Avian brain nomenclature change

Monika Sadananda

The century-old nomenclature that was used to denote regions of the bird brain was based on wrong assumptions of homology to mammalian brain regions. The traditional view held that most of the avian forebrain (cerebrum/telencephalon) was predominantly made of parts of the basal ganglia with only a small part in the roof of the forebrain constituting a cortical pallium (Figure 1 *a*). Edinger[1], father of comparative neuroanatomy, noted that brain evolution from fishes through mammals followed a chronological order: basic brain structures such as the spinal cord, hindbrain, midbrain, thalamus, cerebellum and cerebrum occurred in all, with cerebral structures being progressively added in a step-wise manner resulting in a correspondingly increased encephalization. Thus 'primitive' cerebral fish structures were found in all higher vertebrates, while newer cerebral structures were added in amphibians, reptiles, birds and mammals.

The forebrain of stem reptiles, the amniotic ancestor of both birds and mammals, was said to consist of a meagre cortical mantle called the pallium, and a disproportionately large basal ganglia. In mammals, the former evolved to become the enormously hypertrophied and elaborate multi-layered neocortex (Figure 1 *b*), responsible for complex behaviour such as learning and memory. In birds, however, the latter structure became the large-sized and complex basal ganglia (Figure 1 *a*), thought to be important for instinctive behaviour. The avian forebrain was accordingly classified[2] into regions with the suffix 'striatum', indicating 'striatal' nature. The avian cerebrum constitutes five main regions: the paleostriatum, archistriatum, neostriatum hyperstriatum and ectostriatum (Figure 1 *a*). Only the dorsal-most part of the hyperstriatum constituted the pallium. All the other structures were considered homologous to the mammalian basal ganglia (Figure 1 *a*). The 'paleo' (oldest) striatum was found in fishes, the 'archi' (archaic) striatum was added in amphibians, the 'neo' (new) striatum was a reptilian structure, while 'hyper'(above) and 'ecto'(outside), were exclusively bird structures.

A name for a particular brain area denotes origin, type, identity, function and relationality to other brain areas. Bird neuroscience suffered under the bane of erroneous naming of brain regions for about a century. Preliminary research on the avian cerebrum soon made it clear that only the ventral part is striatal in nature. Evidence proving that the dorsal regions which made most of the cerebrum are in fact responsible for complex learning-related behaviour and not just instinctive, stereotyped, vegetative behaviour, made nomenclature change imminent. For over five decades now, research in bird brain and behaviour using behavioural, lesion-behavioural, hodological and neurochemical methods has not only made it clear that birds are in no way inferior to mammals, but has also disproved that most of the avian cerebrum is only the basal ganglia, and shown that major parts are indeed comparable to the mammalian cortex, claustrum and amygdala.

Neurochemical studies screening for neuronal enzymes and neurotransmitter profiles showed that only the medial and lateral parts of the paleostriatum are striatal in nature (Figure 2 *a*), and suggested that the neostriatum, ectostriatum and hyperstriatum are cortical in nature[3]. Subsequent studies profiling neuropeptides, and developmental studies using homeobox genes and transcription factors showed that ventral parts of the paleostriatum (paleostriatum primitivum and ventral paleostriatum) develop from the subpallium and are comparable to mammalian sub-pallial, pallidal structures: globus pallidus and ventral pallidum respectively (Figure 2 *a*, *b*)[4]. Pathway-tracing studies revealed discrete brain nuclei in the neostriatum, ectostriatum and hyperstriatum in birds where visual, auditory and somatosensory inputs from the brain stem terminate (Figure 2 *a*), comparable to layers of the cortex (Figure 2 *b*) in mammals[5]. Instead of the layered cortical organization seen in mammals, birds have a nuclear organization of sensory processing centres.

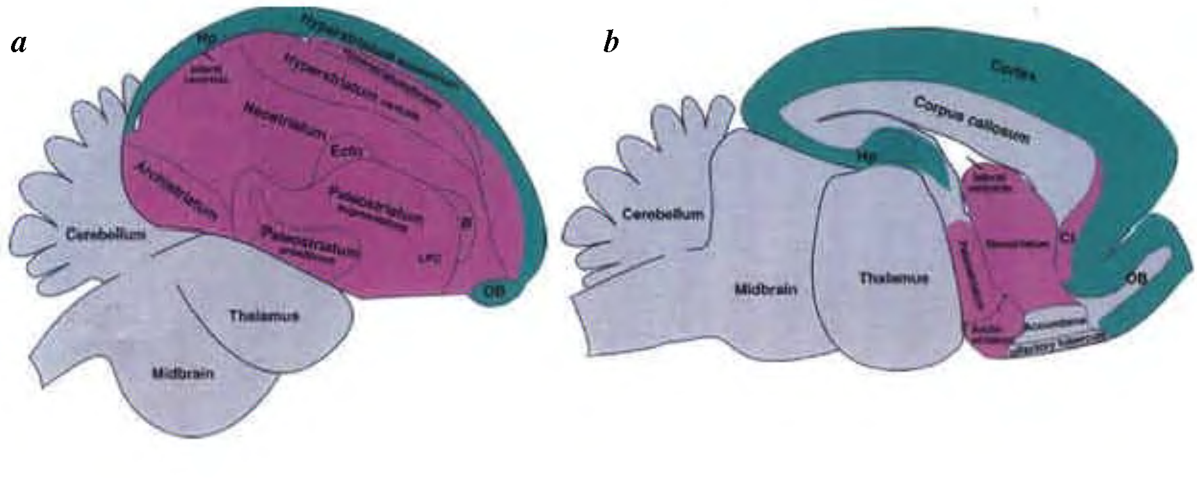

Figure 1. Historical view of brain organization in bird (***a***) and mammal (***b***). Most of the avian forebrain (purple in ***a***) was considered similar to the mammalian striatum (purple in ***b***). Only the hyperstriatum accessorium (green in ***a***) was considered equivalent to the cortex (green in ***b***). B, Basorostral nucleus; Cl, Claustrum; Ecto, Ectostriatum; Hp, Hippocampus; LPO, Lobus parolfactorious and OB, Olfactory bulb.

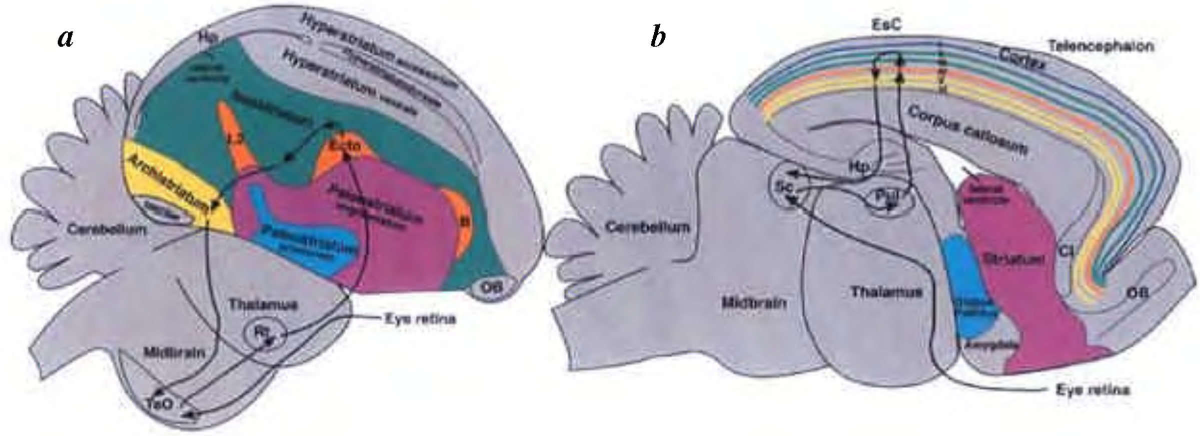

Figure 2. Pathway tracing studies and neurochemical studies in both birds (***a***) and mammals (***b***) showed that only the paleostriatum augmentatum (purple) is equivalent to the mammalian striatum (purple), while paleostriatum primitivum (light blue) is homologous to globus pallidus (light blue), and parts of the neostriatum, ectostriatum, archistriatum and hyperstriatum are comparable to layers of the cortex (yellow, green). The circuitry shown is that of a homologous visual pathway in both birds (***a***) and mammals (***b***). EsC, Extrastriate cortex; Pul, Pulvinar; Rt, Rotundus; Sc, Superior colliculus; TeO, Optic tectum.

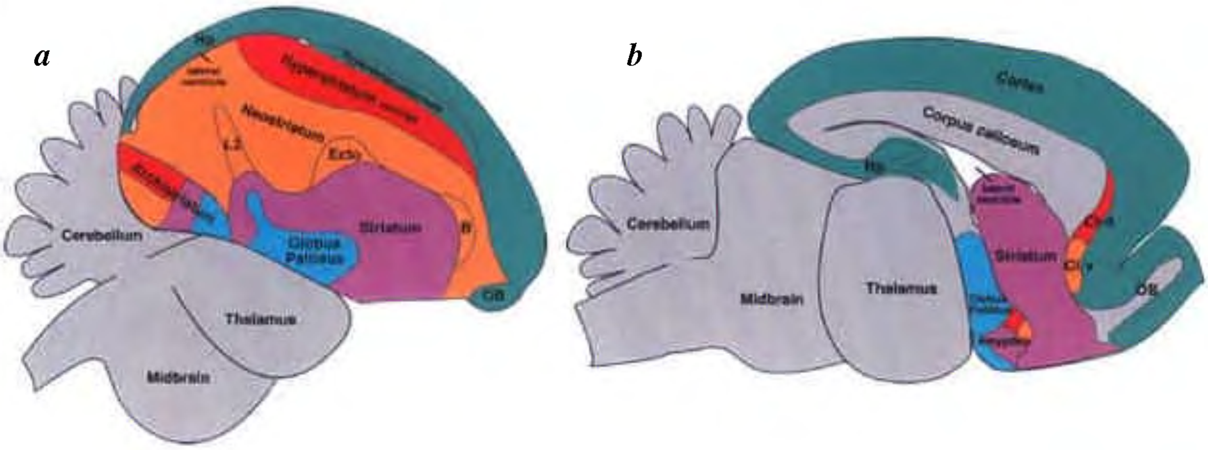

Figure 3. Developmental gene marker distribution in both bird (***a***) and mammal (***b***) showed that avian forebrain regions hyperstriatum ventrale, neostriatum, and parts of the archistriatum (***a***) are an extension of, and are comparable to the mammalian claustrum-amygdala (***b***). Hyperstriatum ventrale is similar to dorsal claustrum (red), while neostriatum is similar to ventral claustrum (orange), and parts of archistriatum are comparable to mammalian amygdala. Cl-d, Dorsal claustrum; Cl-v, Ventral claustrum. All figures from the Avian Brain Nomenclature Forum, courtesy Erich Jarvis.

The same molecular embryological studies[4] also showed that the hyperstriatum, neostriatum and archistriatum, which form major chunks of the avian cerebrum and stain positively for pallial-specific transcription factors Emx-1, Pax-6 and Tbr-1, arise from the developing pallium. The hyperstriatum ventrale and neostriatum are comparable to the dorsal and ventral claustrum respectively, while parts of the archistriatum are similar to the mammalian amygdala (Figure 3 *a*, *b*). The other parts of the archistriatum form descending pre-motor and motor pathways by extending extratelencephalic projection neurons, are sensory in nature and involved in sensori-motor learning.

Today we know that birds evolved independent of, and ~ 50–100 million years after mammals, and have evolved cognitive abilities that are far more complex than in many mammals. Thus, the ‘neo’ cortex thought to be an exclusively mammalian entity required for malleable, complex behaviours to adapt to their environments, is in fact an ‘old’ structure. Birds are not impoverished in their adaptive learning skills, but are able, through learning and memory to vocalize, learn human or other birds’ vocalization and respond[6], something unrivalled by any species in the animal kingdom, save cetaceans and humans themselves[7]. They are also able to remember thousands of food-caches, demonstrate episodic memory[8], make and use tools[9], and memorize and categorize objects and visual patterns, to mention just a few of the enormously complex forms of behaviour requiring a networking on par with that of the mammalian cortex to carry them off.

The need for rectification of such a grossly erroneous nomenclature led to deliberations that began in 1997. In 2000 a group of 28 international (from seven countries) avian brain scientists formed a forum to look into the issues and recommended changes in 2002. The scientific results along with detailed tables of changes to nomenclature which were published in a mega publication in the *Journal of Comparative Neurology*[10] in 2004, were followed by a more homology-based one in *Nature Reviews Neuroscience*[11] in 2005. The latter caused quite a few ripples in Europe and the United States, with lay people's articles appearing in the *New York Times*, *Guardian*, *Washington Post*, MSNBC, ABC, and being carried on the front pages of Yahoo and CNN, Reuters, and other international and small town newspapers. Many from the group were interviewed on various local and international television channels such as BBC, etc.[12–17].

The salient features of the revision include changes to glaringly wrong and misleading nomenclature that were urgently required and re-naming of certain regions in relation to homology with a rationale behind each change. Only the striatal parts of the paleostriatum are now called the medial and lateral striatum, as is appropriate. The pallidal parts of the paleostriatum are called globus pallidus and ventral pallidum. The pallial regions, hyperstriatum, neostriatum, ectostriatum and archistriatum, are now aptly termed hyperpallium, nidopallium, entopallium and arcopallium respectively. Limbic parts of the archistriatum that correspond to parts of the mammalian amygdala have been named accordingly.

However, names of other regions such as the hippocampus, olfactory cortex and olfactory bulb that are uncontroversial, remain unchanged. Various telencephalic and brainstem nuclei misnomers have been changed, denoting more precisely their neurochemical nature, affiliation to a particular brain region or system, and proven homology to mammalian brain nuclei. Names of telencephalic laminae and fibre tracts have also been changed to reflect current understanding. Efforts have been made to retain, wherever possible, the old, familiar abbreviations for the newer Latin terms in order to retain continuity with the innumerable bird brain publications of the past.

With regard to functional organization and evolution of the avian and mammalian forebrain, particularly of the pallial regions, as of now, two hypotheses[18] exist. Results from pathway-tracing studies led to the nuclear-to-layered hypothesis. The discrete nuclei in the avian pallium where somatosensory (basorostral nucleus B in Figure 2 *a*), auditory (auditory centre L2 in Figure 2 *a*) and visual (Ecto in Figure 2 *a*) inputs terminate, are comparable to the primary somatosensory, auditory and visual (extrastriate) cortices, with adjacent parts (green and yellow regions in Figure 2 *a*) being comparable to layers II, III, V and VI of the mammalian cortex (Figure 2 *b*). The newer nuclear-to-claustrum/amygdalar hypothesis that arose mainly from results of developmental gene marker studies, postulates that major parts of the avian pallium are an elaboration of the mammalian amygdala and claustrum (Figure 3 *a*, *b*).

With this nomenclature change, avian brain researchers can now be better understood by their mammalian counterparts, leading to a more fruitful interaction in comparative neurobiology. Besides the goal of promoting better understanding among comparative neurobiologists, changes to brain nomenclature make bird results more accessible and acceptable to mammalian neuroscientists, and rectify a century of misunderstanding of the functional organization of the brain of birds and their evolutionary relationship to mammals.

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Monika Sadananda is in the Department of Applied Zoology, Mangalore University, Mangalagangothri 574 199, India
e-mail: monika@vasnet.co.in