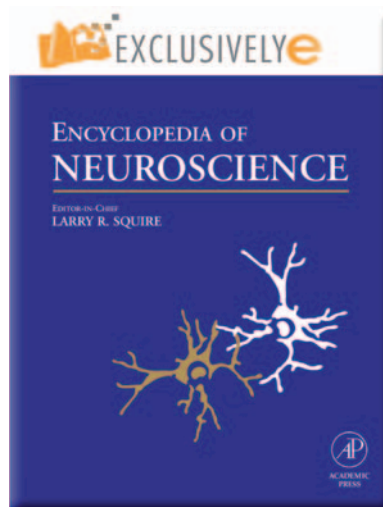


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Bird Brain: Evolution

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The classical century-old view of bird brain evolution was based on a theory of linear and progressive evolution, where the vertebrate cerebrum was argued to have evolved in lower to higher anatomical stages, with birds at an intermediate stage. As such, the avian cerebrum was thought to consist mostly of basal ganglia territories, and these were thought to control mostly primitive behaviors. This view, although slowly challenged, was not formally changed until 2004 and 2005, when a forum of neuroscientists that reevaluated brain terminologies and homologies for birds and other vertebrates published a new nomenclature that reflects a modern understanding of bird brain evolution. This view proposes that the avian cerebrum was inherited as a package with pallial (or cortical-like), striatal, and pallidal regions from its recent reptilian and distant stem amniote ancestors. The avian pallial domain is organized differently from the mammalian pallium or cortex in that the avian is nuclear and the mammalian is layered. However, the pallia of both groups perform similar functions and have some similar connectivity. The avian striatal and pallidal domains are organized more similar to those of mammals and, likewise, perform similar functions in both groups. This article reviews these classical and modern views for bird brain evolution in the context of vertebrate brain evolution.

The Classical View

The classical view of telencephalic evolution had its origin in the late nineteenth and early twentieth century following the impact of Darwin's theory of evolution. Inspired by Darwin's theory, Ludwig Edinger formulated an evolution-based model of brain organization from 1885 to 1908. Edinger and others combined Darwin's concept of 'evolution' with the nineteenth-century version of Aristotle's 'scala naturae,' resulting in the view that evolution was unilinear and progressive, from fish to amphibians, reptiles, birds and mammals, primates, and, finally, humans, ascending from 'lower' to 'higher' intelligence in a chronological series. They believed that the brains of extant vertebrates retained the ancestral structures and, therefore, that the origin of specific human brain subdivisions could be traced back in time by examining the brains of extant nonhuman vertebrates.

Although the spinal cord, hindbrain, midbrain, thalamus, and cerebellum appeared to be well conserved across vertebrates, Edinger noted that the internal organization of the telencephala or cerebrum exhibited the most pronounced differences across vertebrates. In mammals, the outer part of the telencephalon had prominently layered gray matter (**Figure 1(b)**, green), whereas the inner part had nuclear gray matter (**Figure 1(b)**, purple). The inner part was located ventral to the lateral ventricle. In nonmammals, the outer and inner parts of the telencephala had mostly nuclear gray matter, and most of it was located ventral to the lateral ventricle in birds and reptiles (**Figure 1(b)**, purple).

On the basis of these considerations, Edinger proposed that telencephalic evolution occurred in progressive stages of increasing complexity and size, culminating with the human cerebrum. He argued that the stages proceeded in a ventral-to-dorsal direction, with each new vertebrate group acquiring a more advanced cerebral subdivision. He argued that first there was the old brain, the paleoencephalon (also called the basal ganglia or subpallium), which controlled instinctive behaviors, followed by the addition of a new brain, the neoencephalon (also called the pallium or mantle at the top), which controlled learned and intelligent behaviors. The telencephalic subdivisions within each vertebrate group were further named by him, Ariëns-Kappers, and others with the prefixes 'paleo' (oldest), 'archi' (archaic), and 'neo' (new) to designate the presumed relative order of evolutionary appearance of each subdivision. To these prefixes the root word 'striatum' was added for the presumed paleoencephalic subdivisions and 'pallium' (meaning mantle) or 'cortex' (meaning bark) for the presumed neoencephalic subdivisions. The term striatum was used because a large part of the basal ganglia (i.e., paleoencephalon) in mammals, which is now commonly called caudate putamen, contains fiber bundles coursing through it, giving it a striated appearance.

The classical view that became dominant in the context of bird brain was that the bird subpallium consisted of 'paleostriatum' (old striatum) inherited originally from fish, said to be the antecedent of the human globus pallidus, and devoted to olfactory information processing. Above the paleostriatum, birds were said to have inherited an 'archistriatum' (archaic striatum) originally from amphibians, said to be the antecedent of the human amygdala. Above and adjacent to the archistriatum, birds were said to have inherited a 'neostriatum' (new striatum) from their closest relative, reptiles, said to be the antecedent of the human caudate and putamen. Reptiles were

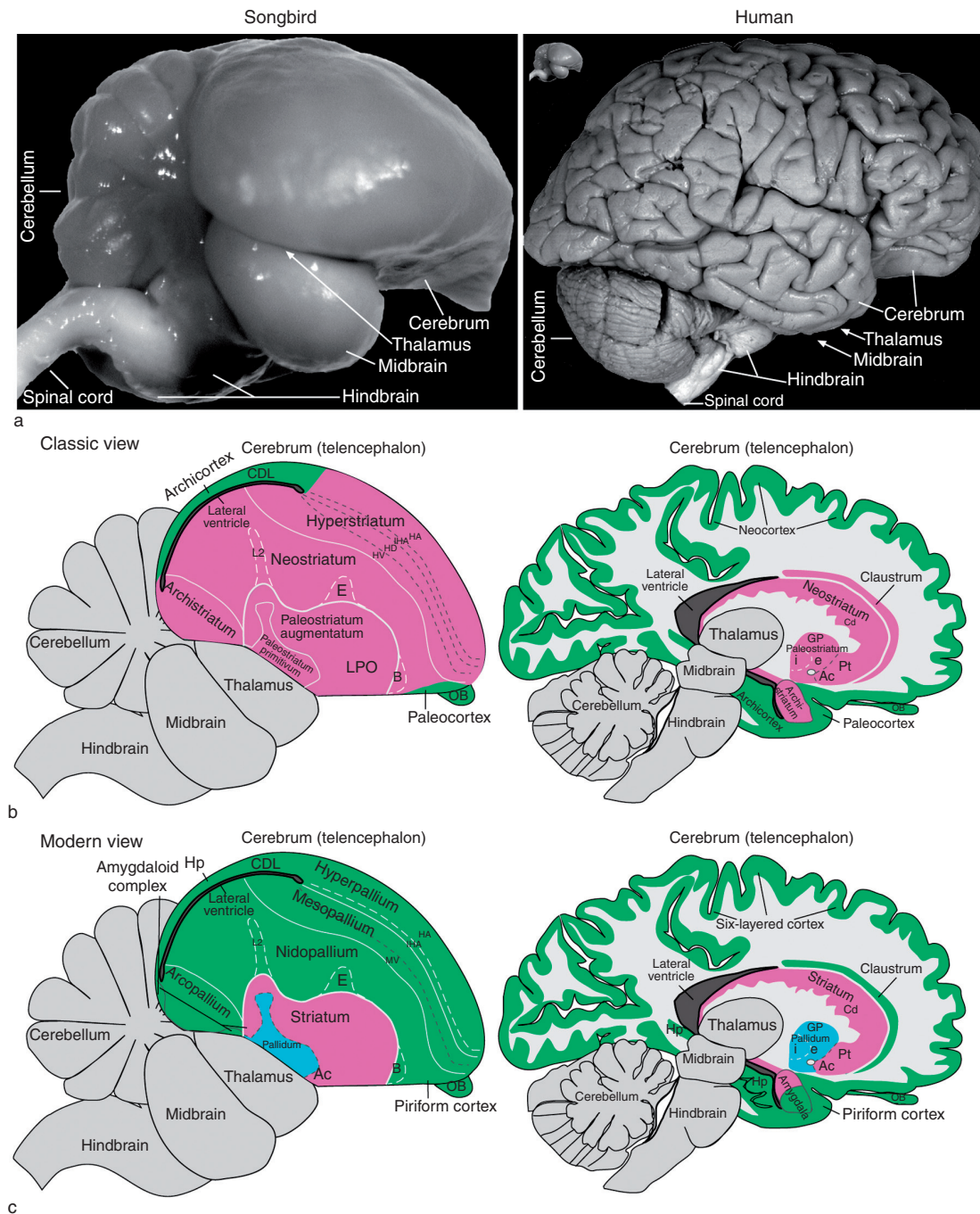


Figure 1 Avian and mammalian brain relationships. (a) Side view of a songbird (zebra finch) and human brain to represent avian and mammalian species. In this view, the songbird cerebrum covers the thalamus; the human cerebrum covers the thalamus and midbrain. Left inset next to the human brain is the zebra finch brain to scale with that of the human. Human brain image is from John W. Sundsten of the Digital Anatomist Project (<http://www9.biostr.washington.edu/da.html>) and used with permission. (b) Classic view of avian and mammalian brain relationships. Although past authors had differing opinions regarding which brain regions are pallium versus subpallium, the images are color-coded to the meaning of the names given. (c) Modern view of avian and mammalian brain relationships according to the conclusions of the Avian Brain Nomenclature Consortium. White solid lines are lamina, cell-sparse zones separating brain subdivisions. Large white areas in the human cerebrum are axon pathways called white matter. Dashed lines divide regions that differ by cell density or cell size; dashed white lines separate primary sensory neuron populations from adjacent regions. Classic view: Ac, accumbens; B, nucleus basalis; Cd, caudate nucleus; CDL, dorsal lateral corticoid area; E, ectostriatum; GP, globus pallidus (i, internal segment; e, external segment); HA, hyperstriatum accessorium; HD, hyperstriatum dorsale; HV, hyperstriatum ventrale; IHA, interstitial hyperstriatum accessorium; L2, field L2; LPO, lobus parolfactorius; OB, olfactory bulb; Pt, putamen. Modern view where different: B, basorostralis; E, entopallium; HA, hyperpallium apicale; Hp, hippocampus; IHA, interstitial hyperpallium apicale; MV, mesopallium ventrale. (b, c) Adapted from Jarvis ED, Gunturkun O, Bruce L, et al. (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* 6: 151–159, with permission.

additionally thought to have elaborated the paleostriatum into an older part (the primitivum) and a newer part (the augmentatum), which was passed onto birds. Birds were then thought to have evolved a large additional basal ganglia subdivision, the 'hyperstriatum' (hypertrophied striatum), considered unique to birds.

The bird pallium was said to consist of a 'paleocortex' inherited from fish pallium and believed to be the antecedent of the human olfactory cortex. Birds were said to have inherited an 'archicortex,' also thought to be olfactory and primitive, from amphibians and believed to be the antecedent of the human hippocampus. Birds were thought not to have evolved any further pallial regions. In contrast, mammals were thought to have evolved from the paleocortex and/or archicortex, a 'neocortex.' The archicortex and/or paleocortex with their two or three cell layers were assumed to be primitive; the neocortex with its six layers was assumed to be more recently evolved and a substrate for more sophisticated behavior. This classical view was codified in the major comparative neuroanatomy text by Ariëns-Kappers, Huber, and Crosby in 1936 and became pervasive throughout neuroscience. This view is now known to be incorrect.

The Modern View

In 2004 and 2005, an international consortium of specialists in avian, mammalian, reptilian, and fish neurobiology – the Avian Brain Nomenclature Consortium – published several reports on a new nomenclature that represents the current understanding of avian telencephalic organization and homologies with mammals ([Figure 1\(c\)](#)). The consortium concluded that the avian telencephalon is organized into three main, developmentally distinct domains that are homologous in fish, amphibians, reptiles, birds, and mammals: pallial, striatal, and pallidal domains ([Figure 1\(c\)](#)). For birds, they renamed these domains and their respective subdivisions with homology-based terms or roots that allow reference to named regions in mammals. In doing so, they eliminated all phylogeny-based prefixes (paleo-, archi-, and neo-) that erroneously implied the relative age of each subdivision.

The avian paleostriatum was simply renamed striatum after its mammalian homolog ([Figure 1\(c\)](#)). The paleostriatum primitivum and adjacent ventral region was renamed pallidum also after its mammalian homolog. Similar to the mammalian pallidum, the avian pallidum has a sparse distribution of cells, giving the region its pale appearance and its name. The dorsal part of the avian pallidum was determined to be homologous to the mammalian globus pallidus

and renamed as such, whereas the ventral part was determined to be homologous to the mammalian ventral pallidum. The dorsal pallidum, however, differs between mammals and birds. In mammals, it consists of two segments with distinct connectivity, the internal and external globus pallidus, whereas in birds neurons with both phenotypes are intermingled ([Figure 1\(c\)](#)).

The avian pallium was determined to be organized not into three striatal subdivisions (hyperstriatum, neostriatum, and archistriatum) but, rather, into four pallial subdivisions renamed as hyperpallium (hypertrophied pallium; upper part of old hyperstriatum), mesopallium (middle pallium; lower part of old hyperstriatum), nidopallium (nest pallium; old neostriatum), and arcopallium (arched pallium; most of old archistriatum) ([Figure 1\(c\)](#)). Several neuronal populations adjacent to the arcopallium and the posterior part of what had been regarded as archistriatum were considered homologous to pallial and subpallial parts of the mammalian amygdala, and they were renamed as the avian amygdaloid complex. Other regions that were widely recognized to be homologous among vertebrates – the hippocampus, olfactory (piriform) cortex, and olfactory bulb – did not require name changes.

Some Anatomical and Molecular Parallels

Some key similarities between avian and mammalian subpallium include a high enrichment of dopaminergic axon terminals in the striatum that originate from the substantia nigra pars compacta and ventral tegmental area neurons of the midbrain. Both avian and mammalian striatum contain two major classes of spiny neuron types, those with the neuropeptide substance P (SP) and those with the neuropeptide enkephalin (ENK), which project to two different neuron populations in the pallidum. In both birds and mammals, the SP neurons seem to be involved in promoting planned movement, whereas the ENK neurons seem to be involved in inhibiting unwanted movements. Both the avian and the mammalian striatum participate not only in instinctive behavior and movement but also in motor learning. Developmental studies indicate that the avian and mammalian subpallium consists of two separate histogenetic zones that express different sets of transcription factors: (1) a dorsal zone that corresponds to the lateral ganglionic eminence and that selectively expresses the transcription factors *Dlx1* and *Dlx2* but not *Nkx2.1* and (2) a ventral zone that corresponds to the medial ganglionic eminence and selectively expresses all three transcription factors. The lateral ganglionic eminence gives rise to the striatum and the medial ganglionic eminence

gives rise to the pallidum. Similar striatal and pallidal territories have been found in reptiles.

Some similarities between avian and mammalian pallium (i.e., mammalian cortex) include direct projections of sensory visual, auditory, and somatosensory input from the thalamus. The corresponding avian brain regions subserve the same type of sensory information processing as is performed by the mammalian cortex. Likewise, the avian hyperpallium and arcopallium give rise to major descending projections to premotor and motor neurons of the brain stem and spinal cord, as do mammalian corticobulbar and corticospinal pathways. These avian brain regions subserve critical roles in motor control and sensorimotor learning, similar to the mammalian cortex. The pallial relationships between these avian and mammalian brain regions are also supported by molecular embryology studies. During development, the avian hyperpallium, mesopallium, and nidopallium and the mammalian pallium selectively express the pallium-specific transcription factors *Emx1*, *Pax6*, and *Tbr1*. In adult birds and mammals, comparative expression profiles of the neurotrophic factor brain-derived neurotrophic factor and the glutamate receptor mGluR2 indicate that the avian arcopallium express these pallial-specific mRNAs at high levels, as does the mammalian cortex.

A Modern View of Telencephalic Evolution

The organization of the true basal ganglia of birds relative to mammals and other vertebrates (i.e., distinct nuclear striatal and pallidal domains) is quite conserved. In contrast, the organization of their pallial

domains differs to a greater degree. The nuclear type of organization of the pallium found in birds is also present in reptiles. The avian hyperpallium possesses a unique organization so far found only in birds; it consists of semilayered subdivisions, and it might have evolved more recently than the mammalian six-layered cortex since birds evolved well after mammals (by ~50–100 million years) (Figure 2). The region below the ventricle, called the dorsal ventricular ridge (DVR), contains mesopallium, nidopallium, and arcopallium, and it is a nuclear pallial organization that is unique to birds and reptiles. The six-layered cortex is a pallial organization unique to mammals. Because all major groups of living mammals (monotremes, marsupials, and placentals) have a six-layered cortex, it was presumably inherited from their common therapsid ancestor more than 200 million years ago (Figure 2). Furthermore, mammals may not have arisen from reptiles but, rather, from therapsids, because reptile and mammal lineages apparently had their last common ancestor in stem amniotes. Because all nonmammalian therapsids are extinct (Figure 2), it is difficult to trace from stem amniotes to mammals the evolutionary history of mammalian telencephalic organization – layered, nuclear, or otherwise. Thus, the reptilian nuclear pallial organization cannot be assumed to represent the ancestral condition for mammals, as it is for birds.

In general, the evidence suggests that pallial, striatal, and pallidal domains exist in most or all vertebrates. Thus, it has been hypothesized that the telencephalon of early fishes possessed all three domains, which were then inherited as a package by later vertebrates, including birds, and independently

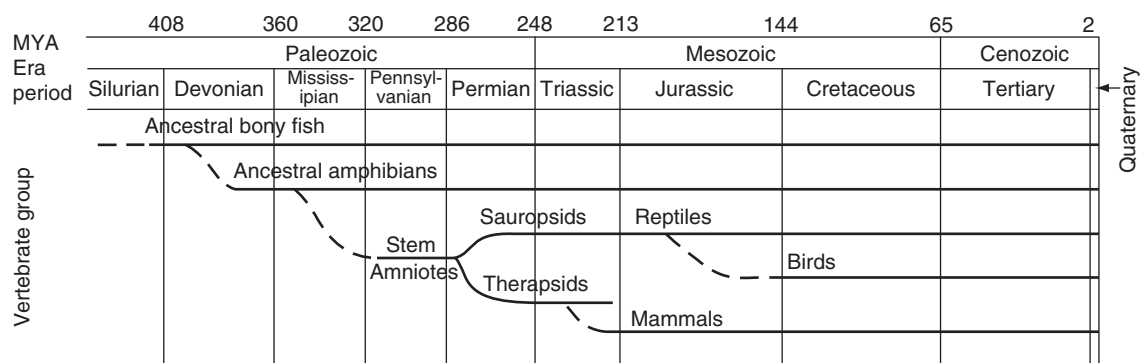


Figure 2 Simplified modern view of vertebrate evolution. The diagram begins with the fish group that contains the most recent ancestor to land vertebrates. This view differs from the classic view in that instead of giving rise to reptiles, ancestral amphibians are thought to have given rise to stem amniotes. Stem amniotes then split into at least two major groups: the sauropsids, which gave rise to all modern reptiles as we know them today, and the therapsids, which, through a series of now-extinct intermediate forms, evolved into mammals. Many sauropsids (reptiles) are currently living. Solid horizontal lines indicate temporal fossil evidence. Dashed lines indicate proposed ancestral links from other types of data. MYA, millions of years ago. Based on Carroll RL (1987) Fossils and relationships. In: *Vertebrate Paleontology and Evolution*, pp. 1–13. New York: Freeman; and Evans SE (2000) General discussion II: Amniote evolution. In: Bock GR and Cardew G (eds.) *Evolutionary Developmental Biology of the Cerebral Cortex*, no. 228, pp. 109–113. Chichester, UK: Wiley.

modified in them. The conserved organization of striatal and pallidal domains indicates that there might be constraints on how the basal ganglia can be organized. The diverse organizations of the pallial domains suggest that there are fewer constraints on how the pallium can be organized.

Detailed Views That Need Further Testing

When the modern view of bird brain evolution was developing, it was accompanied by several new hypotheses about one-to-one homologies between specific avian and mammalian pallial subdivisions. These hypotheses are under active investigation and make up a large area of research on bird brain evolution. They are classified into two main categories: nuclear-to-layered hypotheses and nuclear-to-claustrum/amygdala nuclei hypotheses.

Nuclear-to-Layered Hypotheses

First proposed by Karten, these hypotheses ([Figure 3\(a\)](#)) state that the similarities in connectivity between the avian hyperpallium, nidopallium and arcopallium of birds, and the six-layered cortex of mammals stem from a common origin of these structures – that is, they are homologous. Karten proposed that the common ancestor of birds, reptiles, and mammals possessed a nuclear pallium that was transformed into a laminar pallium early in the mammalian lineage, maintaining connectivity of the ancestral nuclear network. In this regard, he argued that the avian pallium is divided into three sets of serially connected types of neurons – thalamorecipient neurons (field L2, entopallium, and basorostralis), pallio-pallial neurons (nidopallium), and extratelencephalic projection neurons (arcopallium) – with cell types and interconnectivity similar to those of mammalian cortical layers IV, II and III, and V and VI, respectively ([Figure 3\(a\)](#)). Similar arguments were made by others for the avian upper hyperpallium (also known as the Wulst), which also has serially connected neuron types that resemble those found in the mammalian cortex. In this view, avian L2 neurons are homologous to layer IV neurons of mammalian primary auditory cortex, basorostralis neurons to layer IV of primary somatosensory cortex, entopallium neurons to layer IV of extrastriate visual cortex, and the interstitial hyperpallium apicale neurons to layer IV of striate visual cortex. Supporting this hypothesis, gene expression studies have shown that avian thalamorecipient nuclear fields (L2, entopallium, basorostralis, and interstitial hyperpallium) and the mammalian thalamorecipient layer IV of cortex selectively express some of the same genes. Avian extratelencephalic projection neurons (in the arcopallium but not in the hyperpallium) and mammalian

extratelencephalic projection neurons (layer V neurons of cortex) both selectively express some of the same genes. Thus, although the avian pallium is not organized cytoarchitectonically into layers, its nuclear subdivisions bear marked similarities in connectivity and molecular profiles to different layers of the mammalian cortex.

Nuclear-to-Clastrum/Amygdala Hypotheses

These hypotheses differ from the nuclear-to-layered hypotheses with regard to mammalian homologies with the avian DVR (mesopallium, nidopallium, and arcopallium; [Figure 3\(b\)](#)). In an early formulation of the nuclear-to-claustrum/amygdala hypotheses, Bruce and Neary proposed that the avian DVR represents an elaboration of parts of the mammalian amygdala. Subsequently, Striedter proposed that the avian DVR represents an elaboration of the mammalian amygdala and claustrum, and that the connectivity that the DVR shares with the neocortex evolved independently. Support for this view is based on findings that both the avian DVR and mammalian claustrum/amygdala are nuclear in organization, that both the avian DVR and part of the mammalian amygdala have similar connections, and that both have conserved developmental expression patterns of regulatory genes that play key roles in brain regionalization and morphogenesis. Puelles and colleagues proposed that the common topographic expression patterns of the transcription factors *Emx1* and *Pax6* in the avian mesopallium and in the mammalian dorsal claustrum and basolateral amygdala indicate that these structures commonly arose from the lateral pallium ([Figure 3\(b\)](#)). They argued that the absence of *Emx1* but the presence of other pallial genes in the avian nidopallium and in the mammalian ventral claustrum and lateral anterior amygdala indicate that these structures commonly arose from the ventral pallium. They further argued that the avian arcopallium and mammalian amygdala consist of subpallial parts derived from striatal and pallidal cell groups and, by this association, that the avian arcopallium is homologous to the mammalian amygdala, as originally proposed by Edinger.

Both categories of hypotheses have their limitations. For the nuclear-to-layer hypotheses, developmental studies have not been conducted to test whether the three types of serially connected neurons in birds arise from cell types similar to those that give rise to the cortical layers in mammals. Furthermore, not all gene expression patterns support one-to-one molecular relationships between avian pallial subdivisions and mammalian cortical layers. Neither do all findings support the nuclear-to-claustrum/amygdala nuclei hypotheses. More investigation is required. This is an active area of research and debate, but the

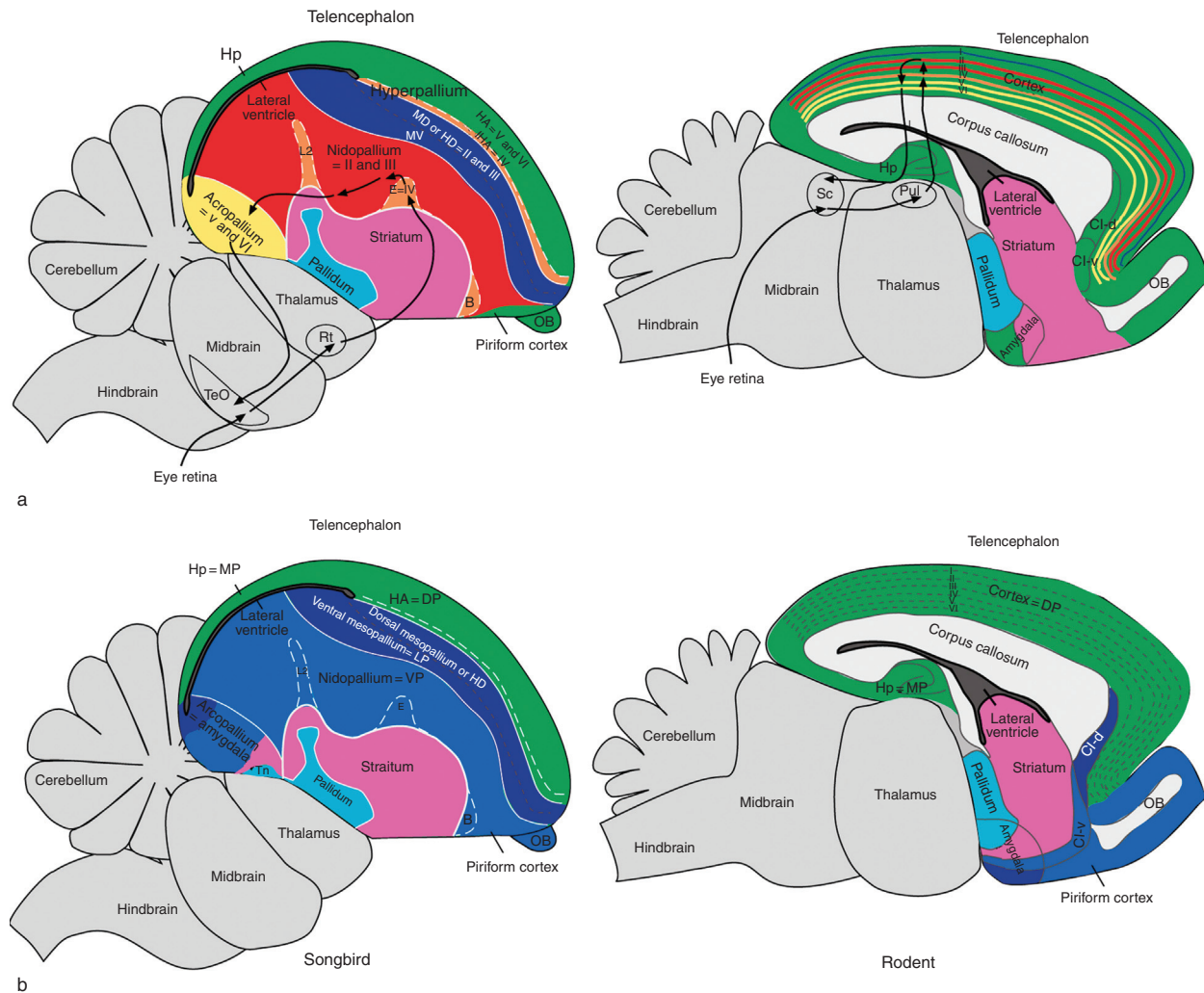


Figure 3 Working hypotheses on avian and mammalian pallial homologies in the context of the new avian brain nomenclature. (a) An example of a nuclear-to-layered hypothesis. Connectivity of tectofugal visual pathways in avian (songbird, left) and mammalian (rat, right) brains is shown. Color coding indicates proposed homologies between birds and mammals. (b) An example of a nuclear-to-claustrum/amygdala hypothesis. B, basorostralis; Cl-d, claustrum, dorsal part; Cl-v, claustrum, ventral part; DP, dorsal pallium; E, entopallium; HA, hyperpallium apicale; HD, hyperpallium densocellulare; Hp, hippocampus; L2, field L2; LP, lateral pallium; MD, dorsal mesopallium; MP, medial pallium; MV, ventral mesopallium; OB, olfactory bulb; Pul, pulvinar nucleus; Rt, nucleus rotundus; Sc, superior colliculus; TeO, optic tectum; Tn, nucleus taenia; VP, ventral pallium. Adapted from Jarvis ED, Gunturkun O, Bruce L, et al. (2005) Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews Neuroscience* 6: 151–159, with permission.

new avian terminology is compatible with adoption of any one-to-one homology hypothesis should future evidence be more convincing.

Avian Cognition and Brain Function

Based on the modern view, the adult avian pallium, as in mammals, comprises approximately 75% of the telencephalic volume. This realization of a relatively large and well-developed avian pallium that processes information in a similar manner to mammalian sensory and motor cortices may help explain some of the

cognitive abilities of birds. As summarized by the Avian Brain Nomenclature Consortium, pigeons can memorize up to 725 different visual patterns, learn to categorically discriminate objects as ‘human-made’ versus ‘natural,’ discriminate cubistic and impressionistic styles of painting, communicate using visual symbols, rank patterns using transitive inferential logic, and occasionally ‘lie.’ New Caledonian crows make tools out of leaves or novel human-made material, use them appropriately to retrieve food, and are believed to pass this knowledge on to other crows through social learning. Magpies develop an understanding

of object constancy at an earlier relative age in their life span than any other organism tested and can use this skill to the same extent as humans. Scrub-jays show episodic memory, recall for events that take place at a specific time or place, once thought to be unique to humans. This same species modifies its food-storing strategy according to the possibility of future stealing by other birds and therefore displays a behavior that would qualify as theory of mind. Owls have a highly sophisticated capacity for sound localization, used for nocturnal hunting, that rivals that of humans and that is developed through learning. Parrots, hummingbirds, and oscine songbirds possess the rare skill of vocal learning. This trait is a critical substrate in humans for spoken language, and with the exceptions of cetaceans and possibly bats and elephants, it is not found in any other mammal. Parrots, in addition, can learn human words and use them to communicate reciprocally with humans. African gray parrots in particular can use human words in numerical and relational concepts – abilities once thought unique to humans. These vocal behaviors are controlled by vocal learning pathways through both pallial and subpallial regions.

In general, these cognitive functions are carried out by the telencephalon, including the six-layered cortex in mammals but by nuclear pallial areas in birds. That is, the mammalian six-layered cortical architecture is not the only neuroarchitectural solution for the generation of complex cognitive behaviors. Pallial-cortical folding is also not required. Birds apparently cannot use cortical folding because of the nuclear organization of their telencephalon; among mammals, such folding is related more to absolute brain size than to behavioral complexity. Rather, the presence of specific brain subdivisions and connections is a more important factor for the generation of behavioral complexity. This suggests that there is an avian method to perform complex behaviors and a mammalian method.

Conclusion

The avian telencephalon is thought to have been inherited from its common ancestors with reptiles and mammals as a package containing pallidal, striatal, and pallial domains. It conserved the pallidal and striatal domains but modified the pallial domains. The pallial domain still performs similar functions as the pallial regions of mammals, such as the six-layered cortex and amygdala. To determine more specific homologies between avian and mammalian pallia, additional investigations are necessary, and such investigations should help determine the basic functions of specific cell types in the vertebrate brain.

See also: Basal Ganglia: Evolution; Bird Song Systems: Evolution; Brain Asymmetry: Evolution; Brain Connectivity and Brain Size; Brain Evolution: Developmental Constraints and Relative Developmental Growth.

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