Songbirds and the Revised Avian Brain Nomenclature

ANTON REINER,[a] DAVID J. PERKEL,[b] CLAUDIO V. MELLO,[c] AND ERICH D. JARVIS[d]

[a]*Department of Anatomy and Neurobiology, University of Tennessee Health Science Center, Memphis, Tennessee 38163, USA*

[b]*Departments of Biology and Otolaryngology, University of Washington, Seattle, Washington 98195-6515, USA*

[c]*Neurological Sciences Institute, Oregon Health and Science University, Beaverton, Oregon 97006-3499, USA*

[d]*Department of Neurobiology, Duke University Medical Center, Box 3209, Durham, North Carolina 27710, USA*

ABSTRACT: It has become increasingly clear that the standard nomenclature for many telencephalic and related brainstem structures of the avian brain is based on flawed once-held assumptions of homology to mammalian brain structures, greatly hindering functional comparisons between avian and mammalian brains. This has become especially problematic for those researchers studying the neurobiology of birdsong, the largest single group within the avian neuroscience community. To deal with the many communication problems this has caused among researchers specializing in different vertebrate classes, the Avian Brain Nomenclature Forum, held at Duke University from July 18–20, 2002, set out to develop a new terminology for the avian telencephalon and some allied brainstem cell groups. In one major step, the erroneous conception that the avian telencephalon consists mainly of a hypertrophied basal ganglia has been purged from the telencephalic terminology, and the actual parts of the basal ganglia and its brainstem afferent cell groups have been given new names to reflect their now-evident homologies. The telencephalic regions that were incorrectly named to reflect presumed homology to mammalian basal ganglia have been renamed as parts of the pallium. The prefixes used for the new names for the pallial subdivisions have retained most established abbreviations, in an effort to maintain continuity with the pre-existing nomenclature. Here we present a brief synopsis of the inaccuracies in the old nomenclature, a summary of the nomenclature changes, and details of changes for specific songbird vocal and auditory nuclei. We believe this new terminology will promote more accurate understanding of the broader neurobiological implications of song control mechanisms and facilitate the productive exchange of information between researchers studying avian and mammalian systems.

Address for correspondence: Anton Reiner, Department of Anatomy and Neurobiology, University of Tennessee Health Science Center, Memphis, Tennessee 38163, USA. Voice: 901-448-8298; fax: 901-448-7193.

areiner@utmem.edu; <http://cns.utmem.edu/faculty/Reiner/Reiner_cv.html>

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A BRIEF HISTORY OF AVIAN TELENCEPHALIC NOMENCLATURE

The advent of improved techniques for cutting and staining brain tissue resulted in a wealth of new knowledge on brain structure in various vertebrate species at the turn of the 19th century and the beginning of the 20th century.[1] Based on his interpretation of such material, Ludwig Edinger formulated a theory of cerebral evolution[2–4] that, as further developed by his colleague C.U. Ariëns-Kappers[5,6] and subsequently refined and widely promulgated in Ariëns-Kappers and colleagues,[7] became the dominant view, and led to an avian telencephalic nomenclature that has continued to be used into the early years of the 21st century (FIG. 1A). According to this view, birds and mammals inherited from their fish ancestors, via the fish to amphibian to reptile lineage, an old basal ganglia structure that was called the paleostriatum (old striatum; corresponding largely to the globus pallidus of mammals), and a newer structure from their reptilian ancestors that Ariëns-Kappers called the neostriatum (new striatum; including most of the caudate and putamen in mammals). Reptiles were thought to have elaborated the paleostriatum further into two distinct parts, one Ariëns-Kappers called the paleostriatum primitivum (comparable to a primitive mammalian globus pallidus) and another part he called the paleostriatum augmentatum (i.e., an augmentation of globus pallidus), and both subdivisions were assumed to have been passed onto birds. Similarly, the neostriatum was also thought to have become enlarged in birds and to have given rise to a novel overlying territory that Edinger and colleagues[3] and Ariëns-Kappers[5,6] called the hyperstriatum, in the be-

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FIGURE 1. (**A**) Classical view of avian and mammalian brain relationships according to the historical nomenclature. Although past authors had differing opinions as to which brain regions are part of the pallium versus subpallium, the images are color-coded according to the meaning of the actual names given to these brain regions. *White lines* represent laminae, cell-sparse regions separating brain subdivisions. *Large white areas* in the human cerebrum are the fibers bundles making up the white matter. *Dashed lines* divide regions that differ by cytoarchitecture. The abbreviations PA and LPO designate regions as defined by Karten and Hodos,[16] while the spelled-out term paleostriatum augmentatum designates this entire area as defined by Ariëns-Kappers, Huber and Crosby.[7] (**B**) Modern view of avian and mammalian brain relationships according to the new nomenclature. In birds, the lateral ventricle is located in the dorsal part of the pallium, whereas in mammals much of the ventricle is located near the border of the pallium with the subpallium. ABBREVIATIONS, classical view: Ac=accumbens; Ap=posterior archistriatum; 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; HIS=hyperstriatum intercalatum superior; HD=hyperstriatum dorsale; HV=hyperstriatum ventrale; L2=field L2, LPO=lobus parolfactorius, OB=olfactory bulb; PA=paleostriatum augmentatum; Pt=putamen; Tn=nucleus taeniae. ABBREVIATIONS, modern view where different from panel **A**: E=entopallium; B=basorostralis; HA=hyperpallium apicale; HI=hyperpallium intercalatum; HD=hyperpallium densocellulare; Hp=hippocampus; LSt=lateral striatum; MSt=medial striatum; PoA=posterior pallial amygdala; TnA=nucleus taeniae of the amygdala; SpA=subpallial amygdala. (Figure adapted from Jarvis and colleagues.[40])

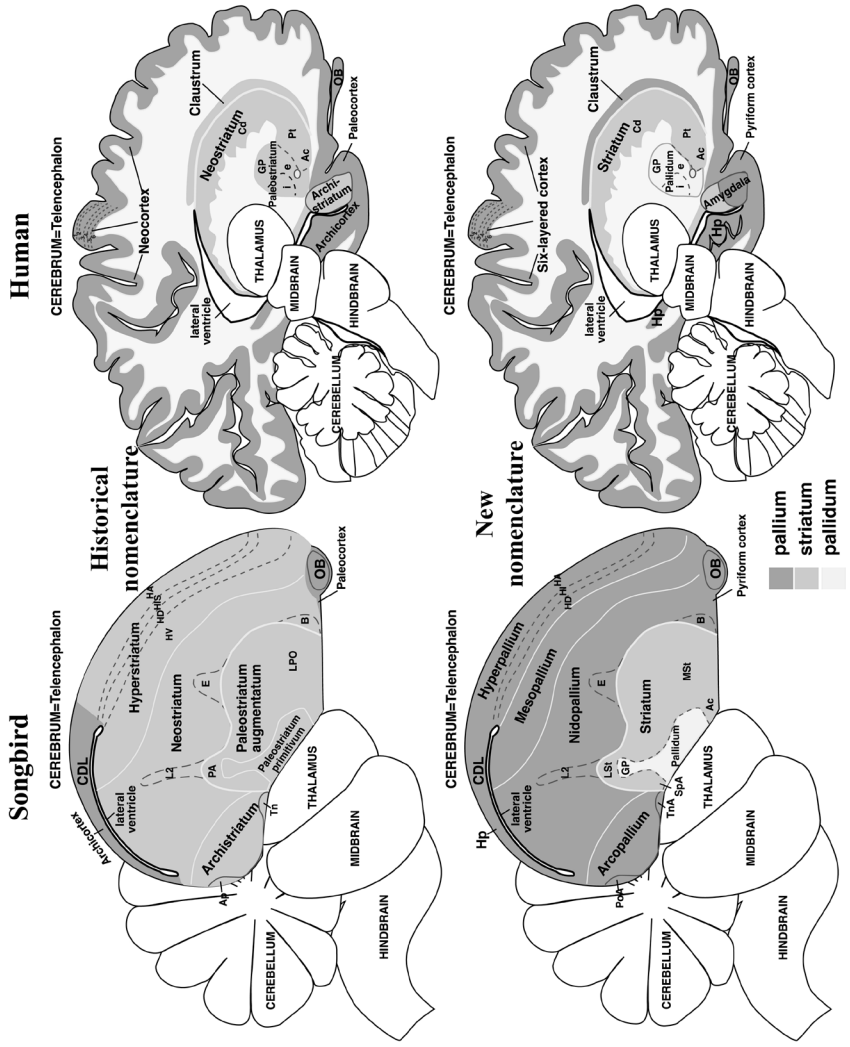

FIGURE 1. *See previous page for legend.*

lief that it was entirely "striatal" in nature and a hypertrophy of the neostriatum. Thus by this view, the avian telencephalon was thought to consist nearly entirely of an enlarged basal ganglia (i.e., what are now commonly called caudate, putamen, and globus pallidus in mammals; FIG. 1A). Finally, mammals, birds, and reptiles were also thought to have inherited an additional subcortical structure that Edinger and Ariëns-Kappers called the archistriatum (in the belief that it was also part of the basal ganglia) from their amphibian ancestors. This brain region in mammals is now called the amygdala, and it is no longer commonly regarded as part of the basal ganglia.

In contrast to the basal ganglia expansion thought to characterize birds, mammals were thought to have expanded the upper, outer part of the telencephalon (the pallium) into a six-layered cortex from a small dorsal cortical region present in the reptile ancestors of mammals.[2–6,8] The novel cortical region in mammals was referred to as neocortex, to distinguish it from the presumed older cortices represented by the olfactory cortex (which they called paleocortex) and hippocampus (which they called archicortex). Ariëns-Kappers and colleagues[7] slightly modified the position of Ariëns-Kappers' earlier works by concluding that a small upper part of the hyperstriatum (largely corresponding to what we now call the Wulst) provided birds with a meager pallial territory comparable to mammalian neocortex. Nonetheless, the view espoused by Ariëns-Kappers and colleagues[7] and by other influential authors[9–12] was that the avian telencephalon consisted mainly of greatly expanded basal ganglia. Except for a dissenting minority,[13–15] this accretionary theory of vertebrate brain evolution became the prevailing view for the first two-thirds of the 20th century. This led to the predominant use of the terms neostriatum, archistriatum, and hyperstriatum to refer to the major sectors of the avian telencephalon above the so-called paleostriatum. The Ariëns-Kappers terminology for the avian telencephalon was, thus, already the most commonly used at the time that Karten and Hodos constructed the first stereotaxic atlas of an avian brain.[16] Although they were aware of possible inaccuracies in this nomenclature, they felt compelled to adopt it because it was entrenched. As a consequence, the Ariëns-Kappers terminology became the standard telencephalic nomenclature for the avian telencephalon.

As neurobiologists have gained deeper insights into the evolution, development, and function of avian and mammalian brains, it has become clear that the accretionary theory of vertebrate telencephalic evolution is incorrect.[1,17–19] Being flawed, the homologies implied by the classical nomenclature have greatly hindered communication between avian and mammalian brain specialists by perpetuating the view that the telencephalon in birds differs qualitatively in structure and function from that in mammals. In particular, the presumed necessity of neocortex for adaptive behavior and higher order cognition[12] and the presumed absence of neocortex in birds have continued to make many believe that birds are incapable of such behavioral abilities. Since the basal ganglia were thought to control instinctive motor behavior and the avian telencephalon was thought to be largely a hypertrophied basal ganglia, all complex behavior in birds had widely been thought to be instinctive.[4,12] As a result of the misconceptions abetted by the Ariëns-Kappers–based terminology, the relevance of the many findings on the avian brain to understanding the functioning of the mammalian brain has been obscured. It is now, however, evident that birds are not uniformly impoverished in their adaptive learning skills. Songbirds, parrots, and hummingbirds show vocal learning abilities not paralleled by any mammals other than humans and cetaceans.[20–25] Crows, members of the oscine songbird family,

show the ability to make and use tools,[26,27] and parrots are capable of learning to communicate with human words and show cognitive skills otherwise evident only in apes and cetaceans among nonhuman species.[23] In parallel with the growing awareness of avian behavioral sophistication, it has become clear that the neural substrate for such behavior is not a hypertrophied basal ganglia but the same general brain region used for such tasks as in mammals (i.e., the pallium), albeit without the laminar morphology characteristic of mammalian neocortex, in combination with a basal ganglia region of the same general size as in mammals.[25,28–35]

While research on all avian species was affected by the outdated terminology for the avian telencephalon, the confusion was especially acute for those studying songbirds, for two major reasons. First, researchers on song control mechanisms now constitute the largest single group within the avian brain research community. Secondly, several major cell groups involved in song perception, learning, or production are located within the part of the brain that in birds has been called the neostriatum. These findings have been habitually misinterpreted by researchers on the mammalian brain, for whom the term "neostriatum" refers to part of the basal ganglia, as pertaining to the functioning of the basal ganglia. This has been the case regardless of the efforts of songbird researchers to provide disclaimers about the use of the term "neostriatum" in birds. A revision in terminology thus is of particular importance for those studying the neural basis of song control.

To address the problems inherent to the old terminology, formal efforts to revise avian brain nomenclature were begun in 1997 by a small group of avian brain specialists, who then sought to involve a more broadly representative group of researchers than had participated in two previous attempts to standardize avian neuroanatomical terms.[36,37] This process culminated in an open Avian Brain Nomenclature Forum, held July 18–20, 2002 at Duke University in Durham, North Carolina, at which an international and multidisciplinary group of neuroscientists adopted a new terminology by consensus. This chapter presents a summary of the decisions made by the Forum, the basic rationale for the revision or retention of existing names (FIG. 1B), and the recommendations relevant to birdsong vocal and auditory nuclei (FIG. 2 and TABLE 1). In the new terminology, the Forum was attentive to the impact of a drastic change in names of pallial structures on continuity in the literature on song control and to the benefits accruing from a more homology-accurate nomenclature than has existed. A full account of the mechanics of the Forum, a description of all structures whose names have been changed, detailed discussions of the evidence, an explanation of the significance of the new nomenclature for understanding vertebrate brain evolution, and a summary of the implications for understanding brain mechanisms of cognition in birds are available[38–40] and a collection of satellite papers is in preparation.[41–47]

NOMENCLATURE AND THE PROBLEM OF HOMOLOGY

Several detailed reviews[18,48–51] address the theoretical issues surrounding the identification of homologous forebrain structures between birds and mammals. It is valuable for the current chapter to define what is meant by homology, and equally importantly, what is not meant. As commonly used in biology, structures in two or more species are considered to be homologous if they are thought to derive from the

same antecedent structure in their common ancestor.[48] Major difficulties arise, however, in identifying homologous brain structures because brain, being a soft tissue, does not fossilize in sufficient detail to make it possible to use the fossil record to trace the natural history of given brain structures. The only remaining approach that can be taken is comparing a variety of features of the structures in question in extant species, including embryological origin, location within the adult brain, afferent and efferent connections, and neurochemical phenotype. In the simplest case, if candidate avian and mammalian homologues (to use sample groups of present interest) arise from the same developmental primordium and have similar adult features and if a similar structure is found in extant reptiles, then a convincing case can be made that the stem amniote common ancestor had an equivalent structure. If, on the other hand, the structures are dissimilar in birds and mammals and/or a comparable structure is not evident in living reptiles, then the compared structures in birds and mammals cannot be said to be demonstrably homologous. It also cannot be automatically said with authority, however, that two morphologically dissimilar structures in birds and mammals are not homologous, since homologous structures can evolve different morphologies.[48] Nonetheless, if the dissimilarities are numerous and living reptiles clearly lack a structure resembling either the compared structure in mammals or the compared structure in birds, then the conclusion that the compared structures in birds and mammals are not homologous is the most likely interpretation.

Terms, such as "analogous," "functionally analogous," or "functionally homologous" have also been used in comparing brain structures. The first two terms mean the same and refer to a circumstance in which structures in different species perform the same function (e.g., bird wings and insect wings), even if they are morphologically different and have evolved independently.[48,52–54] "Analogous" would be the appropriate word to use in this context, and some authors consider the term only to refer to structures of the same function that are independently evolved.[48,52] Note that bat wings and bird wings are analogous as wings but not homologous, since the wings subserve flight in both but the wingedness of the forelimbs was independently evolved. Nonetheless, the forelimbs of bats and birds are homologous as forelimbs, since both inherited their forelimbs from their stem amniote common ancestor. The term "functionally analogous" is redundant with the term "analogous," the latter already implying a functional comparison. The term "functionally homologous" can be ambiguous, meant either as a synonym for analogous (which would be an incorrect use of the word homologous) or to suggest a common origin of a function in two or more species from a function in the common ancestor. The latter misapplies a term commonly used to refer to common ancestry of a morphological entity, i.e., "homologous," to a functional context. The complexities of trying to identify homology at the functional level have been discussed by others.[53,55–57]

Two uses of the term homology by the nomenclature revision effort are one-to-one homology and field homology. In most instances, the term homology is applied to specific structures, such as the humerus of a mouse and the humerus of a chicken. Since they are both derived from the humerus of the stem amniote common ancestor, the humerus of a mouse and chicken would be said to show discrete, or one-to-one, homology.[48,58] This type of homology (which is the type most commonly implied by use of the word) is the type that the Forum required to rename a structure in avian brain with the term used for its mammalian homologue. A second type of homology is field homology. This term, when applied to brain, refers to a circumstance in

TABLE 1. New terminology relevant to songbird vocal and auditory areas

Old Term	Old Abbreviation	New Term	New Abbreviation
		BRAINSTEM	
Nucleus intermedius of the medulla	IM	Hypoglossal nucleus –the twelfth cranial nerve nucleus	nXII
Nucleus nervi hypoglossi the twelfth cranial nerve nucleus	nXII	Supraspinal nucleus	SSp
Area ventralis of Tsai	AVT	Ventral tegmental area or A10	VTA or A10
Nucleus tegmenti-pedunculopontinus, pars compacta	TPc	Substantia nigra, pars compacta or A9	SNc or A9
Anterior nucleus of ansa lenticularis	ALa	Subthalamic nucleus	STN
		SUBPALLIUM PART OF THE TELENCEPHALON	
		Striatal subdivision	
Lobus parolfactorius	LPO	Medial striatum	MSt
–Area X within songbird LPO	X	–Area X within songbird MSt	X
Paleostriatum augmentatum	PA	Lateral striatum	LSt
–Caudal paleostriatum (auditory region)	PC	–Caudal part of the lateral striatum (auditory region)	CSt
		Pallidal subdivision	
Paleostriatum primitivum	PP	Globus pallidus	GP
Ventral paleostriatum	VP	Ventral pallidum	VP
		PALLIUM PART OF THE TELENCEPHALON	
		Hyperpallium subdivision	
Hyperstriatum, Wulst regions	H	Hyperpallium	H
–Hyperstriatum accessorium	HA	–Hyperpallium apicale	HA
–Hyperstriatum intercalatum superior	HIS	–Hyperpallium intercalatum	HI
–Hyperstriatum dorsale	HD	–Hyperpallium dorsale	HD
		Mesopallium subdivision	
Hyperstriatum ventrale	HV	Mesopallium	M
–Nucleus avalanche	Av	–Nucleus avalanche	Av
–Oval nucleus of the hyperstriatum ventrale	HVo	–Oval nucleus of the mesopallium	MO
–Caudal medial hyperstriatum ventrale	CMHV	–Caudal medial mesopallium	CMM
–Caudal lateral hyperstriatum ventrale	CLHV	–Caudal lateral mesopallium	CLM

TABLE 1. (*continued*) New terminology relevant to songbird vocal and auditory

Old Term	Old Abbreviation	New Term	New Abbreviation
		Nidopallium subdivision	
Neostriatum	N	Nidopallium	N
–Hyperstriatum ventrale, pars caudale, or high vocal center, or HVc (letter-based name)	HVC or HVc	–HVC (letter-based proper name)	HVC
–Lateral magnocellular nucleus of the anterior neostriatum	lMAN or LMAN	–Lateral magnocellular nucleus of the anterior nidopallium	LMAN
–Medial magnocellular nucleus of the anterior neostriatum	mMAN or MMAN	–Medial magnocellular nucleus of the anterior nidopallium	MMAN
–Interfacial nucleus	NIf	–Interfacial nucleus of the nidopallium	NIf
–Caudal medial neostriatum	NCM	Caudal medial nidopallium	NCM
–HVC shelf	HVC shelf	–HVC shelf (letter-based proper name)	HVC shelf
–Field L	L	–Field L	L
–Ectostriatum	E	–Entopallium	E
–Nucleus basalis	B or Bas	–Nucleus basorostralis	B or Bas
		Arcopallium subdivisions	
Archistriatum	A	Arcopallium	A
–Robust nucleus of the archistriatum	RA	–Robust nucleus of the arcopallium	RA
–Cup of robust nucleus of the archistriatum	RA cup	–Cup of robust nucleus of the arcopallium	RA cup
–Ventromedial nucleus of the intermediate archistriatum	Aivm	–Ventromedial nucleus of the intermediate arcopallium	AIVM

which homologous parts of developing brain give rise to a set of adult brain structures in two or more species.[59] The adult brain structures would be said to be field homologues, even if the sets included different nuclei in different species.[57,59] This type of homology was of relevance to the efforts of the Forum to rename the subdivisions of the pallial sector of the avian telencephalon. The Forum required for all of its decisions that evidence for one-to-one or field homology be ample, including for the former multiple types of morphological data and the presence of a comparable structure in living reptiles. Since adoption of each new name for birds required 80% approval from the Forum attendees, any acceptance of a homology-based name was, in effect, based on at least 80% agreement on the homology. In cases in which there was not enough evidence to convince 80% or more of the participants of the existence of homology, new names were chosen that differed from those for any specific mammalian brain structure, but retained similarity to the outdated avian terms in abbreviation, syllabication, and/or phonetics.

A REVISED NOMENCLATURE OF THE AVIAN BRAIN: PRINCIPLES

The decisions of the Forum on the renaming of the cell groups in the avian telencephalon were based on current evidence showing that birds, as do mammals, possess a complex forebrain that contains a well-developed upper sector called the pallium and a smaller ventral sector called the subpallium. Pallium means mantle and the term refers to the upper part of the developing telencephalon and its adult derivatives.[51,60] In mammals, the embryonic pallium gives rise to the neocortex, hippocampal complex, piriform cortex, olfactory bulbs, claustrum, and part of the amygdala, while the embryonic subpallium gives rise to the basal ganglia and several additional basal telencephalic cell groups, including part of the amygdala.[51,60] The Forum concluded that developmental, topological, neurochemical, cellular, connectional, and functional data strongly support the conclusion that approximately the dorsal three-fourths of the avian telencephalon is pallial and in adults includes what has been termed the hyperstriatum, neostriatum, ectostriatum, and archistriatum (as defined by Karten and Hodos[16]), as well as nucleus basalis, hippocampus, piriform cortex, and olfactory bulb.[28,31,49,50,60–62] It is thus inappropriate that the root "-striatum" be present in the names of any of these structures. In contrast to the mammalian pallium, the avian pallium does not have a cortical organization, but rather is organized into a largely continuous field of nuclei.[28,31,63] Although these nuclei have similar connectivity and functional properties to those of the mammalian cortex, amygdala, and possibly the claustrum, their histological appearance is more like that of the basal ganglia, explaining, in part, the erroneous conclusions of many early comparative neuroanatomists.

In renaming avian pallial structures, the Forum confronted the issue of whether sufficient data were available to conclude safely and unequivocally that the structures that have been called the archistriatum, neostriatum, and hyperstriatum in birds possess one-to-one homologies with specific structures in adult mammals.[18,28,31,50,51,60,62,64–67] The Forum decided that the evidence was insufficient to conclusively identify one-to-one mammalian homologues for most pallial structures in birds. While it was agreed that the new names for these structures should include the word or root "pallium," several issues needed to be considered in renaming the pallial structures that possessed "-striatum" as a root word in their outdated name. One major issue was the extent to which choosing new names that allowed retention of existing abbreviations was desirable and could be achieved with esthetically pleasing new terms. Alternatively, the possibility had to be considered that a simple and new descriptive terminology that did not retain established abbreviations might be desirable by making the structures of the avian brain easier to learn and more broadly accessible to neuroscientists. In the end, new terms were selected that allowed abbreviations to be retained for the most intensely studied structures of the avian pallium, to provide easy linkage and clear continuity between the old and new terminologies. The accepted homologies of the avian and mammalian hippocampi, piriform cortices, and olfactory bulbs were not disputed, and it was agreed that there was no need to change the name for these regions.

The Forum further concluded that developmental, topological, neurochemical, cellular, connectional, and functional data strongly support the conclusion that the ventral one-fourth of the avian telencephalon is subpallial, and that the subpallial region lateral to the telencephalic ventricle in birds and reptiles contains homologues

of the mammalian basal ganglia, while the subpallial region medial to the lateral ventricle in birds and reptiles contains homologues of the mammalian septum.[60,62,63,68–75] The region lateral to the telencephalic ventricle in birds includes what had been termed the paleostriatum primitivum, the paleostriatum augmentatum, and the lobus parolfactorius. Other subpallial cell groups in birds include the bed nucleus of the stria terminalis, the basal nucleus of Meynert, and the subpallial amygdala. For many subpallial structures, the Forum concluded that there was sufficient evidence to infer one-to-one homologies with mammals. In these instances, the Forum adopted for birds the same name as used for the homologous subpallial structure in mammals. The gain in communication and the already established familiarity of each new avian term, because of their prior use in mammals, were thought to far outweigh disadvantages inherent to abandoning the old names and abbreviations.

The Forum also focused attention on several brainstem cell groups connected with the subpallium or the song control system, for which the homology implied by the name was clearly incorrect, or at best obscure, and for which the true homologue had been amply demonstrated. Below we describe in detail the brainstem, subpallial, and pallial revisions that are relevant to the songbird vocal and auditory nuclei.

SUMMARY OF THE REVISED NOMENCLATURE: THE BRAINSTEM

Nucleus Intermedius (IM) → Hypoglossal Nucleus (nXII)

In the Karten and Hodos atlas[16] of the pigeon brain, a population of motoneurons located ventral to the dorsal motor nucleus of the vagus nerve and the nucleus intercalatus at levels straddling the obex was named the nucleus intermedius, following the practice of Ariëns-Kappers and colleagues.[7] A yet more ventral and somewhat larger population of motoneurons abutting the lateral edge of the medial longitudinal fasciculus was identified as the hypoglossal nucleus. While Ariëns-Kappers and colleagues[7] did suspect that IM innervates lingual and syringeal muscles via bifurcating branches of the twelfth nerve, this has now been demonstrated unambiguously in birds by more recent experimental studies of the innervation of the tongue, trachea and syrinx.[76–84] The IM of Karten and Hodos[16] was thus subsequently renamed the hypoglossal nucleus, or alternatively the 12th cranial nerve nucleus by Nottebohm,[77] and the Forum formally adopted this renaming. Because many investigators had already been using the correct name for this nucleus since 1976, there is no widespread need for investigators to change their customary usage for nXII in birds.

Nucleus Nervi Hypoglossi (nXII) → Supraspinal Nucleus (SSp)

Numerous retrograde labeling studies have demonstrated that the cell group identified by Karten and Hodos[16] as the hypoglossal nucleus actually innervates upper neck musculature (e.g., Mm. complexus, biventer cervicis, splenius capitis, and rectus capitis).[79,80,85–87] This nucleus was thus subsequently renamed supraspinalis,[78,79,88] and the Forum also formally adopted this renaming. It is important to reiterate that most work referring to the hypoglossal nucleus in songbirds has referred to the correct structure, so no change in the customary usage to supraspinalis is needed.

Area Ventralis of Tsai (AVT) → Ventral Tegmental Area (VTA)

The cell group named area ventralis of Tsai in the Karten and Hodos pigeon brain atlas is known to be homologous to the mammalian ventral tegmental area, which was also once commonly called the ventral tegmental area of Tsai[89] and is now also known as the A10 dopaminergic cell group.[90–92] As in mammals, this midbrain-diencephalic cell group sends a massive dopaminergic projection to the basal ganglia, mainly to the medial and ventral part of the region that had been called the lobus parolfactorius (LPO),[91,93–96] including to the song nucleus Area X.[93] To eliminate the eponym "Tsai" (since eponyms are no longer employed according to standard international rules of anatomical nomenclature)[37] and to emphasize the homology with mammals, the Forum renamed the avian area ventralis of Tsai to the ventral tegmental area, with the acceptable alternative name of the A10 dopaminergic cell group.

Nucleus Tegmenti Pedunculopontinus Pars Compacta (TPc) → Substantia Nigra Pars Compacta (SNc)

This cell field, laterally adjacent and continuous with VTA, contains a large population of dopaminergic neurons that send a massive dopaminergic innervation to the dorsal striatal part of the avian basal ganglia (the regions that have been called lobus parolfactorius and paleostriatum augmentatum, the latter including the auditory area PC)[90,91,94,96–99] and therefore is accepted as homologous to the substantia nigra pars compacta of other vertebrates.[71,72,75,92] The name applied to this region, however, incorrectly suggested homology with the pedunculopontine tegmental nucleus of mammals, located in rhombomere 1, which is characterized by cholinergic neurons, but no dopaminergic neurons.[92,100] Moreover, the actual avian pedunculopontine tegmental nucleus (PPT) homologue, which contains cholinergic neurons, has been identified in rhombomere 1 of pigeons.[100] To rectify these misnomers and avoid confusion, the Forum renamed what had been called the nucleus tegmenti pedunculopontinus pars compacta (TPc) in birds to the substantia nigra pars compacta (SNc), or the alternative name, the A9 dopaminergic cell group. While the dopaminergic field of neurons in the avian A9 is not as compact as it is in rodents or as pigmented as it is in humans, the A9 varies in its degree of compactness and blackness (i.e., pigmentedness) even among mammals. For this reason, and because of the gain in using a homology-based term for avian A9, the Forum decided that the descriptive inaccuracies of the terms "compacta" and "nigra" in the avian name for A9 were far outweighed by the benefits obtained in adopting the commonly used term SNc as the name for this structure.

Anterior Nucleus of the Ansa Lenticularis (ALa) → Subthalamic Nucleus (STN)

The avian anterior nucleus of the ansa lenticularis is an inconspicuous cell group located in and along the medial edge of the ansa lenticularis (a fiber bundle interconnecting the basal ganglia with various brainstem cell groups) at rostral diencephalic levels.[68] Based upon its function, the neurochemistry of its inputs and outputs, its developmental profile, its position in the diencephalon, and its apparent presence in reptiles, the ALa is homologous to the subthalamic nucleus (STN) of mammals.[75,101] The Forum therefore renamed the avian ALa as the subthalamic nucleus.

It remains to be determined whether the song nucleus Area X of the basal ganglia is connected with the avian STN.

SUMMARY OF THE REVISED NOMENCLATURE: THE SUBPALLIUM

The basal ganglia in mammals forms within a ventral part of the developing telencephalon called the subpallium. The subpallium, which contains the septal nuclei and several other nuclei in addition to those of the basal ganglia, is notably distinct from the overlying telencephalic region called the pallium in its neurochemistry, in the genes that regulate its development,[102,103] and in its connectivity.[75] Developmental, topological, neurochemical, cellular, connectional, and functional data now strongly support the conclusion that the subpallial region lateral to the telencephalic ventricle in birds and reptiles contains homologues of the mammalian basal ganglia, while the subpallial region medial to the lateral ventricle in birds and reptiles contains the homologue of the mammalian septum.[60,62,63,68–75]

Embryological and developmental molecular studies in both birds and mammals show that the developing avian and mammalian subpallium consists of two separate radially oriented histogenetic zones, a dorsally situated zone that in mammals corresponds to the lateral ganglionic eminence and a ventrally situated zone that in mammals corresponds to the medial ganglionic eminence.[60,104,105,157] Among the derivatives of the lateral ganglionic eminence are the various striatal cell groups, which in mammals make up the dorsal striatum (i.e., the caudate and putamen), the ventral striatum (nucleus accumbens and olfactory tubercle), and the lateral septum. Among the derivatives of the medial ganglionic eminence are the various pallidal cell groups, which in mammals make up the dorsal pallidum (or globus pallidus), the ventral pallidum, and the medial septum. The Forum thus sought to rename the various parts of the avian subpallium so as to more accurately reflect their homologues in mammals. The revisions to the subdivisions that contain vocal and auditory regions are as follows.

Lobus Parolfactorius (LPO), Excluding Its Rostral Ventromedial Part → Medial Striatum (MSt)

Neurochemical, hodological, and developmental evidence indicate that the LPO has striatal traits. The neurochemical and hodological evidence includes a prominent dopaminergic input from the substantia nigra pars compacta and ventral tegmental area, an enrichment in dopamine receptors, a projection back to the SNc/A9 and VTA cell groups, an acetylcholine-rich and cholinesterase-rich neuropil, an enrichment in GABAergic neurons that either contain SP/DYN or enkephalin, and a glutamate receptor pattern very similar to that of the mammalian striatum.[65,72,75,91,93–95,106–111] Developmental evidence includes the finding that the major part of LPO develops from a part of the telencephalic neuroepithelium that expresses the transcription factors *Dlx1* and *Dlx2*, but not the transcription factor *Nkx2.1*, as does the mammalian lateral ganglionic eminence.[60,62] For these and additional reasons summarized by Reiner and colleagues,[75] the Forum replaced the arcane name lobus parolfactorius (meaning lobe next to the olfactory bulb) with the term medial striatum (FIG. 1A,B).

While we recommend that LPO now be called medial striatum in birds, it is also important to note that we do not mean to imply one-to-one homology to the medial part of the mammalian striatum, i.e., the caudate nucleus, and the available evidence seems to be against such a homology. Principal among the reasons against such a notion is that although the avian medial striatum projects predominantly to the substantia nigra, it does not appear to target the pallidal part of the basal ganglia.[68,112,113] By contrast, the caudate nucleus in mammals contains both striatonigral and striatopallidal projection neurons.[75,106,114,115] A second argument against this notion is that the medial striatum in at least some avian species contains pallidal neurons, while such a trait has not been demonstrated for mammalian caudate. These pallidal neurons were first discovered in the specialized song nucleus called Area X within songbird MSt.[116–118] Although the majority of Area X cell types resemble those typical of mammalian striatum in physiology, dendritic morphology, and neurotransmitter features,[108,110,117,118] this sparse but important cell type appears to be pallidal in its aspiny morphology, its probable input from spiny striatal neurons, its GABAergic, inhibitory projection to the thalamus, its neurochemistry, and its physiological features.[110,113,117–119] Compelling evidence now exists showing that the lateral part of MSt outside of Area X and the lateral part of MSt of avian species lacking an Area X also contains pallidal-type neurons.[118–121] Consistent with these observations, developmental studies have suggested that ventrolateral parts of the chicken medial striatum abutting the pallidum may ontogenetically be a pallidal territory that is heavily invaded by striatal cells during development and thereby becomes predominantly striatal in its cell type composition.[60,122] If further study shows such striatal-pallidal neuron mixing in medial striatum to be a general avian trait absent from mammals, it might be advisable to recognize some unique striato-pallidal subdivision within medial striatum and attach to it a suitable name. The Forum concluded, however, that sufficient data were not yet available on the location of this region, on the prevalence of striatal and pallidal cell mixing as an avian trait, and on its absence from mammals. It was also clear to the Forum that what has been called LPO has predominantly striatal cellular traits,[75,91] and so it is appropriate for now to simply rename LPO as the medial striatum, and emphasize the evidence against one-to-one homology with mammalian caudate.

Paleostriatum Augmentatum (PA) → Lateral Striatum (LSt)

Similar lines of evidence demonstrate that PA also has striatal traits and together with MSt makes up the avian dorsal striatum. These traits in PA include a prominent dopaminergic input from the substantia nigra pars compacta, an enrichment in dopamine receptors, an acetylcholine-rich and cholinesterase-rich neuropil, an enrichment in GABAergic neurons that either contain SP/DYN or enkephalin, projections to the paleostriatum primitivum (now to be called the globus pallidus), and a glutamate receptor pattern very similar to that of the mammalian striatum.[28,60,65,72,75,91,93–95,106,107,109,111,121] Additionally, the PA develops from the *Dlx1/2*-rich and *Nkx2.1*-poor neuroepithelial zone corresponding to the mammalian lateral ganglionic eminence.[60,62] For these reasons, and additional ones summarized by Reiner and colleagues,[75] the Forum replaced the name paleostriatum augmentatum with the term lateral striatum (FIG. 1A,B). Similar to LPO, this change is attended by the qualification that there is no compelling evidence that the lateral

striatum of birds is homologous in a one-to-one manner with the lateral part of the mammalian striatum, namely the putamen. Principal among the reasons against such a notion is that avian lateral striatum projects predominantly to the pallidal part of the basal ganglia and very little to the substantia nigra.[68,73,123–125] By contrast, the putamen in mammals contains both striatonigral and striatopallidal projection neurons.[75,106,114,115]

Area X → Area X

While Area X of songbirds resides within the avian medial striatum,[29,113] its own name is unaffected by the change of the name of LPO to medial striatum. Thus, the Forum recommended that Area X retain its name (FIG. 2A). A change to nucleus X was proposed, to reflect the clear boundaries of this structure; after discussion, the Forum took no position on whether Area X should be called nucleus X.

Caudal Paleostriatum (PC) → Caudal Striatum (CSt)

The Forum did not discuss renaming of the PC, an auditory region of the caudal lateral striatum. This region possibly receives auditory input from the thalamus and pallium,[126,127] and it shows audition-related gene expression and electrophysiological activity.[25,128,129] Here, we suggest renaming the caudal paleostriatum (PC) to the caudal part of the lateral striatum or more simply the caudal striatum (FIG. 2B). We have not included the letter L for lateral, to simplify the abbreviation.

Ventromedial Rostral LPO → Nucleus Accumbens (Ac)

Although there are no known auditory or vocal regions within the avian nucleus accumbens, a revision to the location of nucleus accumbens relative to LPO, and thus

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FIGURE 2. Vocal and auditory pathways of the songbird brain within the context of the new avian brain nomenclature. Only the most prominent and/or most studied projections are indicated. For the vocal pathways (**A**), *black arrows* show connections of the components (*dark grey*) of the posterior vocal pathway, *white arrows* show connections of the components (*white*) of the anterior forebrain pathway, and *dashed lines* connections between the two pathways. For the auditory pathway (**B**), most of the hindbrain connectivity is extrapolated from non-songbird species. For clarity, only the lateral part of the anterior vocal pathway is shown, and the connection from Uva to HVC and reciprocal connections in the pallial auditory areas are not indicated. Note that the NCM and CMM are shown for schematic purposes, as they actually lie in a sagittal plane medial to that depicted, and the pathway from NCM to CMM is not depicted. ABBREVIATIONS: Av=avalanche; CLM=caudal lateral mesopallium; CMM=caudal medial mesopallium; CN=cochlear nucleus; CSt=caudal striatum; DM=dorsal medial nucleus; DLM=dorsal lateral nucleus of the medial thalamus; E, entopallium; B=basorostralis; HVC (no formal name other than HVC); LLD=lateral lemniscus, dorsal nucleus; LLI=lateral lemniscus, intermediate nucleus; LLV=lateral lemniscus, ventral nucleus; MLd=dorsal lateral nucleus of the mesencephalon; LMAN=lateral magnocellular nucleus of the anterior nidopallium; Area X=Area X of the medial striatum; MO=oval nucleus of the mesopallium; NCM= caudal medial nidopallium; NIf= nucleus interface of the nidopallium; nXIIts=nucleus XII, tracheosyringeal part; Ov=ovoidalis; PAm=paraambiguus; RAm=retroambiguus; RA=robust nucleus of the arcopallium; SO=superior olive; Uva=nucleus uvaeformis. (Figure adapted from Jarvis and colleagues.[40])

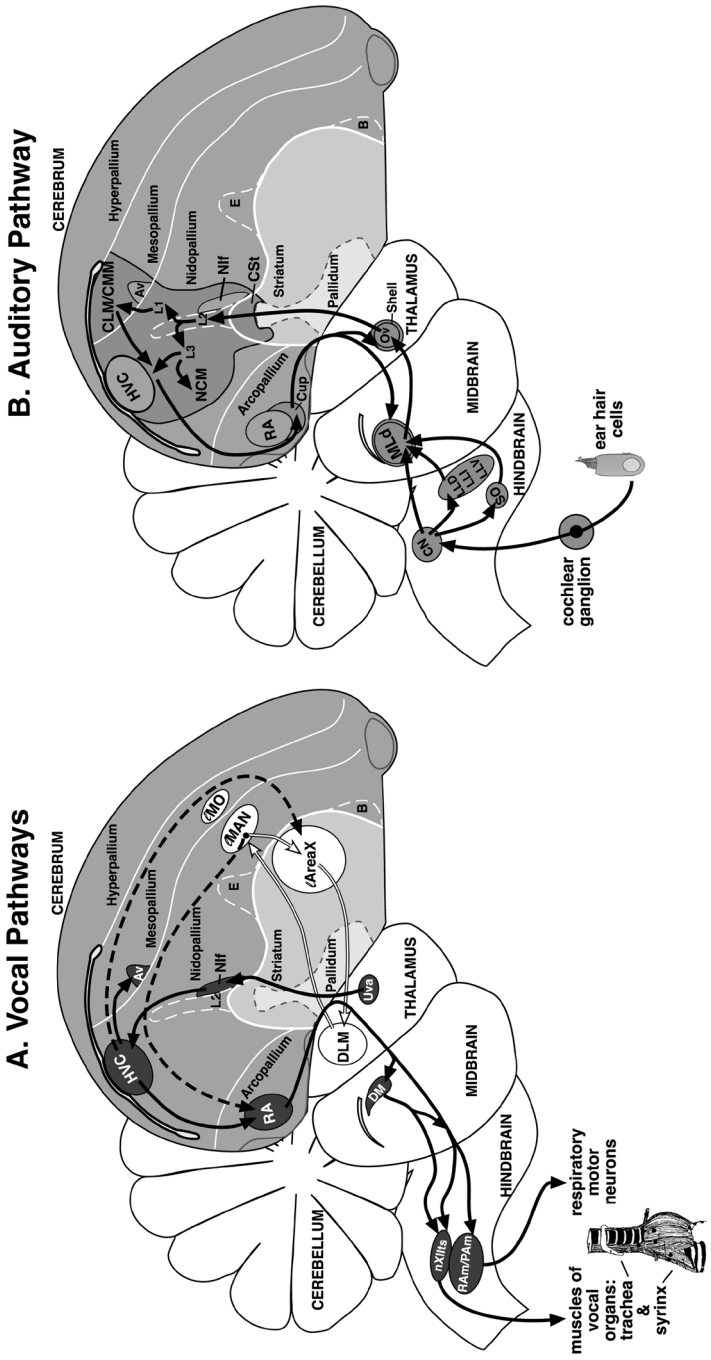

FIGURE 2. *See previous page for legend.*

to Area X within MSt is of relevance. In the Karten and Hodos atlas,[16] nucleus accumbens was identified as a small bulge at the ventral tip of the lateral ventricle extending several millimeters rostral from the level of the anterior commissure. However, based on compelling evidence,[130] the Forum concluded that this region instead is homologous to the lateral part of the mammalian bed nucleus of the stria terminalis (BNST). The Forum further concluded that the region surrounding the tip of the lateral ventricle, at the ventromedial margin of the rostral pole of what has been called LPO in birds possesses the same topographic, hodological, and neurochemical traits as the nucleus accumbens of mammals.[106,124,131–138] This includes for both birds and mammals preferential reciprocal connections with the ventral tegmental area, afferent input from limbic pallial regions (such as the hippocampal complex, amygdala, and cingulate cortex, as well as from frontal pallium), and the frequent co-localization of substance P and enkephalin in spiny projection neurons. By contrast, much of the remainder of what has been called LPO in birds and caudatoputamen in mammals is reciprocally connected with the substantia nigra pars compacta, receives pallial input from somatosensory and somatomotor areas of the pallium, and shows little co-localization of SP and enkephalin in spiny striatal projection neurons.[63,106,112,123–125,131,132,135–137,139] Moreover, a topographically, hodologically, and neurochemically similar cell group has been identified as nucleus accumbens in turtles, lizards, and snakes.[71,106,132,140–143] For these reasons, the Forum recognized and recommended that the rostral ventromedial part of the former LPO of birds be called nucleus accumbens and that the term medial striatum be only used to refer to the remainder of LPO. As in mammals, however, a precise cytoarchitectonic border between the dorsal striatum and nucleus accumbens is not evident, and a neurochemical criterion by which to unambiguously distinguish the two fields has not been identified. Additionally, while the nucleus accumbens of mammals possesses core and shell subdivisions, comparable subdivisions of nucleus accumbens in birds have not been conclusively identified.[135,136]

Paleostriatum Primitivum (PP) → Globus Pallidus (GP)

Although there are no described auditory or vocal nuclei within avian pallidal regions, it is important to be acquainted with the renaming of pallidal subdivisions within the context of subpallial nomenclature revisions. Diverse lines of evidence indicate that the avian PP is derived from the avian equivalent of the medial ganglionic eminence and has traits comparable to those of the dorsal pallidum (globus pallidus) in mammals.[60,63,68,74,75,91,122,131,144–149] In both birds and mammals, the projection neurons of these regions possess large cell bodies and smooth dendrites, derive from an *Nkx2.1*-expressing neuroepithelium, and give rise to the motor output projections of the basal ganglia. In birds and mammals, these neurons are also GABAergic, contain the neuropeptide LANT6, receive inputs with a woolly fiber morphology from either SP/DYN-containing or ENK-containing striatal neurons, receive a prominent glutamatergic input from the subthalamic nucleus, and share similar electrophysiological properties.[75,101,121,150] Thus, the Forum renamed the avian paleostriatum primitivum as the globus pallidus (FIG. 1A,B). This term is appropriate for descriptive reasons, as the avian GP and its mammalian counterpart are pale. Nonetheless, there are some differences between avian GP and mammalian GP. Avian GP neurons, for example, migrate farther laterally than do mammalian pallidal neurons,

with the result that avian GP is more laterally situated than adult mammalian GP.[60,122] The GP in mammals is separated into two segments, the internal and external, with distinct connectivity and neurochemistry, whereas in birds the neuronal types of the two segments are intermingled.[75] The avian globus pallidus as a cell field is also not as globular in shape as the comparable cell field is in mammals, but different mammalian species show variation in the shape of the GP as well. Thus, the Forum concluded that despite any differences, the advantages in the use of the homology-based term globus pallidus as the new name for PP in birds outweighed any slightly misleading implications as to its shape or organization.

Ventral Paleostriatum (VP) → Ventral Pallidum (VP)

A group of GABAergic neurons within the medial forebrain bundle (MFP; also called the fasciculus prosencephali medialis, FPM) has been demonstrated in birds. This cell group has also been called the ventral paleostriatum.[151] It has the cellular neurochemistry, receives the ventral striatal inputs (including from nucleus accumbens), and has the outputs characteristic of the ventral pallidum of mammals.[106,135,144–146] Its glutamate receptor expression profile is identical to that of GP of both birds and mammals.[65] In addition, in both mammals and birds, the neurons of this region arise from the same *Nkx2.1*-expressing histogenetic subpallial neuroepithelium as the GP.[60] A comparable cell group is present in turtles, crocodilians, and lizards.[69,140,141,145,152,153] The Forum thus renamed this cell group as the avian ventral pallidum (TABLE 1). The word ventral is used because it provides the VP with a positional term that distinguishes it from its more dorsal somatic counterpart, the GP, which has also alternatively been termed the dorsal pallidum. Note that the ventral pallidum in birds overlaps a field of cholinergic neurons that spans the medial and lateral forebrain bundles. These cholinergic neurons send diffuse projections into the pallium, including the pallial song control nuclei.[154,155] Since the ventral pallidum in mammals also overlaps a similar field of cholinergic neurons with projections to the pallium,[156] the Forum recommended these neurons in birds be given a name similar to those in mammals, the basal magnocellular cholinergic nucleus (NBM).

SUMMARY OF THE REVISED NOMENCLATURE: THE PALLIUM

The structures constituting the pallium in adult birds and mammals derive from a large histogenetic zone located dorsal to the subpallium and distinguishable from the subpallium in the developmentally regulated genes it expresses.[60,157] Owing to the flawed identification of brain regions by Edinger and his followers, the major pallial sectors of the lateral telencephalic wall in birds have the incorrect root word "-striatum" in their names (hyperstriatum, neostriatum, ectostriatum, archistriatum), and in some cases possess prefixes with questionable evolutionary implications (e.g., "neo-" and "archi-"). The perceived need to correct these errors was the main driving force behind the Forum. The reasoning used by the Forum in selecting the new names is briefly reviewed below (FIG. 1B), followed by specific recommendations of the Forum for vocal and auditory areas (FIG. 2; TABLE 1).

Rationale for New Names for Hyperstriatum, Neostriatum, Ectostriatum, and Archistriatum

Hyperstriatum

In revising the terminology for the hyperstriatum, a guiding consideration was that the hyperstriatum ventrale (HV) should have a name distinct from that for the hyperstriatal subdivisions composing the Wulst [i.e., the hyperstriatum accessorium, (HA), the hyperstriatum intercalatus superior (HIS), and the hyperstriatum dorsale (HD) in the outdated nomenclature]. It has been apparent for some time, from developmental, hodological, neurochemical, and functional studies, that HV and the Wulst are distinct telencephalic subdivisions.[15,50,65,111,158–164] After consideration of various possibilities, the Forum decided to replace the term "hyperstriatum" in HA, HIS, and HD with hyperpallium, replacing the secondary terms of accessorium with apicale, intercalatus superior with intercalatum, and dorsale with densocellulare, and replacing HV with mesopallium (FIG. 1A,B; TABLE 1). Since the prefix "hyper-" refers to an enlarged entity, "hyper-" in hyperpallium was considered acceptable, as the Wulst is an enlarged (bulging) structure at the upper aspect of the pallium. In addition, "hyper" possesses the merits that it is a commonly employed neuroanatomical term, already having been used in the names for the subregions of the Wulst, and it offers easy linking of the new term to the old, with abbreviations retained. "Meso-" as a prefix is descriptive of the location of this region (the former hyperstriatum ventrale) between the hyperpallium and the subdivision below it (the former neostriatum). Of course, the use of mesopallium as a replacement for hyperstriatum ventrale means that abbreviations for this region must change. The Forum did not consider this a serious disadvantage, since relatively few subregions have been named in the literature on the mesopallium.

Neostriatum and Ectostriatum

In revising the terminology for the neostriatum, a guiding principle was to devise a suitable and acceptable prefix that is descriptive of the region and that maintains abbreviations with the past literature. The Forum decided that the prefix "nido-," derived from the Latin word for nest (nidus) met these requirements, resulting in the new term nidopallium as a replacement for neostriatum (FIG. 1A,B). The prefix "nido-" is apt for the neostriatum, since it is the pallial structure in which the overlying pallial structures are nested. Moreover, the prefix "nido-" offers an aural link to the existing prefix for this region (i.e., "neo-"), and allows abbreviation retention. In revising the term ectostriatum, the Forum noted that the term ectostriatum, broken into its prefix and root word, means "outside the striatum." as the striatum is now recognized in birds, and is therefore semantically appropriate. Thus, ectostriatum could have been retained without any erroneous denotation. Nonetheless, the term ectostriatum was linked to the set of incorrect names for the avian pallium by the root word "-striatum", and could be misconstrued as being part of the striatum. For this reason, the name for the ectostriatum was changed to the entopallium, which means "within (ento-) the pallium". This new term also retains existing abbreviations for this region and possesses an aural linkage to the term ectostriatum.

Archistriatum

In revising the terminology for the archistriatum, a number of issues had to be considered. These included defining the boundaries of the archistriatum, as different reports had set different boundaries,[16,165] and coming to consensus on any homologies between the avian archistriatum (or its parts) with cell groups of the mammalian telencephalon. The avian archistriatum has been thought to be, at least in part, homologous to the mammalian amygdala,[3,4,7,60,64,165] a structure that itself is now known to possess both pallial and subpallial portions.[103] In revising the terminology for the avian archistriatum, the relationship of its subfields (including nucleus taeniae, also known as the taenia) to the pallial and subpallial parts of the mammalian amygdala needed to be addressed. Based on neurochemical and developmental data, the Forum concluded that the evidence overwhelmingly indicates that all parts of the avian archistriatum, i.e., structures with archistriatum in their names in the pigeon and chicken brain atlases,[16,151] are pallial.[65,166,167] As part of the discussion on the pallial versus subpallial nature of the archistriatum, the Forum concluded that the taenia has typically been regarded as a part of the archistriatal complex, although this was not reflected in its name,[165,168–170] but that much or all of it is subpallial.[104,170,171] Thus, the conclusion that the structures with archistriatum in their name, as their limits have been traditionally defined (excluding the taenia), are entirely pallial, made it appropriate that the new name for the archistriatum and its subdivisions have "-pallium" as part of the name.

Given the desirability of retaining existing abbreviations for the archistriatum, the Forum considered a number of possible prefixes beginning with the letter "A". "Archi-" was ruled out because of its questionable evolutionary implications. Consideration was given to the idea that "amygdalo-" be used, based on the interpretation that all of the archistriatum was amygdaloid in developmental origin and homologous as a field to all or part of the amygdala in mammals.[60,64] The Forum concluded that while the evidence for an amygdaloid nature of the taeniae and the posterior archistriatum was supported by hodological, developmental, neurochemical, and behavioral evidence,[60,123,135,165,170,172] the anterior, the intermediate, and at least parts of the medial archistriatum appeared to have largely somatic features, making them unlike the amygdala.[65,123,165,166,173,174] While it was further acknowledged that perhaps these regions were homologous to some parts of the mammalian amygdala and had evolved divergently in birds, the Forum concluded that this had not been demonstrated unequivocally. In addition, even if such an evolutionary relationship were established, the concern was expressed that it would be misleading and inappropriate to attach a name with viscerolimbic functional implications (i.e., the term "amygdala") to a field with somatic functional traits.[175–177] In the end, the Forum decided that only the posterior archistriatum and taenia warranted the designation of amygdala (PoA and TnA, FIG. 1B). For the remaining parts of the archistriatum, the Forum decided to replace archistriatum with the term arcopallium, with the prefix "arco-" referring to the arched contour of the upper boundary of the field (FIG. 1B). This choice does not foreclose the future option of replacing "arco-" with "amygdalo-" for specific arcopallial subdivisions if the evidence for this homology becomes more convincing. The subpallial region inferior to the globus pallidus was renamed the subpallial amygdala (SpA, FIG.1B).

Vocal and Auditory Regions of the Mesopallium

Nucleus Avalanche (Av)→ Nucleus Avalanche (Av)

This is a little-studied vocal nucleus in the old named HV that receives a projection from HVC[178] (FIG. 2A) and shows vocalization-associated gene expression.[179] A similar mesopallial nucleus has been identified by vocalization-associated gene expression in budgerigars and hummingbirds.[25,34] Because the name given to this nucleus in songbirds did not have hyperstriatum ventrale in it, no name change is necessary.

Oval Nucleus of the Hyperstriatum Ventrale (HVo) → Oval Nucleus of the Mesopallium (MO)

First described in parrots,[32,33] a similarly positioned, oval-shaped nucleus in the anterior part of songbird HV that shows vocalization-associated gene expression has been noted.[180] With the renaming of the HV, the Forum recommended renaming this nucleus to the oval nucleus of the mesopallium (MO, FIG. 2A). Here the abbreviation for "oval" is capitalized, as the Forum decided to capitalize the letters representing the main words of each name, with only subordinate letters or words in lowercase.

Caudal Medial Hyperstriatum Ventrale (CMHV) → Caudal Medial Mesopallium (CMM)

The caudal medial HV is a distinct region that is part of the telencephalic auditory pathway and that shows auditory-induced gene expression and neural activity.[25,127–129,181–185] With the renaming of the HV, this region becomes the caudal medial mesopallium (CMM, TABLE 1). CMM also has a lateral auditory counterpart that was called the caudal lateral hyperstriatum ventrale (CLHV).[127] This becomes the caudal lateral mesopallium (CLM, FIG. 2B).

Vocal and Auditory Regions of the Nidopallium

HVC (Higher Vocal Center) or HVc → HVC

This nucleus was the first identified part of the telencephalic song control circuit.[29] It was thought to occupy the caudal-most part of the hyperstriatum ventrale, and was thus named the hyperstriatum ventrale, pars caudale, and abbreviated HVc. Subsequent work, however, recognized that this region is in actuality located within the pallial field that had been called the neostriatum[30] (FIG. 2A). To retain the abbreviation, which had already become entrenched, but eliminate the inaccurate location implied by its name, Nottebohm[186] suggested calling this region the higher vocal center, and abbreviating it with all capital letters HVC. Subsequently, the concern was raised that HVC was arguably not the apex of a hierarchy of vocal centers of the brain, making the name unwarranted.[187] Thus, Fortune and Margoliash[188] and Brenowitz and colleagues[189] recommended use of "HVc" as a letter-based proper name for the nucleus. However, the use of "high (or higher) vocal center" has persisted in published reports by some investigators, while "HVc" used as a proper name has been employed by others. In order to unify the field behind a single name, the Forum solicited feedback from the songbird research community, who overwhelmingly supported using HVC as the proper name (i.e., letter-based name only, all caps) and recommended against using HVc or any form of the term "higher vocal center."

Lateral and Medial Magnocellular Nucleus of the Anterior Neostriatum (lMAN and mMAN) → Lateral and Medial Magnocellular Nucleus of the Anterior Nidopallium (LMAN and MMAN)

The magnocellular nucleus of the anterior neostriatum (MAN) is a vocal nucleus of the anterior telencephalon that is necessary for song learning[113,190–192] and is active during singing.[179,193] This nucleus has two named subdivisions, the lateral and medial (typically abbreviated lMAN and mMAN). With the renaming of the neostriatum, the name for each of these is altered by substituting nidopallium for neostriatum; the established abbreviations remain the same (FIG. 2A; TABLE 1). Based upon feedback from songbird researchers, the Forum recognized that using the lowercase letter "l" for the word "lateral" in the abbreviation for the lateral magnocellular nucleus of the anterior nidopallium causes confusion due to the resemblance of the lowercase letter "l" to the number "1" or to the capital letter "I." Using all capital letters in this case (LMAN and MMAN) eliminates this confusion.

Nucleus Interface (NIf) → Nucleus Interface of the Nidopallium (NIf)

The nucleus interface (NIf) is a telencephalic constituent of the song control circuit that projects to HVC[178] (FIG. 2A), and shows singing-associated neural activity and gene expression.[180,194] While this nucleus is located in what has been called the neostriatum, the word neostriatum does not appear in the established name for NIf. To emphasize its location, the Forum adopted the official name nucleus interface of the nidopallium (or its Latin equivalent), and its abbreviation remains the same (TABLE 1).

Caudal Medial Neostriatum (NCM) → Caudal Medial Nidopallium (NCM)

The caudal medial neostriatum is a large and well-studied region of the avian auditory circuit, subjacent to the caudal medial mesopallium (CMM). It shows specialized auditory processing properties in response to species-specific sounds.[128,195–199] With the renaming of the neostriatum, the name is altered to caudal medial nidopallium (NCM), and the established abbreviation remains the same (FIG. 2B; TABLE 1).

HVC (or HVc) Shelf → HVC Shelf

The HVC shelf is an auditory region continuous with NCM dorsally, and is located immediately ventral to HVC[126,128,174] (FIG. 2B). Because the word neostriatum is not in the name, there is no change. However, due to the Forum recommendation that HVC serve as a proper name, it is similarly recommended that the HVC part of the term "HVC shelf" be a letter-based proper name.

Field L → Field L

The nidopallial region containing the primary auditory thalamo-recipient zone was not recognized as a distinct region in the Karten and Hodos atlas[16] and was not assigned a name. However, the experimental work of Karten[200] established that this zone largely coincided with the cytoarchitectonic region named Field L by Rose,[13] and this name subsequently became entrenched in the literature on this region.[126,127,181,183,201–203] Given its identification as Field L in a large number of

studies, and given that the term has no erroneous evolutionary implications, the existing name was retained. The Forum recognized, however, that an inconsistency exists in the literature in the extent of the territory to which the term Field L is applied. In many studies, Field L is taken to mean the region in the caudal medial neostriatum (now nidopallium) defined by Rose[13] and identified by Karten[200] as receiving a prominent input from nucleus ovoidalis (Ov, FIG. 2B). The work of Scheich and colleagues[183,204,205] led to the recognition that the auditory field in the caudal medial nidopallium was actually larger than the ovoidalis-recipient Field L alone. Thus, the main ovoidalis thalamo-recipient zone was named L2, and the regions immediately adjacent to L2, which receive L2 input as well as a smaller amount of thalamic input from the ovoidalis shell region, were named L1 and L3 (FIG. 2B). As a consequence of the presence of subfields, the term "Field L" has come to have two different definitions in the recent literature, one in which it refers to L2 alone and one in which it refers to L1, L2, and L3 together. Similar problems exist for what the Forum has renamed the entopallium,[161,206–209] and for the nucleus basalis (renamed nucleus basorostralis by the Forum).[78,210–212] The Forum concluded that it would be desirable to develop a uniform and consistent terminology for core and shell subdivisions of these three sensory fields in the nidopallium, and will make recommendations in a separate publication devoted to this issue.[46]

Vocal and Auditory Regions of the Arcopallium

Robust Nucleus of the Archistriatum (RA) →
Robust Nucleus of the Arcopallium (RA)

The robust nucleus of the arcopallium (RA) is a specialized nucleus within the intermediate archistriatum of songbirds, required for and active during the production of learned song.[29,177,179,213] With the renaming of the archistriatum, the name for this nucleus becomes the robust nucleus of the arcopallium (RA), and the existing abbreviation is retained (FIG. 2A).

Cup of the Robust Nucleus of the Archistriatum (RA cup) →
Cup of the Robust Nucleus of the Arcopallium (RA cup)

The RA cup is a region within the songbird auditory pathway located immediately rostroventral to the vocal nucleus RA[126,128,174,180] (FIG. 2B). A similar region has been found in the intermediate arcopallium of other vocal learning birds, as well as in vocal non-learning birds.[25,34,181] In pigeons, this region has been called the ventromedial nucleus of the intermediate archistriatum (AIVM).[181] With the new nomenclature, archistriatum in these names is replaced by arcopallium, and the existing abbreviations are retained (TABLE 1).

CONCLUSIONS

The understanding of avian brain organization and function has advanced enormously in the past one hundred years.[3,5–7,12,13,18,28,31,38,40,60,75] The facts that have emerged have shown the existing terminology for the avian telencephalon and many

brainstem cell groups related to it to be erroneous. These errors perpetuated misconceptions about birds and the avian brain. The Avian Brain Nomenclature Forum was the culmination of a growing awareness of how these errors have affected the understanding of the avian brain and of the communication problems caused by the faulty and outdated terminology. The Forum thus sought to devise a new terminology that is free of errors and promotes accurate understanding of avian brain organization and evolution. The Forum was scrupulous in its renaming efforts to use names implying homology only when it was confident that the names would not later prove to be in error. We believe the nomenclature we have devised can serve the field well, and we thus urge all avian brain researchers, birdsong neurobiologists included, to adopt the new nomenclature. Further information and avian brain images depicting this new nomenclature are available in our related papers[39,40,167] and on the Avian Brain Nomenclature Exchange website (<http://avianbrain.org>).

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