



Avian pallial circuits and cognition: A comparison to mammals

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Abstract

Cognitive functions are similar in birds and mammals. So, are therefore pallial cellular circuits and neuronal computations also alike? In search of answers, we move in from bird's pallial connectomes, to cortex-like sensory canonical circuits and connections, to forebrain micro-circuitries and finally to the avian "prefrontal" area. This voyage from macro- to micro-scale networks and areas reveals that both birds and mammals evolved similar neural and computational properties in either convergent or parallel manner, based upon circuitries inherited from common ancestry. Thus, these two vertebrate classes evolved separately within 315 million years with highly similar pallial architectures that produce comparable cognitive functions.

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Introduction

The last two decades witnessed a revolution in our understanding of avian brain and cognition. For long, birds were seen as cognitively limited animals with small non-cortical pallia. Now, new studies reveal that corvids and parrots are cognitively on par with apes [1,2]. Consequently, avian brains moved into the focus of new inquiries. These studies demonstrated four major insights. First, the avian pallium is homologous to that of mammals and occupies about the same proportion of the

forebrain [3]. Second, the nidopallium caudolaterale (NCL) of birds is an associative pallial area that is not homologous but functionally equivalent to the prefrontal cortex (PFC) [1]. Thus, both mammals and birds convergently evolved pallial structures that generate executive processes by similar neurobiological means [4]. Third, especially songbirds and parrots have twice the number of neurons per gram pallium than mammals. In addition, these avian orders allocate more than half of their neurons within the pallium while comparable numbers in primates hover around 19% [5]. Fourth, several studies discovered cellular homologies between neurons of the mammalian cortex and the avian pallium [6–8] but see [9].

As important these discoveries are, only unravelling the computational properties emerging from similar circuits of the avian pallium will permit a deeper understanding of the neuronal fundamentals of bird cognition. The developments in the recent years have enabled several insights into this topic. We will present and integrate these developments in four steps by moving from macro to meso and thence to micro-scale avian circuitries, before placing these findings into a broader evolutionary framework.

Macroscale circuitries: the avian pallial connectome

Connectomes are neuronal connectivity patterns which may be analyzed by graph theory to reveal principles of information flow at macro-scale level. For birds, up to now only the connectome of the pigeon telencephalon has been analyzed. It shows a small-world network with two levels of modularity and a connective core of central hub nodes that are extensively connected to the remaining network [10]. At the first look, there is nothing special about this finding, since even the connectome of *Caenorhabditis elegans* integrates input from specialized cells within a small core of hub neurons from where it fans out into networks that organize the systems output [11]. What is remarkable about the pigeon connectome; however, are the identities of its modules and hubs. The modules are either of associative, limbic, premotor, or sensory nature while the structural core consists of prefrontal, parahippocampal, and premotor hubs [10]. This is identical to mammals

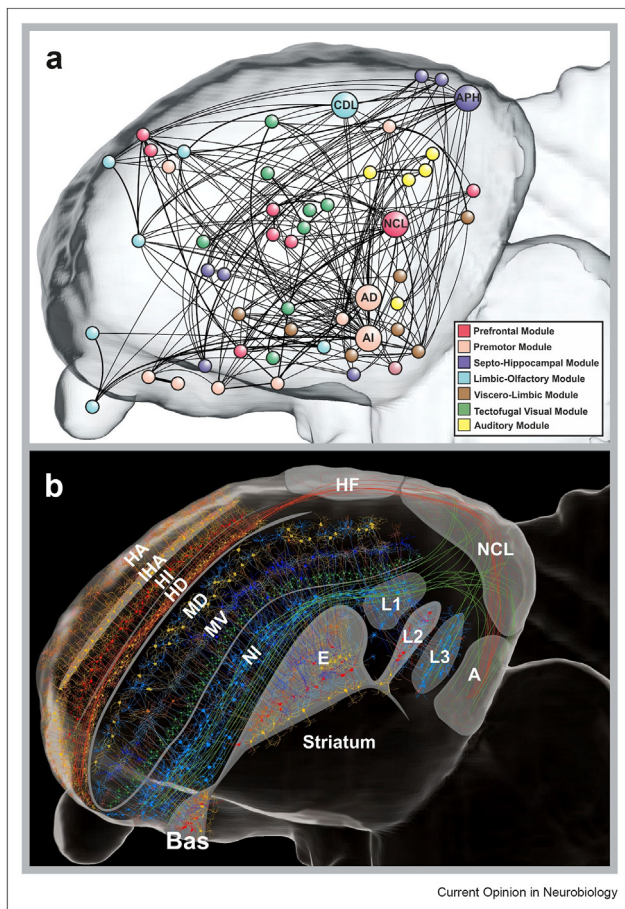
[12]. Thus, macro-scale information flow in the pigeon's pallium is functionally remarkably similar to that in mammals (Figure 1a).

Mesoscale circuitries: the avian sensory cortex

The non-cortical nuclear organization of the avian pallium was always perceived as inferior when compared with the canonical circuits of the six-layered neocortex. In the recent years, however, detailed analyses of the local connectivity patterns of the auditory and visual tectofugal areas discovered column- and layer-like connectivity patterns [13–15]. Recently, Stacho et al. [16] demonstrated that the entire sensory

pallium encompassing the wulst (somatosensory, visual thalamofugal) and the dorsal ventricular ridge (DVR; trigeminal, visual tectofugal, auditory) is characterized by an orthogonal pattern of tangentially and radially organized fibers. Tracing of local connectivities uncovered columnar canonical iterative circuits that are highly similar in both regions of the brain (wulst and DVR) and sensory domains (somatosensory, visual, auditory) in avian species (pigeon, barn owl). Both wulst- and DVR-circuits are tangentially intersected by long-range fiber systems that cross-connect columns and link them to hippocampal, prefrontal and (pre) motor structures (Figure 1b). It is important to emphasize that this cortical organization is only visible in the sensory pallial areas and does not encroach into the associative and motor areas of the posterior and medial pallium, which display a nuclear arrangement.

Figure 1



(a) Connectome of the pigeon cerebrum in sagittal view. Nodes are colored according to module membership. Based on the study by Shanahan et al. [10]. (b) Sagittal view of the pigeon forebrain with a highly schematized depiction of local connections in hyperpallium and DVR. Abbreviations: A: Arcopallium; AD: Arcopallium dorsale; AI: Arcopallium intermedium; APH: Area parahippocampalis; Bas: *N. basalis* prosencephali; CDL: Area corticoidea dorsolateralis; E: Entopallium; HA: Hyperpallium apicale; HD: Hyperpallium dorsale; HF: Hippocampal formation; HI: Hyperpallium intercalatum; IHA: *N. interstitialis* hyperpallii apicalis; L1-3: Field L1-3; MD: Mesopallium dorsale; MV: Mesopallium ventrale; NCL: Nidopallium caudolaterale; NI: Nidopallium intermedium.

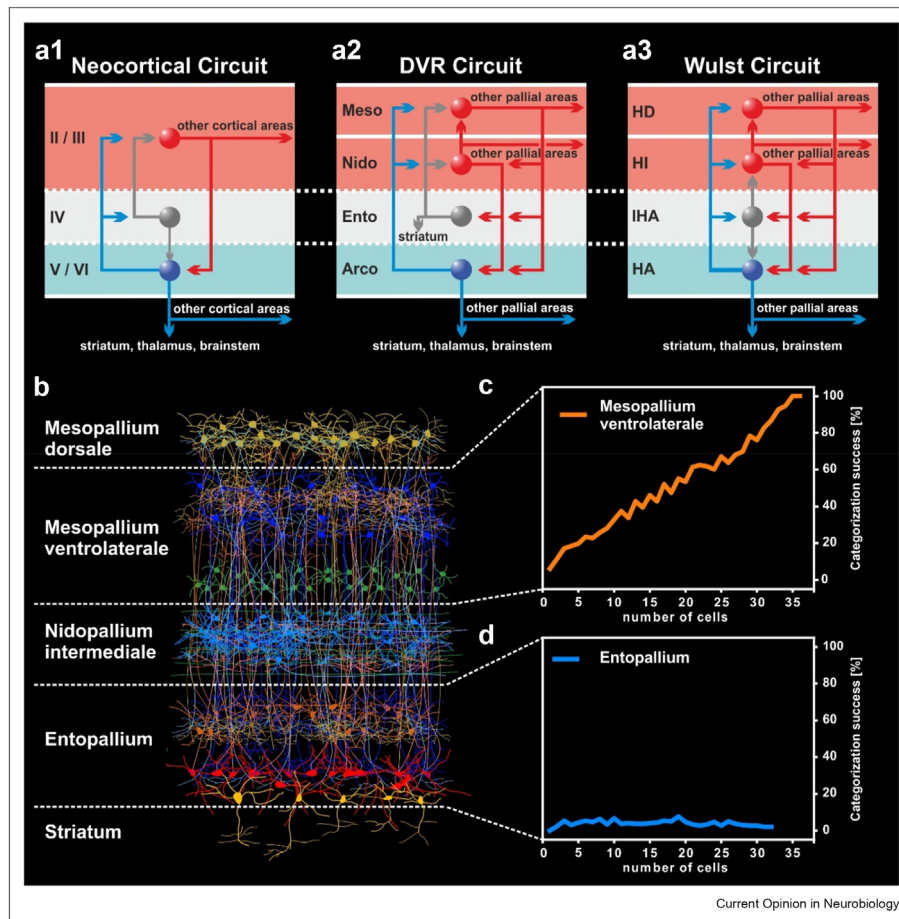
Overall, the organization of the columns of the avian sensory cortex is highly similar to those of the mammalian cerebral cortex (Figure 2). There are, however, also some differences. While cortical lamina IV receives rather modest input from other columnar layers [17], the avian sensory input zones receive massive feedback from all layers [16]. In addition, the avian equivalent of layer IV cells in DVR have direct striatal projections while the descending thalamic projections of DVR circuits are routed via the (pre)motor arcopallium.

Microscale circuitries: cellular computations

The histological similarity of mammalian and avian canonical circuits suggests that they could generate similar cellular dynamics. This indeed was already shown for different sensory domains. Electrophysiological recordings from the auditory field L-area in zebra finches demonstrated that the avian auditory pallium shows information-processing principles that resemble those of the mammalian auditory cortex [18]. This is reflected by different parameters like short response latencies of neurons in field L2 where the auditory thalamic input terminates (Figure 1b). Significantly longer latencies in responses to auditory input were found in adjacent superficial (L1 and CML) as well as deep and secondary auditory areas (L3 and NC). Additional measures such as receptive field separability and linearity as well as spike-timing correlations further indicated the existence of a mainly feed-forward hierarchical information-processing system in the avian auditory forebrain—a defining hallmark of the mammalian neocortical microcircuit. Thus, cell types with similar circuit patterns [13] and response characteristics [18] have been identified in both the avian and mammalian auditory pallium/cortex.

At the circuit level, neuronal response patterns of the avian tectofugal visual DVR demonstrate layer-specific

Figure 2



Simplified canonical circuitries of the mammalian cerebral cortex (**a1**) as well as the avian DVR (**a2**) and wulst (**a3**). Color codes outline conceivable correspondences between cortical layers and layer-like entities in birds. The grey lamina represents the thalamopallial input area. Note that the wulst is depicted upside down to have the descending projections at the bottom. Based on the study by Stacho *et al.* [16]. Abbreviations as in figure 1. (**b**) Schematic representation of the visual DVR and its constituent layers. (**c**) The classification performance of a linear classifier in the Mesopallium ventrolaterale (MVL) incrementally increases as a function of population size. Thus, a growing MVL population accumulates categorical information that can be read out by a linear classifier. (**d**) Despite an increasing cell population, the classification success in the entopallium persists at low levels. Thus, no readable category information is present at the level of the thalamorecipient entopallium. Based on the study by Azizi *et al.* [20].

response patterns during categorization tasks in awake pigeons [19,20]. Here, pigeons saw visual stimuli belonging to different categories like animate or inanimate objects, without being required to categorize them. Post hoc analysis of neural population responses revealed that category representation was absent in the thalamorecipient entopallium but emerged in higher visual layers like the MVL (Figure 2). The experimental approach prevented reward contingencies from influencing the neuronal responses, thereby revealing feed-forward information processing within the hierarchical avian visual tectofugal DVR cortex. This response pattern is comparable to results obtained in the visual cortex of mammals [21].

The sensory DVR circuitry connects to the prefrontal NCL by way of tangentially projecting nidopallial neurons. Despite the non-cortical layout of the NCL, a rich

set of electrophysiological studies show that neuronal computations in the NCL closely reflect the cellular properties of neurons in the layered PFC. For example, activity in NCL neurons reflect upcoming decisions [22,23], stimulus-associated value [24], maintenance of information in working memory [25–28], numerical competence [29,30] and abstract rules about task contingencies [31]. Nieder *et al.* [32] even discovered neural correlates of sensory consciousness in the NCL, a finding that was primarily known from the primate brain [33,34]. Together, these results strongly indicate that birds, especially corvids are not only “feathered apes” on the behavioral level [35,36], but also demonstrate a striking similarity in their cellular computations. However, the non-cortical layout of the NCL suggests that a nuclear structure can support complex cognition while sensory computations possibly require the spatial layout of a cortical architecture.

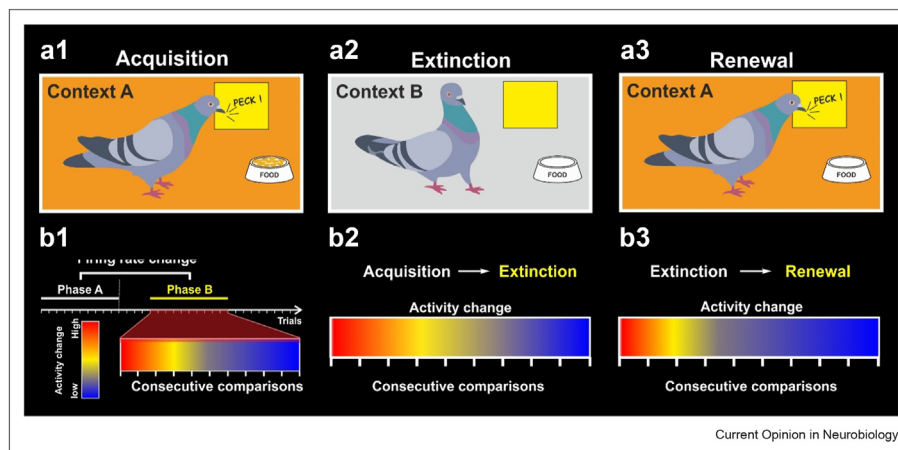
These findings are remarkable and highly illuminating since they demonstrate the extent of similarities between avian and primate findings on prefrontal coding properties. This especially becomes clear when studying prefrontal functions like fast, feedback-based updating of the network. The possible role of the NCL in the reward prediction error (RPE) network was investigated by Packheiser et al. [37] who studied the neural dynamics of RPEs in pigeons. While several studies have reported RPE-like signals in both the PFC and NCL [22,38], it remains largely unclear what these signals represent and how they are used for trial-by-trial updates of associations between stimuli and reward, decision-making and learning. Wang et al. [39] provided a computational model suggesting that prefrontal structures are involved both at early and late stages of the RPE network. Initially, they process dynamic updates of environmental changes of stimulus–outcome associations that are then transmitted to other neural structures in which the complete RPE is computed such as the ventral tegmental area or the substantia nigra [40]. In return, RPEs are then sent back to prefrontal areas to guide decision-making. Trial-by-trial analyses of NCL recordings supported this notion as population activity in this region initially signaled the mismatch between expected and received outcome during an operant extinction learning task (Figure 3). However, once the animals started to change their behavior later on during learning, choice-related signals started to change accordingly in NCL neurons. Furthermore, signal changes during outcome re-emerged merely by a

change in the ambient context following extinction. Thus, this study could illustrate that RPEs are purely expectancy driven even without modulating the quantity or quality of reward. Since the results of the study by Packheiser et al. [37] were correlative, it will however require causal interventions to determine the functional role of the NCL in the RPE network, conclusively. Here, future studies should make use of the recent establishment of optogenetics in pigeons [41] that allow for trial-by-trial modifications of neural activity.

Evolution of cognitive structures

Until recently, not much was known about the evolution of the associative pallium within the avian lineage. Now, for the first time, an NCL-like structure has been described in a member of the Crocodylia, the closest living relatives of birds [42]. A detailed analysis of catecholaminergic fiber innervation of the central nervous system of the Nile crocodile (*Crocodylus niloticus*) identified a field within the caudal nidopallium that demonstrated a high comparability to the avian NCL. The area is situated adjacent to the lateral border in between the dorsal arcopallium and the lateral ventricle and it receives a denser dopaminergic innervation compared to that of the surrounding nidopallium. Part of the fibers is organized as characteristic “baskets.” This is a distinct morphological feature where fibers coil around a large unstained perikarya, possibly making multiple presynaptic contacts and indicating close dopaminergic control of the underlying cell [43]. Even though the presence of the NCL-like area in the caudal nidopallium

Figure 3

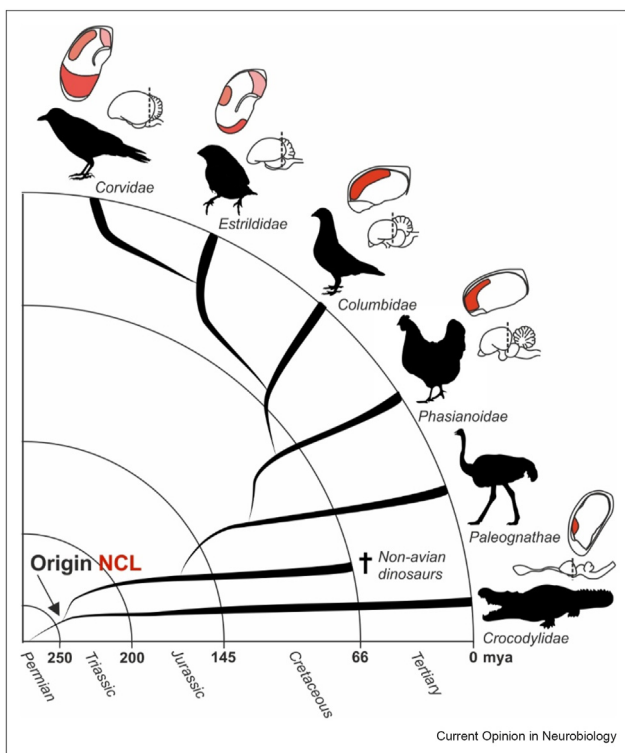


Behavioral task and NCL population response from Packheiser et al. [37]. The behavioral task comprised one singular session during which pigeons learned a stimulus–outcome association in context A (acquisition phase, **a1**), extinguish this association in context B (extinction phase, **a2**) and were then tested for the behavioral response back in context A (renewal phase, **a3**). During this test, conditioned responses towards the stimulus resurfaced only due to the contextual change back to the acquisition context (known as the renewal effect). (**b1**) To quantify temporally precise changes of the NCL population, we compared the activity at the end of the last phase to the beginning of the next phase trial-by-trial. (**b2**) At the transition from acquisition to extinction, we found strong activity changes in the NCL population owing to the omission of reward suggesting RPE signaling. (**b3**) At the transition from extinction to renewal, we found comparable activity changes in the NCL. Importantly, however, there was no change in reward contingencies as food was continuously omitted during the renewal phase.

of the Nile crocodile could be an example of convergent evolution, a more parsimonious explanation would be that the stem archosaurian possessed a primordial NCL. In this scenario, a tentative origin of the NCL can be dated to the split of crocodiles and birds approximately 245 million years ago (mya [44], Figure 4).

In mammals, the evolutionary selection for cognitive control resulted in changes of absolute and relative size of prefrontal areas and associated networks, but also in the extent of parcellation and the number of subdivisions [45]. Namely, compared to rodents, primates, and great apes and humans in particular, have an expanded frontal lobe that can be parcellated in additional subdivisions [46,47], with an extended and intensified dopaminergic innervation pattern [48]. A recent study delineated the NCL in different species of birds to elucidate if and how this executive structure varies depending on species and cognitive capacities

Figure 4



Evolution of the associative pallium in simplified phylogenetic tree of archosaurs. The origin of the NCL is dated to the stem archosaur that existed approximately 245 million years ago (mya). Across extant archosaurs the NCL differs in size and number of subdivisions. Crocodyliidae have a small uniform area situated in the caudal lateral part of the pallium. Currently nothing is known about the NCL of Paleognathae. Next, the NCL appears expanded in basal birds such as chicken (Phasianoidae) and pigeon (Columbidae), but situated in approximately the same location. In Passeriformes, such as members of Estrildidae and Corvidae, the NCL stretches across the entire back of the caudal pallium and can be parcellated in additional subdivisions.

[49]. The results showed that more basal birds, such as pigeon and chicken, are characterized by an NCL situated as a singular field below the lateral ventricle. In contrast, the NCL of members of Passeriformes, such as zebra finch and carrion crow, consists of at least three parcellated subareas that span across the entire caudal nidopallium. These findings reveal striking parallels to the evolution of the PFC in mammals; avian species with more elaborate cognitive capacities have an expanded and more parcellated executive structure that is more diversely and densely innervated by dopaminergic fibers [49]. These parallel lines of evidence provide strong support that the computational power required for the execution of complex cognition relies on the size, parcellation, and dopaminergic innervation of a higher order associative structure such as the PFC or NCL.

The evolution of avian pallial circuitries

The last decade has seen an unprecedented surge of new information on the structural and functional organization of the avian pallium. These insights reveal more similar neural computational principles in birds and mammals than previously anticipated—a finding that could explain why cognitive properties of these two vertebrate classes are so alike. Similar findings have been obtained in weakly electric fish where principles and circuitries for active sensing and spatial learning have independently evolved in the South American gymnotiform and the African mormyrid fish [50,51]. But did these comparable circuitries at macro-, meso-, and micro-scale level evolved in birds and mammals also evolve independently or were they inherited as homologous cellular connectivity patterns from common ancestors [52,7,6]? A detailed inspection of the aforementioned discoveries provides some hints.

The macroscale telencephalic connectomes of mammals and birds are highly similar [10] but partly constituted by non-homologous and convergently evolved nodes like NCL/PFC [53,1] (Figure 1a). Thus, the connectomes of these two vertebrate classes cannot fully derive from common ancestry, but must have resulted from parallel evolution in which first an ancient core connectome was inherited from a common ancestor. Subsequently, both mammals and birds possibly elaborated this network step-by-step incorporating functionally similar nodes that are newly evolved during the evolution of both taxa.

The avian “cortical” mesoscale network (Figure 1b) shows remarkable similarities to its mammalian counterpart [16]. However, the excitatory DVR neurons in this network have transcription factors akin to the mammalian ventral pallium [54]. Thus, avian DVR and cerebral cortex must have emerged from different neurodevelopmental pallial regions and therefore cannot

be homologous. The striking parallels between avian and mammalian microcircuits seem to arise from the action of overlapping effector genes that shape local networks into similar computational units [54]. Such computations may be ancient, since lampreys have a lateral pallial three-layered microcircuit with sensory input and motor output units and also weakly electric fish show signatures of laminar and columnar organization in their dorsolateral pallium [50,55]. Consequently, it is likely that the basic pallial circuitry of extant amniotes may stem from an ancient ancestor and was reshaped by both birds and mammals. But why do birds still retain a nuclear arrangement in their associative and motor DVR? Cortical organizations represent and process sensory input that already arrives with a spatial code (visual or tactile position, frequency). If birds indeed evolved their sensory cortex mostly independent from mammals, they may have selectively exploited the benefits of a spatially arranged cortical organization for their sensory input while leaving other non-sensory pallial domains in their ancestral nuclear design. Thus, the ventral pallial origin of the DVR may allow for multiple and distinct kinds of computations for different functions.

If both macroscale and mesoscale networks of birds and mammals became comparable by similar selection pressures for increasingly complex computations, it is easy to see why microscale functions of birds reveal coding properties akin to the mammalian cerebral cortex [18–20]. This is to be expected when both birds and mammals in parallel develop iteratively repeated columnar canonical circuits across pallial layers. By this arrangement, both taxa achieve computational properties that permit a detailed analysis of the thalamic input along the radial, and a widespread association with other processes along the tangential domain. Similarly, an enlargement and sub-differentiation of prefrontal areas in cognitively advanced species increases the number of associative parallel computing units in both birds and mammals.

Resume

The unexpected discovery of the outstanding cognitive abilities of birds refreshed interest in the avian pallium. These studies reveal that birds and mammals evince mostly comparable neural circuitries and computations from macro- to micro-scale level. Detailed analyses show that these properties emerged by parallel and/or convergent evolutionary forces that molded joint primitive ancient circuits in both taxa into an astonishingly similar design. Thus, the two cognitively advanced vertebrate classes evolved very similar pallial circuits partly independently from each other. Such an outcome is only possible when the degrees of freedom to develop neural designs for complex cognition are highly limited. Consequently, if both birds and mammals are selected for similar cognitive behaviors, their pallial circuits also

evolve comparable properties. Thus, nothing in neuroscience makes sense, except in the light of behavior.

Author contributions

Concept: OG; writing: OG, KvE, JP, RP; figures: OG, KvE, JP, RP.

Conflict of interest statement

Nothing declared.

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