral pallium in lampreys contains distinct visual and somatosensory areas, as well as an adjacent motor region with long descending projections [Ocaña et al., 2015; Suryanarayana et al., 2020]. On the basis of these findings, they suggested that “the basic sensorimotor representa-

tion of the mammalian neocortex, as well as the sensory thalamocortical relay, had already evolved in the last common ancestor of cyclostomes and gnathostomes around 560 million years ago” [Suryanarayana et al., 2020, p. 639]. These data and interpretations are clearly at odds with our proposal, since they imply that the dorsal pallium is an ancient vertebrate structure and homologous across the extant vertebrates. Therefore, additional discussion is warranted.

One important question is whether the data of Grillner and colleagues contradict the earlier claims that the olfactory bulbs in lampreys project broadly throughout the pallium [Suryanarayana et al., 2020]. Suryanarayana et al. [2021] present neuroanatomical and physiological evidence that axons from the olfactory bulb terminate in what we call the ventral portion of the lateral pallium (L-v in Fig. 3a, b; their ventral pallium) and that this region then projects to the dorsal portion of the lateral pallium (L-d; their dorsal pallium). However, Suryanarayana et al. [2017] had previously shown that pallial neurons with long descending projections (many of which are located in the dorsal portion of the lateral pallium; Fig. 3c) respond monosynaptically to electrical stimulation of axons from the olfactory bulb. Thus, if these motor cortex-like neurons [Ocaña et al., 2015] represent part of a dorsal pallium, then this dorsal pallium receives secondary olfactory projections. Alternatively, the dorsal pallium in lampreys may be limited to the visual and somatosensory neurons that Suryanarayana et al. [2020] identified in the more medial portion of the dorsal lateral pallium. This region seems to receive few or no secondary olfactory projections [Northcutt and Puzdrowski, 1988], but it remains unclear whether the dendrites of the sensory cortex-like neurons in lampreys extend laterally into the olfactory bulb’s pallial termination zone. In any case, physiological evidence that the visual or somatosensory neurons in the lamprey pallium do *not* respond to olfactory input have not, so far, been presented.

A second open question is whether the visual and somatosensory neurons in the lamprey pallium receive a direct thalamic input, as the dorsal pallium does in amniotes. Neuroanatomical data had previously indicated that the thalamus projects sparsely to much of the lamprey pallium (Fig. 3b) but projects most heavily to the medial pallium rather than the region identified by Grillner and colleagues as the dorsal pallium [Polenova and Vesselkin, 1993; Northcutt and Wicht, 1997; Suryanarayana et al., 2020]. Suryanarayana et al. [2017] did confirm through retrograde labeling that some thalamic neurons project to the lamprey’s lateral pallium, and they provided physio-

logical evidence for monosynaptic projections to the ventral division of the lateral pallium. However, the only published evidence for direct thalamic input to the visual and somatosensory areas in the lamprey pallium are illustrations of one neuron in the visually responsive region that extends a dendrite into a fiber tract that carries ascending thalamic axons (and, most likely, other axons) (Fig. 3d). It may seem reasonable to assume that visual and somatosensory information *must* reach the pallium via the thalamus, but as the data from ray-finned fishes have shown (see The Ray-Finned Fish Revolution), other routes are possible.

Third, we wonder whether the visual and somatosensory areas in the lamprey pallium could be part of what we would call the medial pallium or part of the lateral pallium rather than a distinct dorsal pallium. These suggestions may seem like definitional legerdemain but, as we mentioned previously, nonolfactory sensory representations are found in the lateral and medial pallial regions of teleosts (see The Ray-Finned Fish Revolution). Analogous ascending sensory projections to these pallial divisions may well exist in lampreys without requiring the presence of a dorsal pallium homologous to that of amniotes. Testing this hypothesis will probably require the discovery of transcription factors or other molecular markers that selectively label the embryonic medial or lateral pallial divisions (including their dorsal portions) or the embryonic dorsal pallium in a variety of vertebrates, including anamniotes. We are not aware of any such markers. It is interesting to note, however, that the transcription factor *Emx* duplicated independently in cyclostomes and jawed vertebrates, and that *emxB* of lampreys is selectively expressed in the caudodorsal pole of the lamprey pallium [Tank et al., 2009]. Unfortunately, it remains unclear which adult brain areas correspond to this embryonic precursor region. Still, these data suggest that the lamprey pallium undergoes some lamprey- or cyclostome-specific differentiation that could, potentially, include the formation of a phylogenetically unique pallial zone.

Although the lamprey data require further elaboration and clarification, they should stimulate further research on nonolfactory sensory areas in the pallium of other amniotes, even in species that exhibit widespread secondary olfactory projections. For example, it is already known that the pallium in hagfishes receives some minor and diffusely organized projections from the thalamus [Wicht and Northcutt, 1998], but it remains unclear whether the recipient pallial neurons also respond to olfactory stimuli. As noted earlier, it is entirely possible that the pallium

Fig. 4. Evo-devo model of how dorsal pallia may emerge. **a** The diagrams depict a conceptually flattened forebrain, adapted from Puelles [2011] and Binks et al. [2019]. It shows that the dorsal pallium in amniotes develops as an island within the pallium and that pallial cell fates are specified by diffusible morphogenetic signals originating from the pallium's periphery (arrows with gradient shading). **b** Our suggestion that a dorsal pallium (DP) emerges whenever the embryonic pallium expands tangentially to such an extent that the morphogenetic signals specifying ventral, lateral, and medial pallial fates fail to reach the pallium's central region [Striedter and Northcutt, 2020]. We recently became aware that this basic idea was first proposed by Puelles [2001].

of the earliest vertebrates received some nonolfactory inputs, but we hypothesize that the target neurons also received olfactory information.

Our Model, Stated Succinctly

Given these data and considerations, we now state our model of dorsal pallial evolution as three interrelated hypotheses: (1) secondary olfactory projections to the pallium were widespread in the earliest vertebrates, covering most or all of the pallium, but then receded in several vertebrate lineages; (2) pallial territory that became devoid of secondary olfactory projections was "invaded" by additional ascending nonolfactory sensory inputs, which were conveyed through the thalamus or other lower brain regions; and (3) as the pallium expanded in some vertebrate lineages, a novel pallial zone appeared in the pallium's central region, in between the medial and lateral pallia and far from signaling centers along the pallium's periphery (Fig. 4). These dorsal pallial regions may or may

not coincide with the nonolfactory sensory regions but are, in any case, not homologous across all vertebrates.

We are not the first to argue in favor of these, or very similar, hypotheses. The small brain hypothesis was developed by an earlier generation of comparative neuroanatomists (see Previous Ideas about Pallial Evolution), and Wullimann and Vernier [2009] clearly stated that "a dorsal pallium may have arisen several times independently in chondrichthyans (i.e., cartilaginous fishes), teleosts and amniotes." Doubts about the existence of a dorsal pallium homolog in various anamniotes, as well as an evo-devo scenario for its emergence, have also been expressed before [Puelles, 2001; Holmes and Northcutt, 2003]. Still, we had not anticipated reaching these conclusions when we began writing our book and, therefore, would argue that they are not widely considered or, certainly, accepted in the field.

More important than establishing priority is to determine what kinds of data would allow for tests of the proposed hypotheses. Regarding our first hypothesis, it will be important to complement neuroanatomical data on

the distribution of secondary olfactory projections in various anamniotes with physiological data. Specifically, we need to know which neurons respond to olfactory inputs and which do not. Similarly, testing our second hypothesis will require data from multiple anamniotes and the integration of neuroanatomical and physiological data, with a special emphasis on the pathways through which nonolfactory sensory information reaches the pallium. Our third hypothesis appears most difficult to test. A good first step would be to identify molecular markers for the embryonic dorsal pallium in anamniotes that are thought to possess a dorsal pallium and then to determine whether similar expression patterns are found in other vertebrates, including amniotes [Desfilis et al., 2018]. It might also be possible to manipulate the size of the embryonic pallium to see whether experimental expansion causes novel brain regions to emerge (Fig. 4) or, conversely, whether experimental reductions in pallium size cause putative dorsal pallia to disappear. Combining such evo-devo experiments with manipulations of the olfactory inputs to the developing pallium might also yield results relevant to our proposal.

We freely admit that the hypotheses presented here are risky (as one reviewer put it), because they are not supported by extensive evidence and run counter to ideas currently predominant within comparative neuroanatomy. Indeed, we have some doubts ourselves. Still, we believe that the ideas are worth considering and testing thoroughly. In that sense, we share the view of Darwin [1871, p. 385] that, “false facts are highly injurious to the progress of science, for they often long endure; but false views, if supported by some evidence, do little harm, for everyone takes a salutary pleasure in proving their falseness.”

Conclusion

Most comparative neurobiologists, including the two of us, had been assuming that the pallium of all vertebrates conforms to an ancient Bauplan. Specifically, we used to think that the pallium’s division into 4 fundamental zones would be conserved across all vertebrates and that, therefore, all vertebrates *should* possess some kind of dorsal pallium. Once we dropped this assumption, the evidence for a dorsal pallium that is homologous across all vertebrates appeared (to us) surprisingly weak. This realization prompted us to think more deeply about alternative scenarios of pallial evolution.

It can be difficult to imagine how a novel brain region, such as a dorsal pallium, can possibly appear “from noth-

ing” in evolution [Ebbesson, 1980]. Indeed, “morphological structures, and the ontogenies which produce them, do not simply arise from the dust of the earth” [Braun and Northcutt, 1997, p. 263]. However, novel entities certainly can arise in evolution. They do so when ontogenies are modified in such a way that developmental factors are combined in novel ways and, thereby, specify new, additional traits (rather than slightly modifying old ones). Such evolutionary innovations can be difficult to identify with certainty, since one must demonstrate the absence of suitable ancestral homologs, and their developmental bases are likewise difficult to uncover [e.g., see Shigetani et al., 2005]. However, one can certainly imagine, as we have done (Fig. 4b), speculative scenarios that generate true novelties [see also Puelles, 2001].

An interesting implication of our model is that dorsal pallia may have arisen independently in several vertebrate lineages via shared developmental mechanisms, i.e., tangential expansion of the embryonic pallium and its knock-on effects. Because of those shared mechanisms, the independently evolved dorsal pallia may share some adult characteristics (e.g., their topological position between the medial and lateral pallia and the presence of nonolfactory sensory inputs) that are suggestive of homology but are actually the result of parallel evolution [Hall, 2003]. General considerations of this type have given rise to the concept of “developmental homology” [DiFrisco, 2019] but, to our way of thinking, homology requires that the traits being compared can be traced back – via a continuous evolutionary history – to a common ancestral trait [Striedter and Northcutt, 1991; Striedter, 1998]. This would not be the case in the scenario we have proposed.

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Conflict of Interest Statement

The authors have no conflict of interests to declare.

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Both authors made essential contributions to this work.

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