OPINION

Avian brains and a new understanding of vertebrate brain evolution

*The Avian Brain Nomenclature Consortium**

Abstract | We believe that names have a powerful influence on the experiments we do and the way in which we think. For this reason, and in the light of new evidence about the function and evolution of the vertebrate brain, an international consortium of neuroscientists has reconsidered the traditional, 100-year-old terminology that is used to describe the avian cerebrum. Our current understanding of the avian brain — in particular the neocortex-like cognitive functions of the avian pallium — requires a new terminology that better reflects these functions and the homologies between avian and mammalian brains.

One hundred years ago, Edinger, the father of comparative neuroanatomy, formulated a unified theory of brain evolution that formed the basis of a nomenclature that has been used to define the cerebral subdivisions of all vertebrates[1]. This resulted in terms and associated concepts such as palaeostriatum, archistriatum, neostriatum and neocortex that are still in common use. According to this theory, the avian cerebrum is almost entirely composed of basal ganglia, the basal ganglia is involved in only instinctive behaviour, and the malleable behaviour that is thought to typify mammals exclusively requires the so-called neocortex. However, towards the end of the twentieth century, there accumulated a wealth of evidence that these viewpoints were incorrect. The avian cerebrum has a large pallial territory that performs functions similar to those of the mammalian cortex. Although the avian pallium is nuclear, and the mammalian cortex is laminar in organization, the avian pallium supports cognitive abilities similar to, and for some species more advanced than, those of many mammals. To eliminate these misconceptions, an international forum of neuroscientists (BOX 1) has, for the first time in 100 years, developed new terminology that more accurately reflects our current understanding of the avian cerebrum and its homologies with mammals. This change in terminology is part of a new understanding of vertebrate brain evolution.

In this article, we summarize the traditional view of telencephalic evolution before reviewing more recent findings and insights. We then present the new nomenclature that has been developed by the Avian Brain Nomenclature Forum, and discuss its implications for our understanding of vertebrate brain evolution and its associated homologies.

The classical view

The classical view of telencephalic evolution, which is still prevalent in classrooms and textbooks, began in the late nineteenth and early twentieth centuries after the publication of *The Origin of Species* by Darwin[2]. Inspired by Darwin's theory, between 1885 and 1908 Edinger formulated an influential, evolution-based model of brain organization[1,3,4]. Edinger and other early comparative neurobiologists combined Darwin's concept of 'evolution' with the nineteenth-century version of Aristotle's '*scala naturae*', which resulted in the view that evolution was progressive and unilinear[5] — from fish, to amphibians, to reptiles, to birds and mammals, to primates and, finally, to humans — ascending from 'lower' to 'higher' intelligence in a chronological series. They believed that the brains of extant vertebrates retained ancestral structures, and, therefore, that the origin of specific human brain subdivisions could be traced back in time by examining the brains of extant non-human vertebrates. In making such comparisons, they noted that the main divisions of the human CNS — the spinal cord, hindbrain, midbrain, thalamus, cerebellum and cerebrum or telencephalon — were present in all vertebrates (FIG. 1a). Edinger, however, noted that the internal organization of the telencephala showed the most pronounced differences between species. In mammals, the outer part of the telencephalon was found to have prominently layered grey matter (FIG. 1b, green) whereas the inner part had nuclear grey matter (FIG. 1b, purple). The inner part was located ventrally to the lateral ventricle. The outer part was more elaborate and folded in humans than in smaller mammals. In non-mammals, the outer and inner parts of the telencephala were mainly composed of nuclear grey matter, most of which was located ventrally to the lateral ventricle in reptiles and birds (FIG. 1b, 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 suggested that the stages proceeded in a ventral-to-dorsal direction, with each new vertebrate group acquiring a more advanced cerebral subdivision, much as the earth's geological strata formed over time. He proposed that, first, there was the old brain, the palaeoencephalon (also called the basal ganglia or subpallium at the telencephalic base), which controlled instinctive behaviour, followed by the addition of a new brain, the neoencephalon (also called the pallium or mantle at the top of the telecephalon), which controlled learned and intelligent behaviour[4]. He, Ariëns Kappers

Box 1 | Avian Brain Nomenclature Consortium

Authors are ordered alphabetically in two groups: the first group, along with the first two and last two authors, are the core Avian Brain Nomenclature Forum Thinktank group; the second group are professors, postdoctoral fellows and students who also participated in the Avian Brain Nomenclature Forum. (For author affiliations see online supplementary information S1 (box).)

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and others named the telencephalic subdivisions within each vertebrate group with the prefixes 'palaeo' (oldest), 'archi' (archaic) and 'neo' (new) to designate the presumed relative order of evolutionary appearance of each subdivision. In Greek, 'archi' means the oldest, the first, or the most primitive, whereas 'palaeo' means ancient, primitive or old, but not necessarily the oldest. Both Edinger and Ariëns Kappers misinterpreted the meaning of these prefixes and reversed them, naming structures with 'palaeo-' to indicate the oldest or first and 'archi-' to indicate old. They added to these prefixes the root word 'striatum' for the presumed palaeoencephalic subdivisions and 'pallium' or 'cortex' for the presumed neoencephalic subdivisions[1,4,6–8]. The term 'striatum' was used because a large part of the basal ganglia (palaeoencephalon) in mammals, now commonly called the caudate–putamen, has fibre bundles coursing through it that give it a striated appearance.

The classical view that became dominant was that the primordial telencephalon of fishes had a relatively small pallium and a larger subpallium, both of which were entirely devoted to olfactory information processing. The fish subpallium was named 'palaeostriatum' (old striatum), and was thought to be the antecedent of the human globus pallidus (FIG. 1b). Amphibians were thought to have evolved an 'archistriatum' (archaic striatum) above the palaeostriatum, which was proposed to be the antecedent of the human amygdala. Reptiles were thought to have evolved a 'neostriatum' (new striatum) above the archistriatum, which was proposed to be the antecedent of the human caudate and putamen. The palaeostriatum of reptiles was also thought to have elaborated into an older part (primitivum) and a newer part (augmentatum), both of which were considered homologous to the human globus pallidus. Following this, birds were thought to have evolved a large additional basal ganglia subdivision, the 'hyperstriatum' (hypertrophied striatum), which was considered to be unique to birds[9].

The fish pallium was named 'palaeocortex', and was proposed to be the antecedent of the human olfactory cortex. Reptiles were thought to have evolved an 'archicortex', also thought to be olfactory and primitive, that was said to be the antecedent of the human hippocampus. Birds were thought not to have evolved any further pallial regions. By contrast, mammals were thought to have evolved the latest and greatest achievement, a 'neocortex', from the palaeocortex and/or archicortex[6]. The archicortex and/or palaeocortex, with their 2–3 cell layers, were assumed to be primitive; the neocortex, with its 6 layers, was assumed to be more recently evolved and a substrate for more sophisticated behaviour.

There were dissenting voices to the classical view[10–12]. Some of its proponents also made partial or tentative retractions[13,14]. However, alternative views were not widely embraced. Instead, the classical view was codified in the important 1936 comparative neuroanatomy text by Ariëns Kappers, Huber and Crosby[14] and became pervasive throughout neuroscience.

A new view of the subpallium

Substantive challenges to the classical view of the subpallium began in the 1960s and 1970s with the advent of new methods for determining both nervous system connectivity and the anatomical profiles of gene products[5]. These studies found that, in mammals, acetylcholinesterase enzymatic activity was enriched in the neostriatum[15]. In birds, high acetylcholinesterase activity was found only in the palaeostriatum augmentatum and associated lobus parolfactorius (LPO)[15,16] (the LPO was considered to be part of the palaeostriatum augmentatum by Ariëns Kappers *et al.*[14], but was named as a separate region by Karten and Hodos[17]). Other studies found that the mammalian neostriatum was highly enriched with dopaminergic terminals, which originated from midbrain neurons in the substantia nigra pars compacta[18]. In birds, again, only the palaeostriatum augmentatum and LPO were enriched with dopaminergic terminals, and this input originated from neurons in the midbrain[19,20]. During the following decades, using new methods in double-label immunohistochemistry and tract tracing, the mammalian neostriatum was found to be enriched in two types of neuron: those containing the neuropeptide substance P (SP), which project to the internal part of the globus pallidus and substantia nigra, and those containing the neuropeptide enkephalin (ENK), which project to the external part of the globus pallidus[21–24]. In birds, SP and ENK neurons are enriched in the palaeostriatum augmentatum (including the LPO)[24,25], and, like the equivalent neurons in mammals, project to different cell types within the adjacent avian palaeostriatum primitivum. In both birds and mammals, the SP neurons seem to be involved in promoting planned movement, whereas the ENK neurons seem to have a role in inhibiting unwanted movement. Further functional studies revealed that both the mammalian neostriatum and the avian palaeostriatum augmentatum (including the LPO) participate not only in instinctive behaviour and movement, but also in motor learning[26,27].

These apparent relationships between the subpallia of mammals and birds have been supported by molecular embryology studies[24,28–31]. The developing subpallium in birds and mammals consists of two separate histogenetic zones that express different sets of transcription factors: a dorsal zone, which, in mammals, corresponds to the lateral ganglionic eminence and selectively expresses the transcription factors *DLX1* and *DLX2* but not *NKX2.1*; and a ventral zone, which, in mammals, corresponds to the medial ganglionic eminence and selectively expresses all three transcription factors. In mammals, the lateral ganglionic eminence gives rise to the dorsal striatum (neostriatum) and the ventral striatum (nucleus accumbens and part of olfactory tubercle). The homologous developing territory in birds gives rise to the structures that were previously called the palaeostriatum augmentatum (including the LPO) and the olfactory tubercle. The medial ganglionic eminence in mammals gives rise to various pallidal cell groups, including the dorsal pallidum (the globus pallidus) and the ventral pallidum. The homologous developing territory in birds gives rise to the structures that were called the palaeostriatum primitivum and ventral palaeostriatum. These avian and mammalian striatal and pallidal relationships are further supported by studies of the comparative expression patterns of more than 30 other genes in adult birds and mammals[32–36]. Similar striatal and pallidal territories have been found in the so-called palaeostriatal regions of reptiles[37–40].

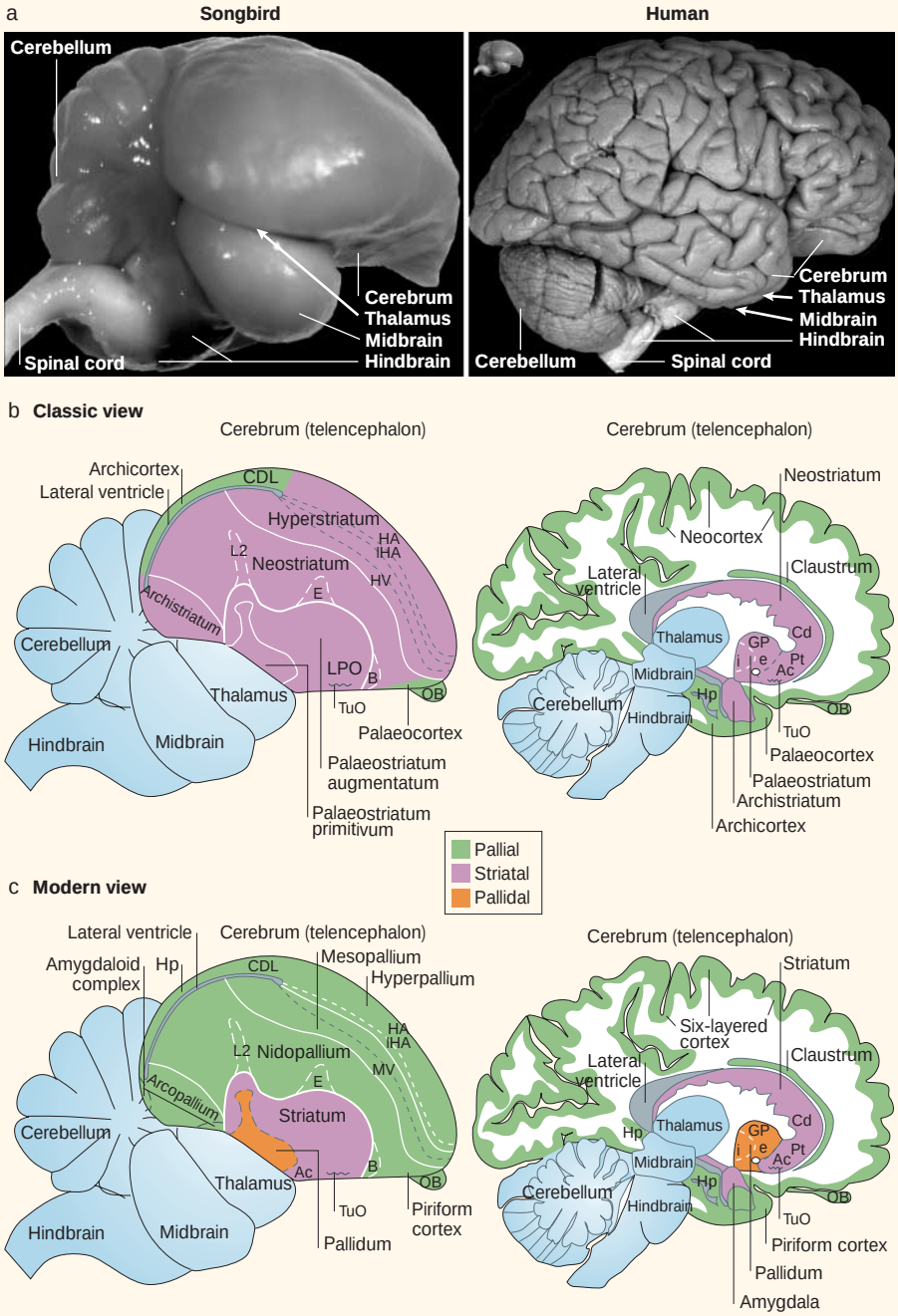


Figure 1 | **Avian and mammalian brain relationships. a** | Side view of a songbird (zebra finch) and human brain to represent avian and mammalian species. In this view, the songbird cerebrum covers the thalamus; the human cerebrum covers the thalamus and midbrain. Inset (left) next to the human brain is the zebra finch brain to the same scale. Human brain image reproduced, with permission, courtesy of John W. Sundsten, Digital Anatomist Project. **b** | Classic view of avian and mammalian brain relationships. Although past authors had different opinions about which brain regions are pallium versus subpallium, we have coloured individual brain regions according to the meaning of the names given to those brain regions. 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; HV, hyperstriatum ventrale; IHA, interstitial hyperstriatum accessorium; L2, field L2; LPO, lobus parolfactorius; OB, olfactory bulb; Pt, putamen; TuO, olfactory tubercle. **c** | Modern consensus view of avian and mammalian brain relationships according to the conclusions of the Avian Brain Nomenclature Forum. Solid white lines are lamina (cell-sparse zones separating brain subdivisions). Large white areas in the human cerebrum are axon pathways called white matter. Dashed grey lines divide regions that differ by cell density or cell size; dashed white lines separate primary sensory neuron populations from adjacent regions. Abbreviations where different from **b**: E, entopallium; B, basorostralis; HA, hyperpallium apicale; Hp, hippocampus; IHA, interstitial hyperpallium apicale; MV, mesopallium ventrale.

Together, these studies indicate that the avian palaeostriatum augmentatum is homologous to the mammalian neostriatum and that the avian palaeostriatum primitivum is homologous to the mammalian globus pallidus.

A new view of the pallium

With these challenges to the classical view of the subpallial relationships among birds, reptiles and mammals came challenges to the classical view of the relationships among their pallia. The mammalian pallium includes the areas known as palaeocortex, archicortex and neocortex; and has been said, more recently, to include both the claustrum and lateral parts of the amygdala[28,41,42] (FIG. 1c; Holmgren[11] originally proposed that the claustrum and part of the amygdala were pallial, but this view was largely ignored at the time). In birds, the finding that the structures that had been called hyperstriatum, neostriatum and archistriatum were neither striatum nor pallidum raised the question of which telencephalic sector these regions did represent. The results that were needed to answer this question also began to appear in the mid-1960s from pathway tracing[16,43–46] and behavioural studies[47–51]. These studies found that the so-called avian neostriatum and hyperstriatum receive visual, auditory and somatosensory input from the thalamus, as does the mammalian neocortex. These avian brain regions also carry out the same type of sensory information processing as is performed by the mammalian neocortex. The so-called avian hyperstriatum accessorium and the archistriatum give rise to important descending projections to the premotor and motor neurons of the brainstem and spinal cord, like those of the mammalian cortico-bulbar and cortico-spinal pathways[43,52–54]. Finally, like the mammalian neocortex, these avian brain regions carry out crucial roles in motor control and sensorimotor learning[55–67].

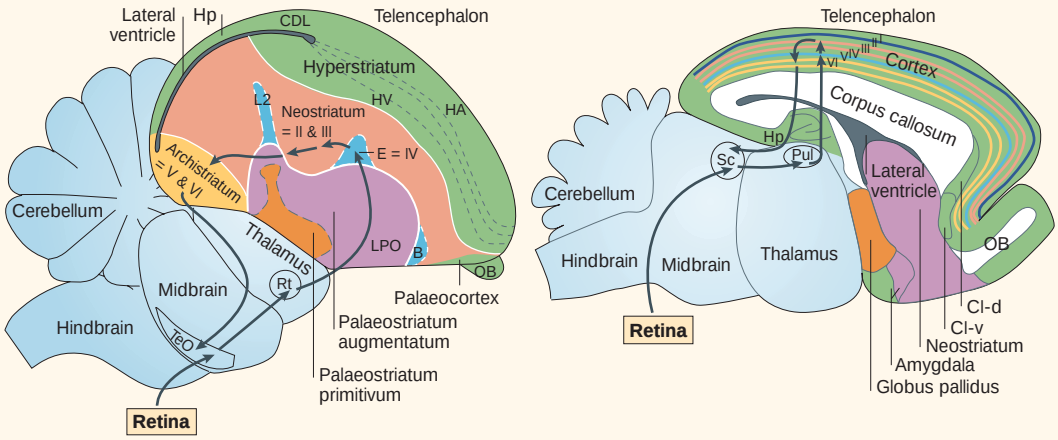
The apparent pallial relationships between these mammalian and avian brain regions were also supported by molecular embryology studies[28,68,69]. During development, both the avian hyperstriatum and neostriatum and the mammalian pallium express the pallium-specific transcription factors *EMX1*, *PAX6* and *TBR1*. The developmental data led to uncertainties about how much of the archistriatum is pallial[28,30]. However, comparisons of the expression of the brain-derived neurotrophic factor (*BDNF*) and the glutamate receptor *mGluR2* in adult birds and mammals indicated that the entire avian archistriatum, as defined in brain atlases[17,70], expresses these pallium-specific mRNAs[34,36]. Further studies of the comparative expression patterns of other glutamate receptors in adult birds and mammals[36]

Box 2 | Working hypotheses on avian and mammalian pallial homologies

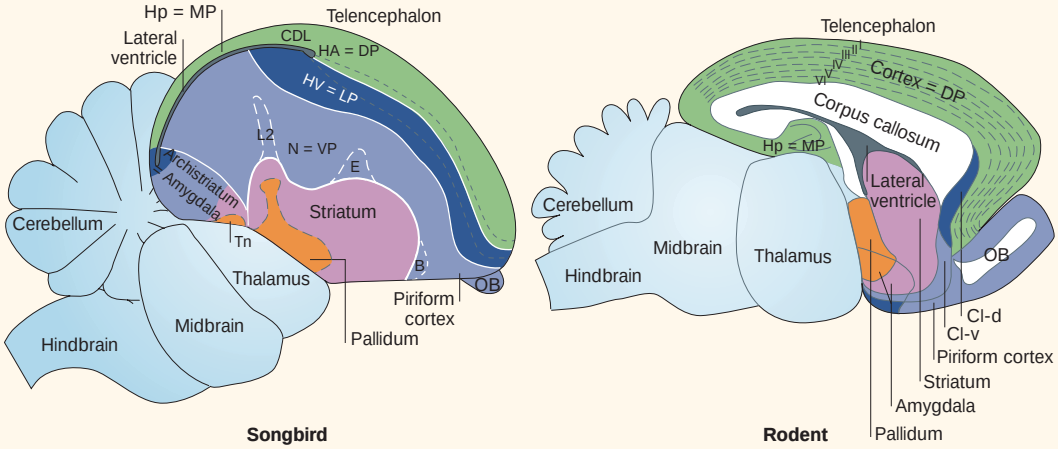
An example of a nuclear-to-layered hypothesis is shown in panel **a**. The connectivity of tectofugal visual pathways in avian (left) and mammalian (right) brains is shown. The hypothesis illustrated is that of Karten[71]. Colour-coding indicates proposed homologies between birds and mammals. An example of a nuclear-to-claustrum/amygdala nuclei hypothesis is shown in panel **b**. The hypothesis illustrated is that of Puelles *et al.*[28].

I–VI, cortical layers I–VI;
B, nucleus basalis;
CDL, dorsal lateral corticoid area;
Cl-d, claustrum, dorsal part;
Cl-v, claustrum, ventral part;
DP, dorsal pallium;
E, ectostriatum;
HA, hyperstriatum accessorium;
Hp, hippocampus;
HV, hyperstriatum ventrale;
L2, field L2; LP, lateral pallium;
LPO, lobus parolfactorius;
MP, medial pallium;
N, Neostriatum;
OB, olfactory bulb;
Pul, pulvinar nucleus;
Rt, nucleus rotundus;
Sc, superior colliculus;
TeO, optic tectum;
Tn, nucleus taenia;
VP, ventral pallium.

a **Nuclear-to-layered hypothesis**



b **Nuclear-to-claustrum/amygdala hypothesis**



support these conclusions. Together, these studies indicate that the avian hyperstriatum, neostriatum, and archistriatum might be homologous to mammalian pallial regions.

This developing view was accompanied by several new proposals about one-to-one homologies between specific avian and mammalian pallial subdivisions. We will consider these in two groups — nuclear-to-layered hypotheses and nuclear-to-claustrum/amygdala nuclei hypotheses.

Nuclear-to-layered hypotheses. First proposed by Karten[16,71], nuclear-to-layered hypotheses (BOX 2) propose that the similarities in connectivity between the so-called hyperstriatum, neostriatum and archistriatum of birds and the neocortex 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 the connectivity of the ancestral nuclear network. In this regard, he argued that the avian pallium is divided into three groups of serially connected neuron types — thalamorecipient neurons (field L2, ectostriatum and basalis), pallio-pallial neurons (neostriatum) and extratelencephalic projection neurons (archistriatum), with cell types and interconnectivity that resemble those of mammalian cortical layers IV, II–III and V–VI, respectively (BOX 2). Similar arguments were later made for the avian upper hyperstriatum (also known as the Wulst), which also has serially connected neuron types that resemble those found in the mammalian neocortex[62]. In this hypothesis, avian L2 neurons are homologous to layer IV neurons of mammalian primary auditory cortex, basalis neurons to layer IV of primary somatosensory cortex, ectostriatal neurons to layer IV of extrastriate visual cortex, and the interstitial hyperstriatum accessorium to layer IV of striate visual cortex. In support of this hypothesis, gene expression studies[36,72,73] have shown that avian thalamorecipient nuclear fields (L2, ectostriatum, basalis and interstitial hyperstriatum accessorium) and the mammalian thalamorecipient layer IV of neocortex selectively express some of the same genes (the steroid transcription factor *ROR-β* and the potassium channel *EAG2*) and express a low level of others (the activity-dependent transcription factor *ZENK* and the AMPA (α-amino-3-hydroxy-5-methyl-4-isoxazole propionic acid) glutamate receptor subunit *GluR1*). Avian extratelencephalic projection neurons (in the archistriatum, but not in the hyperstriatum accessorium) and mammalian extratelencephalic projection neurons (layer V neurons of neocortex) both show selective expression of the transcription factor *ER81*. So, although the avian pallium is not organized cytoarchitectonically into layers, its nuclear subdivisions bear marked similarities in connectivity and molecular profile to different layers of the mammalian neocortex.

Nuclear-to-claustrum/amygdala hypotheses. These hypotheses (BOX 2) provide a different interpretation of mammalian homologies with the avian ventral hyperstriatum, neostriatum and archistriatum, known collectively as the dorsal ventricular ridge (DVR). In an early proposal, Bruce and Neary[74] proposed that the avian DVR represents an elaboration of parts of the mammalian amygdala. Subsequently, Striedter[75] 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 was based on several facts: both the avian DVR and mammalian claustrum/amygdala are nuclear in organization[75]; both the avian DVR and part of the mammalian amygdala have similar connections[74,76,77]; and both have conserved developmental expression patterns of regulatory genes that have important roles in brain regionalization and morphogenesis[28,68]. In the most detailed gene expression study, Puelles *et al.*[28] proposed that the common topographic expression patterns of the transcription factors *EMX1* and *PAX6* in the avian hyperstriatum ventrale and in the mammalian dorsal claustrum and basolateral amygdala indicate that these structures both arose from the lateral pallium (BOX 2). They argued that the absence of *EMX1* but the presence of other pallial genes in the avian neostriatum and in the mammalian ventral claustrum and lateral anterior amygdala indicate that these structures commonly arose from the ventral pallium. They further proposed that the avian archistriatum and mammalian amygdala consist of subpallial parts derived from striatal and pallidal cell groups, and, by this association, that the avian archistriatum is homologous to the mammalian amygdala, as originally proposed by Edinger[1].

Both the above hypotheses have their limitations. For the nuclear-to-layered hypotheses, developmental studies have not been conducted to investigate whether the three types of serially connected neuron 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[78]. In addition, not all findings support the nuclear-to-claustrum/amygdala hypothesis. Although initial studies[28] reported that this hypothesis was supported by the lack of pallial *EMX1* expression in the avian neostriatum (so-called ventral pallium) and the mammalian ventral claustrum and lateral anterior amygdala, recent fate mapping showed that the ventral claustrum contains dispersed *EMX1*-expressing cells and the lateral amygdala contains many *EMX1*-expressing cells[79]. The antiquity of the claustrum has also been debated. One study[80] reported that monotremes (platypus and echidnas) lack a claustrum, whereas a later study[81] reported that echidnas, but not platypus, have a rudimentary claustrum located more ventrally in the white matter relative to the location of the claustrum in other mammals. So, it is possible that some monotreme groups have lost the claustrum; that the echidna has independently evolved it or another deep cortical derivative; or that the claustrum is not an ancestral mammalian trait. Further investigation is required.

A new nomenclature

Despite an extensive revision of our understanding of telencephalic evolution, the common nomenclature used for the avian telencephalon has, until 2004 (REF. 82), retained all of the classical evolution- and *scala naturae*-based terminology. For this reason, findings in 'birdbrains' have been habitually misinterpreted by neuroscientists studying non-avian brains as pertaining to the basal ganglia or as largely irrelevant to mammals. To rectify this problem, an international consortium of specialists in avian, mammalian, reptilian and fish neurobiology — the Avian Brain Nomenclature Consortium (BOX 1) — assembled with the goal of revising the terminology for the avian brain. Through online discussions, an Avian Brain Nomenclature Exchange web site, various meetings held over a period of 6 years and an Avian Brain Nomenclature Forum held at Duke University, North Carolina[83], the group developed a new terminology that represents the current understanding of avian telencephalic organization and its homologies with mammals[82] (FIG. 1c). On the basis of the evidence summarized above, we 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 (FIG. 1c). We renamed the subdivisions within each of these domains in birds with homology-based terms or roots that allow reference to named regions in mammals, and eliminated all phylogeny-based prefixes (palaeo-, archi- and neo-) that erroneously implied the relative age of each subdivision.

The striatal and pallidal domains. We renamed the avian palaeostriatum augmentatum and LPO as the lateral and medial parts of the avian dorsal striatum, and identified a nucleus accumbens and olfactory tubercle as parts of the avian ventral striatum (FIG. 1c). We renamed the region that includes the palaeostriatum primitivum and ventral palaeostriatum as the 'pallidum' (FIG. 1c). Like the mammalian pallidum, the avian pallidum has a sparse distribution of cells[24], giving the region its pale appearance and, therefore, its name. The dorsal region of the avian pallidum was found to be homologous to the mammalian globus pallidus and named 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[25] (FIG. 1c).

The pallial domain. We concluded that the avian pallium is organized into four main subdivisions instead of three striatal subdivisions (hyperstriatum, neostriatum and archistriatum)[7] and renamed them 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) (FIG. 1c). We concluded that several neuronal populations adjacent to the arcopallium and the posterior part of what had been regarded as archistriatum are homologous to pallial and subpallial regions of the mammalian amygdala, and renamed them as members of the 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. After extensive evaluation of the various one-to-one homology hypotheses of the avian and mammalian pallia[28,44,68,74,75,77,84] (BOX 2), we concluded that the evidence is not strong enough for any specific proposed homologies to be incorporated into a new pallial terminology. However, we recognize that this is an area of active research and debate, and designed the new terminology to be compatible with the adoption of any one-to-one homology hypothesis should future evidence be more convincing.

A new view of telencephalic evolution

With this new understanding of the avian telencephalic organization and its homologies

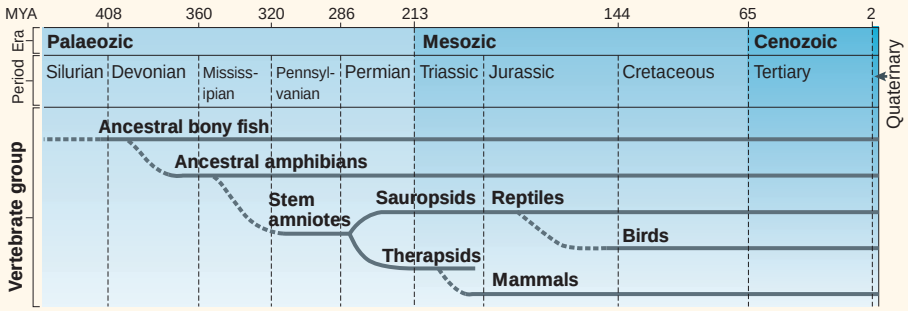


Figure 2 | **Simplified modern view of vertebrate evolution.** The diagram begins with the fish group that contains the most recent ancestors of land vertebrates. This differs from the classic view in that instead of giving rise to reptiles, ancestral amphibians are thought to have given rise to stem amniotes. Stem amniotes then split into at least two 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 based on other types of data. MYA, million years ago Based on REFS 85,86.

with that of mammals, we can generate more informed hypotheses and conclusions about telencephalic evolution in vertebrates. It is now apparent that the organization of the true basal ganglia among birds, mammals and other vertebrates (that is, distinct nuclear striatal and pallidal domains with more dopaminergic input into the striatal domain[24]) is quite conserved. By contrast, the organization of the pallial domains of these groups is more varied. The avian hyperpallium has a unique organization that has so far been found only in birds[69]. This consists of semi-layered subdivisions, and might have evolved more recently than the mammalian six-layered cortex, as birds evolved ~50–100 million years after mammals[85,86] (FIG. 2). The DVR (which, in birds, contains the mesopallium, nidopallium and arcopallium) is a nuclear, grey matter formation that is unique to birds and reptiles. The six-layered cortex is unique to mammals, and, as all the main groups of living mammals (monotremes, marsupials and placentals) have a six-layered cortex[87], it was presumably inherited from their common therapsid ancestor more than 200 million years ago (FIG. 2). Furthermore, new findings indicate that mammals did not arise from reptiles, but from therapsids, and that the last common ancestor of the reptile and mammal lineages was the stem amniotes[86]. As all non-mammalian therapsids are now extinct (FIG. 2), it is difficult to trace from stem amniotes to mammals the evolutionary history of mammalian telencephalic organization — layered, nuclear or otherwise. Therefore, the reptilian nuclear pallial organization cannot be assumed to represent the ancestral condition for mammals.

Further, it is now known that evolution is not invariably progressive or linear, so there is no basis for the view that more recently evolved species or structures are more advanced. In support of this conclusion, we now know that the telencephala of fishes are not devoted mainly to olfactory function, as the olfactory area represents only a limited portion of the fish pallium[88]. In addition, fishes have a hippocampus (archicortex), and the main function of the hippocampus in fishes, reptiles, birds and mammals alike is not olfaction, but memory formation and spatial mapping[89,90].

So, as for birds, it might be best to abandon the use of the terms archicortex, palaeocortex, archistriatum, palaeostriatum and neostriatum for mammals and other vertebrates in favour of the alternatives — hippocampus or hippocampal cortex, piriform cortex, amygdala, striatum and pallidum. However, alternative terms for 'neocortex', such as 'isocortex', have not been universally accepted. 'Neocortex' would be appropriate if taken to refer to the uniqueness of this cortical structure among vertebrates. However, 'neocortex' should not be taken to mean that it is the only unique form of pallial organization, that it evolved out of a palaeo- and/or archicortex, or that it is the newest pallial organization to have evolved. In the absence of a universally accepted alternative to neocortex, for the remainder of this article we use the term 'six-layered cortex'. Although some regions of this cortical domain have fewer than six layers, we justify our use by analogy to the term tetrapods, which refers to all taxa derived from ancestral four-footed vertebrates, including snakes and whales.

Overall, the evidence indicates that there are pallial, striatal and pallidal domains in most or all vertebrates[24]. Therefore, it is reasonable to propose that the telencephala of early fishes possessed all three domains, which were then inherited as a package by later vertebrates, and independently 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 indicate that there are fewer constraints on how the pallium can be organized. This view has important implications for our understanding of neural mechanisms of cognition.

Avian cognition and brain function

On the basis of this new understanding of avian brain organization and its evolutionary relationships, we estimate that, as in mammals, the adult avian pallium comprises about 75% of the telencephalic volume (FIG. 1c; calculated from sagittal series of pigeon and zebra finch brain sections). This realization of a relatively large and well developed avian pallium that processes information in a similar manner to mammalian sensory and motor cortices sets the stage for a re-evaluation of the cognitive abilities of birds, which, since the 1950s, have been increasingly appreciated as far more complex than was originally presumed[91,92]. For example, pigeons can memorize up to 725 different visual patterns[93], learn to categorize objects as 'human-made' versus 'natural'[94], discriminate cubistic and impressionistic styles of painting[95], communicate using visual symbols[96], rank patterns using transitive inferential logic[97] and occasionally 'lie'[98,99]. New Caledonian crows make tools out of leaves or novel human-made material, use them appropriately to retrieve food and are thought to pass this knowledge on to other crows through social learning[100,101]. Magpies develop an understanding of object constancy at an earlier relative age in their lifespan than any other organism tested and can use this skill to the same extent as humans[102]. Scrub-jays show episodic memory — the ability to recall events that take place at a specific time or place, which was once thought to be unique to humans[103]. This same species modifies its food-storing strategy according to the possibility of future stealing by other birds and, therefore, exhibits a behaviour that would qualify as theory-of-mind[104]. Owls have a highly sophisticated capacity for sound localization, used for nocturnal hunting, that rivals that of humans and that is developed through learning[66]. Parrots, hummingbirds and oscine songbirds possess the rare skill of vocal learning[105]. This trait is a prerequisite in humans for spoken language and, with the exceptions of cetaceans and possibly bats, is not found in any other mammal[106]. In addition, parrots can learn human words and use them to communicate reciprocally with humans. African grey parrots, in particular, can use human words in numerical

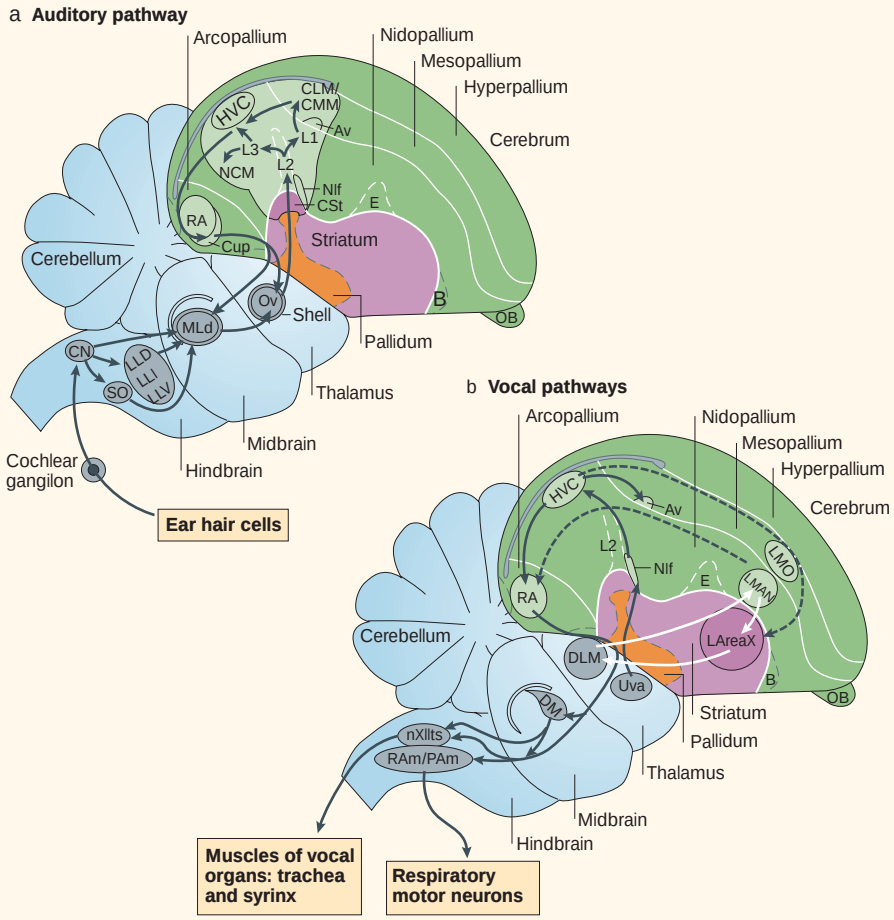


Figure 3 | **Auditory and vocal pathways of the songbird brain within the context of the new consensus view of avian brain organization.** Only the most prominent and/or most studied connections are indicated. **a** | The auditory pathway. Most of the hindbrain connectivity is extrapolated from non-songbird species. For clarity, reciprocal connections in the pallial auditory areas are not indicated. **b** | The vocal pathways. Black arrows show connections of the posterior vocal pathway (or vocal motor pathway), white arrows indicate the anterior vocal pathway (or pallial–basal ganglia–thalamic–pallial loop) and dashed lines show connections between the two pathways. Av, avalanche; B, basorostralis; CLM, caudal lateral mesopallium; CMM, caudal medial mesopallium; CN, cochlear nucleus; CSt, caudal striatum; DLM, dorsal lateral nucleus of the medial thalamus; DM, dorsal medial nucleus; E, entopallium; HVC (a letter-based name); L1, L2, L3, fields L1, L2 and L3; LAreaX, lateral AreaX of the striatum; LLD, lateral lemniscus, dorsal nucleus; LLI, lateral lemniscus, intermediate nucleus; LLV, lateral lemniscus, ventral nucleus; LMAN, lateral magnocellular nucleus of the anterior nidopallium; LMO, lateral oval nucleus of the mesopallium; MLd, dorsal lateral nucleus of the mesencephalon; NCM, caudal medial nidopallium; NIf, interfacial nucleus of the nidopallium; nXIIts, nucleus XII, tracheosyringeal part; OB, olfactory bulb; Ov, ovoidalis; PAm, para-ambiguus; RA, robust nucleus of the arcopallium; RAm, retroambiguus; SO, superior olive; Uva, nucleus uvaeformis.

and relational concepts[107,108], abilities that were once thought to be unique to humans.

So, many birds have cognitive proficiencies that are quite sophisticated, and some birds and mammals have cognitive proficiencies that clearly exceed all other birds or mammals. As these cognitive functions are carried out by the six-layered cortex in mammals[109] but by nuclear pallial areas in birds[58,66,110,111], it is clear that the mammalian six-layered cortical architecture is not the only neuroarchitectural solution for the generation of complex cognitive behaviours. It is also clear that pallial–cortical folding is 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 behavioural complexity[112,113]. The presence of specific brain subdivisions and connections are more important factors for the generation of behavioural complexity.

An example of how avian pallial and subpallial areas can interact to produce complex behaviour in the context of the new view of avian brain organization can be seen in the brain pathways that control learned vocal communication (FIG. 3). Most of the telencephalic auditory processing areas are in the pallium, adjacent to a smaller auditory area in the striatum (FIG. 3a). Likewise, most of the telencephalic vocal control nuclei are in the pallium, with one vocal nucleus in the striatum (FIG. 3b). The vocal nuclei that are involved in the production of learned vocalizations, including human speech in parrots[111], make up a pathway that directly innervates brainstem motor neurons (FIG. 3b, black arrows). This vocal motor pathway is similar to mammalian motor corticobulbar pathways[106]. The vocal nuclei that are involved in the imitation of vocalizations form a pallial–basal ganglia–thalamic–pallial loop (FIG. 3b, white arrows). This vocal learning pathway is similar to mammalian cortical–basal ganglia–thalamic–cortical loops[27,106,114], which are involved in motor learning, sensorimotor integration and addictive behaviours. Other avian sensory and motor systems that are used for cognitive behaviours share a common circuit organization with the auditory and vocal pathways[63,64].

Conclusion

The inaccurate evolution-based terminology for the vertebrate brain that was used throughout the twentieth century became a severe impediment to the communication of scientific discoveries and the generation of new insights. Many of the tenets on which this old view of vertebrate telencephalic evolution was based have been refuted. The problems created by this view and its associated nomenclature have now been rectified for the avian brain with a new terminology that reflects the current understanding of vertebrate brain organization, homologies, evolution and function. This new understanding should facilitate a better assimilation of scientific insights into brain function through the study of birds.

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1. Edinger, L. (Translation from German) *Investigations on the Comparative Anatomy of the Brain* Volumes 1–5 (Moritz Diesterweg, Frankfurt/Main, 1888–1903).
2. Darwin, C. *The Origin of Species* (Murray, 1859).
3. Edinger, L. *The Anatomy of the Central Nervous System of Man and of Vertebrates in General* 5th edn (F. A. Davis Company, Philadelphia, 1896).
4. Edinger, L. The relations of comparative anatomy to comparative psychology. *Comp. Neurol. Psychol.* **18**, 437–457 (1908).
5. Northcutt, R. G. Changing views of brain evolution. *Brain Res. Bull.* **55**, 663–674 (2001).
6. Ariëns Kappers, C. The phylogenesis of the paleo-cortex and archi-cortex compared with the evolution of the visual neo-cortex. *Arch. Neurol. Psychiatry* **4**, 161–173 (1909).

7. Ariëns Kappers, C. The ontogenetic development of the corpus striatum in birds and a comparison with mammals and man. *Proc. Kon. Akad. v. Wetens. te Amsterdam* **26**, 135–158 (1922).
8. Ariëns Kappers, C. Three lectures on neurobiotaxis and other subjects delivered at the University of Copenhagen (Leven and Munksgaard, Copenhagen, 1928).
9. Edinger, L., Wallenberg, A. & Holmes, G. M. Untersuchungen über die vergleichende Anatomie des Gehirns. Das Vorderhirn der Vögel. *Abhandlungen der Senckenbergischen naturforschenden Gesellschaft* **20**, 343–426 (1903).
10. Rose, M. Über die cytoarchitektonische Gliederung des Vorderhirns der Vogel. *J. f. Psychol. Neurol.* **21** (suppl. 1), 278–352 (1914).
11. Holmgren, N. Points of view concerning forebrain morphology in higher vertebrates. *Acta. Zool. Stockh.* **6**, 413–477 (1925).
12. Kuhlenbeck, H. The ontogenetic development and phylogenetic significance of the cortex telencephali in the chick. *J. Comp. Neurol.* **69**, 273–301 (1938).
13. Elliot Smith, G. The term 'archipallium' - a disclaimer. *Anatomischer Anzeiger* **35**, 429–430 (1910).
14. Ariëns Kappers, C. U., Huber, C. G. & Crosby, E. C. *Comparative Anatomy of the Nervous System of Vertebrates, Including Man* (Hafner, New York, 1936).
15. Parent, A. & Olivier, A. Comparative histochemical study of the corpus striatum. *J. Hirnforsch.* **12**, 73–81 (1970).
16. Karten, H. J. in *Comparative and Evolutionary Aspects of the Vertebrate Central Nervous System* (ed. Pertras, J.) 164–179 (1969).
17. Karten, H. J. & Hodos, W. *A Stereotaxic Atlas of the Brain of the Pigeon (Columba livia)* (Johns Hopkins Univ. Press, Baltimore, 1967).
18. Dahlström, A. & Fuxe, K. Evidence for the existence of monoamine-containing neurons in the central nervous system I. Demonstration of monoamines in cell bodies of brainstem neurons. *Acta Physiol. Scand.* **62**, 1–55 (1964).
19. Juorio, A. V. & Vogt, M. Monoamines and their metabolites in the avian brain. *J. Physiol.* **189**, 489–518 (1967).
20. Karten, H. J. & Dubbeldam, J. L. The organization and projections of the paleostriatal complex in the pigeon (*Columba livia*). *J. Comp. Neurol.* **148**, 61–90 (1973).
21. Graybiel, A. M. Neuropeptides in the basal ganglia. *Res. Publ. Assoc. Res. Nerv. Ment. Dis.* **64**, 135–161 (1986).
22. Smeets, W. J. Comparative aspects of basal forebrain organization in vertebrates. *Eur. J. Morphol.* **30**, 23–36 (1992).
23. Steiner, H. & Gerfen, C. R. Role of dynorphin and enkephalin in the regulation of striatal output pathways and behavior. *Exp. Brain Res.* **123**, 60–76 (1998).
24. Reiner, A., Medina, L. & Veenman, C. L. Structural and functional evolution of the basal ganglia in vertebrates. *Brain Res. Brain Res. Rev.* **28**, 235–285 (1998).
25. Jiao, Y. *et al.* Identification of the anterior nucleus of the ansa lenticularis in birds as the homologue of the mammalian subthalamic nucleus. *J. Neurosci.* **20**, 6998–7010 (2000).
26. Graybiel, A. M. The basal ganglia and cognitive pattern generators. *Schizophr. Bull.* **23**, 459–469 (1997).
27. Perkel, D. & Farries, M. Complementary 'bottom-up' and 'top-down' approaches to basal ganglia function. *Curr. Opin. Neurobiol.* **10**, 725–731 (2000).
28. Puelles, L. *et al.* Pallial and subpallial derivatives in the embryonic chick and mouse telencephalon, traced by the expression of the genes *Dlx-2*, *Emx-1*, *Nkx-2.1*, *Pax-6*, and *Tbr-1*. *J. Comp. Neurol.* **424**, 409–438 (2000).
29. Cobos, I., Shimamura, K., Rubenstein, J. L., Martinez, S. & Puelles, L. Fate map of the avian anterior forebrain at the four-somite stage, based on the analysis of quail-chick chimeras. *Dev. Biol.* **239**, 46–67 (2001).
30. Redies, C., Medina, L. & Puelles, L. Cadherin expression by embryonic divisions and derived gray matter structures in the telencephalon of the chicken. *J. Comp. Neurol.* **438**, 253–285 (2001).
31. Marín, O. & Rubenstein, J. L. A long, remarkable journey: tangential migration in the telencephalon. *Nature Rev. Neurosci.* **2**, 780–790 (2001).
32. Veenman, C. L. Pigeon basal ganglia: insights into the neuroanatomy underlying telencephalic sensorimotor processes in birds. *Eur. J. Morphol.* **35**, 220–233 (1997).
33. Sun, Z. & Reiner, A. Localization of dopamine D1A and D1B receptor mRNAs in the forebrain and midbrain of the domestic chick. *J. Chem. Neuroanat.* **19**, 211–224 (2000).
34. Li, X.-C. & Jarvis, E. Sensory- and motor-driven BDNF expression in a vocal communication system. *Soc. Neurosci. Abstr.* 538.8 (2001).
35. Reiner, A., Meade, C. A., Cuthberston, S. L., Laverghetta, A. & Bottjer, S. W. An immunohistochemical and pathway tracing study of the striatopallidal organization of Area X in the zebra finch. *J. Comp. Neurol.* **469**, 239–261 (2004).
36. Wada, K., Sakaguchi, H., Jarvis, E. D. & Hagiwara, M. Differential expression of glutamate receptors in avian neural pathways for learned vocalization. *J. Comp. Neurol.* **476**, 44–64 (2004).
37. Brauth, S. E. & Kitt, C. A. The paleostriatal system of *Caiman crocodilus*. *J. Comp. Neurol.* **189**, 437–465 (1980).
38. Brauth, S. E., Reiner, A., Kitt, C. A. & Karten, H. J. The substance P-containing striatotegmental path in reptiles: an immunohistochemical study. *J. Comp. Neurol.* **219**, 305–327 (1983).
39. Reiner, A., Brauth, S. E. & Karten, H. J. Evolution of the amniote basal ganglia. *Trends Neurosci.* **7**, 320–325 (1984).
40. Smeets, W. J. A. J. *in Phylogeny and Development of Catecholamine Systems in the CNS of Vertebrates* (ed. Smeets, W. J. A. J.) 103–133 (Cambridge Univ. Press, Cambridge, England, 1994).
41. Swanson, L. What is the brain? *Trends Neurosci.* **23**, 519–527 (2000).
42. Reblet, C. *et al.* Neuroepithelial origin of the insular and endopiriform parts of the claustrum. *Brain Res. Bull.* **57**, 495–497 (2002).
43. Zeier, H. & Karten, H. J. The archistriatum of the pigeon: organization of afferent and efferent connections. *Brain Res.* **31**, 313–326 (1971).
44. Karten, H. J. & Shimizu, T. The origins of neocortex: connections and lamination as distinct events in evolution. *J. Cogn. Neurosci.* **1**, 291–301 (1989).
45. Vates, G. E., Broome, B. M., Mello, C. V. & Nottebohm, F. Auditory pathways of caudal telencephalon and their relation to the song system of adult male zebra finches. *J. Comp. Neurol.* **366**, 613–642 (1996).
46. Wild, J. M. The avian somatosensory system: the pathway from wing to Wulst in a passerine (*Chloris chloris*). *Brain Res.* **759**, 122–134 (1997).
47. Shimizu, T. & Hodos, W. Reversal learning in pigeons: effects of selective lesions of the Wulst. *Behav. Neurosci.* **103**, 262–272 (1989).
48. Mello, C. V. & Clayton, D. F. Song-induced *ZENK* gene expression in auditory pathways of songbird brain and its relation to the song control system. *J. Neurosci.* **14**, 6652–6666 (1994).
49. Jarvis, E. D., Mello, C. V. & Nottebohm, F. Associative learning and stimulus novelty influence the song-induced expression of an immediate early gene in the canary forebrain. *Learn. Mem.* **2**, 62–80 (1995).
50. Wild, J. M., Reinke, H. & Farabaugh, S. M. A non-thalamic pathway contributes to a whole body map in the brain of the budgerigar. *Brain Res.* **755**, 137–141 (1997).
51. Laverghetta, A. V. & Shimizu, T. Visual discrimination in the pigeon (*Columba livia*): effects of selective lesions of the nucleus rotundus. *Neuroreport* **10**, 981–985 (1999).
52. Vicario, D. S. Organization of the zebra finch song control system: II. Functional organization of outputs from nucleus robustus archistriatalis. *J. Comp. Neurol.* **309**, 486–494 (1991).
53. Wild, J. M. Descending projections of the songbird nucleus robustus archistriatalis. *J. Comp. Neurol.* **338**, 225–241 (1993).
54. Wild, J. M. & Williams, M. N. Rostral Wulst in passerine birds. I. Origin, course, and terminations of an avian pyramidal tract. *J. Comp. Neurol.* **416**, 429–450 (2000).
55. Nottebohm, F., Stokes, T. M. & Leonard, C. M. Central control of song in the canary, *Serinus canarius*. *J. Comp. Neurol.* **165**, 457–486 (1976).
56. Bottjer, S. W., Miesner, E. A. & Arnold, A. P. Forebrain lesions disrupt development but not maintenance of song in passerine birds. *Science* **224**, 901–903 (1984).
57. Shimizu, T. & Karten, H. J. in *The Neocortex* (ed. Finlay, B. L.) 75–86 (Plenum, New York, 1990).
58. Scharff, C. & Nottebohm, F. A comparative study of the behavioral deficits following lesions of various parts of the zebra finch song system: implications for vocal learning. *J. Neurosci.* **11**, 2896–2913 (1991).
59. Güntürkün, O. in *Neural and Behavioral Plasticity* (ed. Andrew, R. J.) 92–105 (Oxford Univ. Press, Oxford, 1991).
60. Wild, J. M., Karten, H. J. & Frost, B. J. Connections of the auditory forebrain in the pigeon (*Columba livia*). *J. Comp. Neurol.* **337**, 32–62 (1993).
61. Butler, A. B. The evolution of the dorsal pallium in the telencephalon of amniotes: cladistic analysis and a new hypothesis. *Brain Res. Brain Res. Rev.* **19**, 66–101 (1994).
62. Shimizu, T., Cox, K. & Karten, H. J. Intratelencephalic projections of the visual Wulst in pigeons (*Columba livia*). *J. Comp. Neurol.* **359**, 551–572 (1995).
63. Kröner, S. & Güntürkün, O. Afferent and efferent connections of the caudolateral neostriatum in the pigeon (*Columba livia*): A retro- and anterograde pathway tracing study. *J. Comp. Neurol.* **407**, 228–260 (1999).
64. Shimizu, T. & Bowers, A. N. Visual circuits of the avian telencephalon: evolutionary implications. *Behav. Brain Res.* **98**, 183–191 (1999).
65. Brainard, M. & Doupe, A. Interruption of a basal ganglia-forebrain circuit prevents plasticity of learned vocalizations. *Nature* **404**, 762–766 (2000).
66. Knudsen, E. I. Instructed learning in the auditory localization pathway of the barn owl. *Nature* **417**, 322–328 (2002).
67. Mello, C. V. Mapping vocal communication pathways in birds with inducible gene expression. *J. Comp. Physiol. A* **188**, 943–959 (2002).
68. Smith-Fernandez, A. S., Pieau, C., Repérant, J., Boncinelli, E. & Wassef, M. Expression of the *Emx-1* and *Dlx-1* homeobox genes define three molecularly distinct domains in the telencephalon of mouse, chick, turtle and frog embryos: implications for the evolution of telencephalic subdivisions in amniotes. *Development* **125**, 2099–2111 (1998).
69. Medina, L. & Reiner, A. Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends Neurosci.* **23**, 1–12 (2000).
70. Kuenzel, W. J. & Masson, M. *A Stereotaxic Atlas of the Brain of the Chick (Gallus domesticus)* (The Johns Hopkins Univ. Press, Baltimore, 1988).
71. Karten, H. J. Homology and evolutionary origins of the 'neocortex'. *Brain Behav. Evol.* **38**, 264–272 (1991).
72. Mello, C. V. & Clayton, D. F. Differential induction of the *ZENK* gene in the avian forebrain and song control circuit after metrazole-induced depolarization. *J. Neurobiol.* **26**, 145–161 (1995).
73. Dugas-Ford, J. & Ragsdale, C. 23rd Annual J. B. Johnston Club Meeting and 15th Annual Karger Workshop 2003. *Brain Behav. Evol.* 62, 168–174 (2003).
74. Bruce, L. L. & Neary, T. J. The limbic system of tetrapods: a comparative analysis of cortical and amygdalar populations. *Brain Behav. Evol.* **46**, 224–234 (1995).
75. Striedter, G. F. The telencephalon of tetrapods in evolution. *Brain Behav. Evol.* **49**, 179–213 (1997).
76. Bruce, L. L., Kornblum, H. I. & Seroogy, K. B. Comparison of thalamic populations in mammals and birds: expression of ErbB4 mRNA. *Brain Res. Bull.* **57**, 455–461 (2002).
77. Martínez-García, F., Martínez-Marcos, A. & Lanuza, E. The pallial amygdala of amniote vertebrates: evolution of the concept, evolution of the structure. *Brain Res. Bull.* **57**, 463–469 (2002).
78. Haesler, S. *et al. FoxP2* expression in avian vocal learners and non-learners. *J. Neurosci.* **24**, 3164–3175 (2004).
79. Gorski, J. A. *et al.* Cortical excitatory neurons and glia, but not GABAergic neurons, are produced in the Emx1-expressing lineage. *J. Neurosci.* **22**, 6309–6314 (2002).
80. Butler, A. B., Molnár, Z. & Manger, P. R. Apparent absence of claustrum in monotremes: implications for forebrain evolution in amniotes. *Brain Behav. Evol.* **60**, 230–240 (2002).
81. Ashwell, K. W., Hardman, C. & Paxinos, G. The claustrum is not missing from all monotreme brains. *Brain Behav. Evol.* **64**, 223–241 (2004).
82. Reiner, A. *et al.* Revised nomenclature for avian telencephalon and some related brainstem nuclei. *J. Comp. Neurol.* **473**, 377–414 (2004).
83. Reiner, A. *et al.* The Avian Brain Nomenclature Forum: a new century in comparative neuroanatomy. *J. Comp. Neurol.* **473**, E1–E6 (2004).
84. Reiner, A. J. A hypothesis as to the organization of cerebral cortex in the common amniote ancestor of modern reptiles and mammals. *Novartis Found. Symp.* **228**, 83–102; discussion 102–113 (2000).
85. Carroll, R. L. in *Vertebrate Paleontology and Evolution* 1–13 (W. H. Freeman, New York, 1988).
86. Evans, S. E. in *Evolutionary Developmental Biology of the Cerebral Cortex* (eds Bock, G. R. & Cardew, G.) 109–113 (John Wiley & Sons, Chichester, 2000).
87. Northcutt, R. G. & Kaas, J. H. The emergence and evolution of mammalian neocortex. *Trends Neurosci.* **18**, 373–379 (1995).
88. Northcutt, R. G. Visual pathways in elasmobranchs: organization and phylogenetic implications. *J. Exp. Zool. Suppl.* **5**, 97–107 (1990).
89. Suzuki, W. A. & Clayton, N. S. The hippocampus and memory: a comparative and ethological perspective. *Curr. Opin. Neurobiol.* **10**, 768–773 (2000).

90. Rodríguez, F. *et al.* Spatial memory and hippocampal pallium through vertebrate evolution: insights from reptiles and teleost fish. *Brain Res. Bull.* **57**, 499–503 (2002).
91. Marler, P. Characteristics of some animals calls. *Nature* **176**, 6–8 (1955).
92. Thorpe, W. H. The learning of song patterns by birds, with special reference to the song of the chaffinch, *Fringilla coelebs*. *Ibis* **100**, 535–570 (1958).
93. von Fersen, L. & Delius, J. D. Long-term retention of many visual patterns by pigeons. *Ethology* **82**, 141–155 (1989).
94. Lubow, R. E. High-order concept formation in the pigeon. *J. Exp. Anal. Behav.* **21**, 475–483 (1974).
95. Watanabe, S., Sakamoto, J. & Wakita, M. Pigeons' discrimination of paintings by Monet and Picasso. *J. Exp. Anal. Behav.* **63**, 165–174 (1995).
96. Lubinski, D. & MacCorquodale, K. 'Symbolic communication' between two pigeons (*Columba livia*) without unconditioned reinforcement. *J. Comp. Psychol.* **98**, 372–380 (1984).
97. von Fersen, L., Wynne, C. D. L., Delius, J. D. & Staddon, J. E. R. Transitive inference formation in pigeons. *J. Exp. Psychol. Anim. Behav. Process.* **17**, 334–341 (1992).
98. Lanza, R. P., Starr, J. & Skinner, B. F. 'Lying' in the pigeon. *J. Exp. Anal. Behav.* **38**, 201–203 (1982).
99. Munn, C. Birds that cry 'wolf'. *Nature* **319**, 143–145 (1986).
100. Weir, A. A., Chappell, J. & Kacelnik, A. Shaping of hooks in New Caledonian crows. *Science* **297**, 981 (2002).
101. Hunt, G. R. & Gray, R. D. Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proc. R. Soc. Lond. B* **270**, 867–874 (2003).
102. Pollok, B., Prior, H. & Güntürkün, O. Development of object-permanence in the food-storing magpie (*Pica pica*). *J. Comp. Psychol.* **114**, 148–157 (2000).
103. Clayton, N. S. & Dickinson, A. Episodic-like memory during cache recovery by scrub jays. *Nature* **395**, 272–274 (1998).
104. Emery, N. J. & Clayton, N. S. Effects of experience and social context on prospective caching strategies by scrub jays. *Nature* **414**, 443–446 (2001).
105. Jarvis, E. D. *et al.* Behaviourally driven gene expression reveals song nuclei in hummingbird brain. *Nature* **406**, 628–632 (2000).
106. Jarvis, E. D. Learned birdsong and the neurobiology of human language. *Ann. NY Acad. Sci.* **1016**, 749–777 (2004).
107. Pepperberg, I. in *The Alex Studies: Cognitive and Communicative Abilities of Grey Parrots* 96–167 (Harvard Univ. Press, Cambridge, Massachusetts, 1999).
108. Pepperberg, I. M. & Shive, H. R. Simultaneous development of vocal and physical object combinations by a Grey Parrot (*Psittacus erithacus*): bottle caps, lids, and labels. *J. Comp. Pyschol.* **115**, 376–384 (2001).
109. Gazzaniga, M. S. (ed.) *The New Cognitive Neurosciences* (MIT Press, Cambridge, Massachusetts, 1999).
110. Delius, J. D. & Hollard, V. D. Orientation invariance of shape recognition in forebrain-lesioned pigeons. *Behav. Brain Res.* **23**, 251–259 (1987).
111. Lavenex, P. B. Lesions in the budgerigar vocal control nucleus NLc affect production, but not memory, of English words and natural vocalizations. *J. Comp. Neurol.* **421**, 437–460 (2000).
112. Van Essen, D. A tension-based theory of morphophogenesis and compact wiring in the central nervous system. *Nature* **385**, 313–318 (1997).
113. Striedter, G. F. in *Principles of Brain Evolution* 345–361 (Sinuaer Associates, Massachusetts, 2004).
114. Bottjer, S. W. & Johnson, F. Circuits, hormones, and learning: vocal behavior in songbirds. *J. Neurobiol.* **33**, 602–618 (1997).

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Competing interests statement
The authors declare no competing financial interests.

Online links

DATABASES
The following terms in this article are linked online to:
Entrez Gene:
http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=gene
BDNF | *DLX1* | *DLX2* | *EAG2* | *EMX1* | *ENK* | *ER81* | *GluR1* | *mGluR2* | *NKX2.1* | *PAX6* | *ROR-β* | SP | *TBR1* | *ZENK*

FURTHER INFORMATION
Avian Brain Nomenclature Exchange web site:
http://avianbrain.org/
Digital Anatomist Project:
http://www9.biostr.washington.edu/da.html
Access to this interactive links box is free online.

SCIENCE AND SOCIETY

fMRI in the public eye

Eric Racine, Ofek Bar-Ilan and Judy Illes

Abstract | The wide dissemination and expanding applications of functional MRI have not escaped the attention of the media or discussion in the wider public arena. From the bench to the bedside, this technology has introduced substantial ethical challenges. Are the boundaries of what it can and cannot achieve being communicated to the public? Are its limitations understood? And given the complexities that are inherent to neuroscience, are current avenues for communication adequate?

Functional neuroimaging techniques, such as functional MRI (fMRI) and positron emission tomography (PET), have evolved as key research approaches to studying both disease processes and the basic physiology of cognitive phenomena in contemporary neuroscience. In the clinical domain, they carry hope for guiding neurosurgical mapping, monitoring drug development and providing new approaches to disease diagnosis and management at early, possibly even presymptomatic stages. However, issues relating to these capabilities, such as technical readiness and the possibility of disease screening in advance of effective therapeutic intervention, raise substantial ethical challenges for investigators, health care providers and patients alike. In basic neuroscience, increasing numbers of non-health-related fMRI studies that touch on our personal values and beliefs have also forced us to expand our ethical perspectives[1]. The wide dissemination of this research, growing applications of the technology and continuously improving resolution have not escaped the attention of the neuroscience and neuroethics communities, the media or the broader public[2–6]. However, are the boundaries of what this technology can and cannot achieve being effectively communicated to the public? Are its limitations understood? Are the applications of the technology viewed as useful and meaningful? Are some studies more conducive to misinterpretation than others? What are the associated risks to society? From a scientific perspective, important methodological and technical assumptions guide fMRI research. However, from the public's point of view, once research results are publicized, especially when they concern personality, self-identity and other social constructs, they are bound to interact with lay conceptions of these phenomena.

To understand this complex interaction between neuroscience and society, we focused on the coverage of fMRI — as one model of frontier neurotechnology — in the print press. We investigated how both neuroscience and the media shape the social understanding of fundamental aspects of our reality and how this, in turn, points to issues of scientific communication and public involvement in neuroscience. To this end, we frame our arguments according to three trends that we have observed in press coverage of fMRI — 'neuro-realism', 'neuro-essentialism' and 'neuro-policy' — and explore how neuroethics can attend to the related ethical, legal and social issues by promoting multidirectional communication in neuroscience.

fMRI in the public eye

The increasing investigation of cognitive and social phenomena using fMRI[1] represents a relatively new venture for neuroscience. Neuroscientists who pursue such research hope for new insights into behaviour, culture and personality. However, they face new challenges in trying to convey this knowledge meaningfully to the public. Journalists, from their purview, must report these results in an adapted communication style that differs from scientific communication and adheres to a separate set of standards[7]. This creates a context in which the wider significance of research results and efforts for public outreach intermingle with the reporting of neuroscientific findings.

To understand this context specifically in relation to neuroimaging, and to launch a discussion of these issues, we carried out a press content analysis[8] of samples of print media coverage of fMRI. Using this method, we were able to capture salient messages about the research as they are conveyed to readers.