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The Avian Brain Nomenclature Forum: Terminology for a New Century in Comparative Neuroanatomy

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Abstract

Many of the assumptions of homology on which the standard nomenclature for the cell groups and fiber tracts of avian brains have been based are in error, and as a result that terminology promotes misunderstanding of the functional organization of avian brains and their evolutionary relationship to mammalian brains. Recognizing this problem, a number of avian brain researchers began an effort

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to revise the terminology, which culminated in the Avian Brain Nomenclature Forum, held at Duke University from July 18 to 20, 2002. In the new terminology approved at this Forum, the flawed conception that the telencephalon of birds consists nearly entirely 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 names reflecting their now evident homologies. The telencephalic regions that were erroneously named to reflect presumed homology to mammalian basal ganglia were renamed as parts of the pallium, using prefixes that retained most established abbreviations (to maintain continuity with the replaced nomenclature). Details of this meeting and its major conclusions are presented in this paper, and the details of the new terminology and its basis are presented in a longer companion paper. We urge all to use this new terminology, because we believe it will promote better communication among neuroscientists.

Indexing terms

pallium; basal ganglia; telencephalon; brainstem; evolution; terminology; birds; mammals

The view of telencephalic evolution that became widespread during the first 60 years of the 20th century was that both birds and mammals shared several basal ganglia structures, namely, an older structure inherited from fish called the paleostriatum (now called the globus pallidus in mammals) and a newer basal ganglia structure that evolved in amphibians but expanded in reptiles and more so in birds, called the neostriatum (then considered equivalent to the supposedly newer parts of the caudate and putamen; Edinger et al., 1903; Edinger, 1908; Ariëns-Kapper 1922, 1928; Johnston, 1923; Ariëns-Kappers et al., 1936; Herrick, 1948, 1956). Reptiles were thought to have also elaborated the two parts of the paleostriatum of fish, the primitivum and the augmentatum (the latter considered equivalent to older parts of mammalian caudatoputamen) into distinct regions and passed on this trait to birds, whereas the neostriatum in birds was thought to have given rise to a novel overlying structure called the hyperstriatum. Birds and mammals were also thought to share a caudobasal subcortical structure termed the archistriatum, now called the amygdala in mammals. Because an equivalent of laminated mammalian neocortex was not evident in birds, their telencephalon was considered to consist primarily of a hypertrophied basal ganglia. Although some investigators such as Kuhlenbeck, Rose, and Källén dissented from these views of avian brain organization and evolution (Rose, 1914; Kuhlenbeck, 1938; Källén, 1953), the accretionary theory of vertebrate brain evolution, as espoused in major books by Ariëns-Kappers et al. (1936) and Herrick (1948, 1956), became the prevailing view and led to the predominant use of the terms neostriatum, archistriatum, and hyperstriatum to refer to the major sectors of the telencephalon above the so-called paleostriatum in birds and to the term neocortex for the major telencephalic sector in mammals.

In 1967, Karten and Hodos published their stereotaxic atlas of the pigeon brain, which provided the first comprehensive effort to identify and name all parts of the brain in birds. For the diverse subtelencephalic structures, prior studies offered simple and uncontroversial terms that Karten and Hodos adopted (Huber and Crosby, 1929; Craigie, 1931; Kuhlenbeck, 1937, 1939; Meessen and Olszewski, 1949; Olszewski and Baxter, 1954). Karten and Hodos, however, recognized that the choice of a terminology for avian telencephalon was more problematic, because they were aware that the structures termed the archistriatum, neostriatum, ectostriatum, and hyperstriatum by Ariëns-Kappers et al. (1936) were unlikely to be parts of the basal ganglia. Despite their misgivings, Karten and Hodos chose to use these terms because they were already entrenched. Subsequent atlases for other avian species (Kuenzel and Masson, 1988) largely used the same terminology as Karten and Hodos. Although much of this terminology has stood the test of time, many of the interpretations of telencephalic homology implied by the terminology of Ariëns-Kappers et al. (1936) have been overwhelmingly shown to be erroneous.

Additionally, the mammalian homologues of some brainstem cell groups connected with the telencephalon, which were not known at the time the Karten and Hodos atlas was completed, have also become clear. As deeper insight has been gained into the evolution, development, and function of the brains of birds and mammals, the flawed homologies implied by the terms of Ariëns-Kappers et al. for avian telencephalon and some now evident errors in brainstem terminology have greatly hindered communication among avian and mammalian brain research specialists and perpetuated an outdated view of avian brain evolution.

This issue came to be of increasing concern to avian neurobiologists over the past 10 years, and formal efforts to revise avian brain nomenclature were begun 5 years ago by a small group of avian brain specialists. To develop widely acceptable new terms, this group sought to involve a greater number of researchers than had participated in two previous attempts to standardize avian neuroanatomical nomenclature (Baumel, 1979, 1993). Accordingly, the group discussing such a revision eventually grew to an international collection of multidisciplinary neuroscientists, and 2 years ago the group decided to hold an open Nomenclature Forum, at which a new terminology would be adopted. This Forum was held July 18–20, 2002 at Duke University in Durham, North Carolina, and it was preceded by in-depth discussions by E-mail and telephone of the need for a terminology change and specific recommendations as to the nature of the new terms. This report describes the pre-Forum preparatory period, the Forum logistics, and the decision-making process. The new terminology itself and the rationale for individual changes are presented in detail in a companion paper (Reiner et al., 2004).

AVIAN BRAIN NOMENCLATURE FORUM

Rationale and overview of meeting

Armed with 2 years of formal preparation, an international team of experts in the fields of avian, mammalian, reptilian, and fish brain research assembled at Duke University and took on the task of devising a new avian telencephalic nomenclature. This group critically evaluated the evidence, as detailed in various published and soon-to-be-published studies, for specific, possible new terms. We concluded that an overwhelming body of data supports the interpretation that most of the dorsal three-fourths of the cerebrum in birds (including what has been termed the neostriatum, hyperstriatum, and archistriatum) is pallial in nature and therefore homologous as a field to the brain sector that in mammals includes the neocortex, claustrum, piriform cortex, and pallial amygdala (Karten, 1969, 1991; Güntürkün, 1991; Butler, 1994; Reiner et al., 1998; Smith-Fernandez et al., 1998; Medina and Reiner, 2000; Puelles et al., 2000). Accordingly, we have now designated the major subdivisions of the dorsal three-fourths of the telencephalon in birds with terms that contain the root word “-pallium” rather than the Ariëns-Kappers et al. term “-striatum.” We have also revised prefixes with questionable evolutionary implications. We further concluded that the approximately ventral one-fourth of the cerebrum in birds contains the homologues of such subpallial structures in mammals as the basal ganglia proper (including dorsal striatal and pallidal subdivisions), the more ventrally located limbic striato-pallidal complex (sometimes called the ventral basal ganglia), the medial and lateral bed nuclei of the stria terminalis, the basal nucleus of Meynert, and part of the subpallial amygdala. The new names chosen for these subpallial structures reflect these homologies.

Meeting planning and preparation

In organizing and planning the Nomenclature Forum, several goals were paramount. First, it was necessary to devise means by which the researchers interested in the issue of nomenclature change could communicate and develop their thoughts about suitable name changes. This was achieved through two E-mail list servers, one for all avian brain researchers and one for songbird specialists. Typically messages were posted to both lists. By means of these two E-

mail list servers, the discussion of nomenclature change was open to the broad community of avian brain researchers, and all had the opportunity to contribute. Additionally, those interested in nomenclature change met as a group one evening at the annual Society for Neuroscience Meeting for each of the several years preceding the Forum and discussed issues related to avian brain nomenclature revision.

Second, a planning group of 13 neurobiologists was established for the Nomenclature Forum. This group also communicated openly by E-mail, supplemented by individual face-to-face or telephone conversations. In forming this group, which constituted the core of those attending the Forum, we sought to include major experts in avian neurobiology, as well as in fish, amphibian, reptilian, and mammalian neurobiology. This group included Laura L. Bruce, Ann B. Butler, András Csillag, Erich D. Jarvis, Harvey J. Karten, Wayne Kuenzel, Loreta Medina, George Paxinos, David J. Perkel, Anton Reiner, Toru Shimizu, Georg Striedter, and Martin Wild. Many members of this group possess expertise in more than one vertebrate group, some have considerable experience in brain atlas construction, and some are conversant with classical languages.

Third, to provide concrete ideas for nomenclature revision, proposals for specific nomenclature change were solicited by the core group and then extensively discussed (principally by E-mail) as to their strengths and weaknesses prior to the meeting. The open nature of the E-mail communication within the avian brain research community made it possible to gauge the reactions of diverse members of the community to specific proposals.

Fourth, to foster planning for the meeting and dissemination of ideas and information related to the nomenclature revision effort, a website called the Avian Brain Nomenclature Exchange (<http://jarvis.neuro.duke.edu/nomen/index.html>, renamed recently to <http://avianbrain.org/nomen/index.html>) was established. The expectation was that Forum attendees would be well versed in the need for the terminology change, in specific suggestions as to which structures needed a name change, specific proposals as to the new names, and the rationale or data supporting any given proposed name change.

Meeting format

Schedule—The 3-day Forum was organized into three major goal-oriented blocks. On the first day, the rationales for specific suggested name changes for subpallial and some related brainstem cell groups were reviewed and evaluated, and the Forum voted on the name changes. For the subpallium and related brainstem cell groups, the parties recommending name changes differed little among each other in the cell groups recommended for name change or in the specifics of the proposed new names. The discussion mainly focused on the evidence for the homologies underpinning the specific recommended name changes. On the second day, the rationales and merits for various specific suggested name changes for the neostriatum and hyperstriatum were presented and discussed. Voting was completed on new names for these structures on the morning of the third day, and the remainder of the third day was devoted to the rationales for specific proposed name changes for the archistriatal complex and voting for new names for this region. The discussion about the pallial terminology focused on cytoarchitectonic boundaries, the limits of what the data could conclusively prove about homology to mammalian structures, and the esthetics and practicalities (impact on the accessibility of the avian brain literature) of the specific proposed name changes for the pallium. The overall discussion and evaluation process on each day involved use of computers, projectors, video-interfaced microscopes, and internet connections to display the data and images required to assess published and unpublished data favoring or opposing particular proposals. Discussion was open, and focus was maintained by a moderator for each session. Discussion/Data sessions typically were 2–3 hours in length, separated by 15–30-minute breaks

that were largely characterized by spontaneous small group discussions on the topic of the preceding formal session.

Attendees—The meeting was attended by 19 faculty-level neuroscientists (Gregory F. Ball, Laura L. Bruce, Ann B. Butler, András Csillag, Sarah Durand, Onur Güntürkün, Erich D. Jarvis, Wayne Kuenzel, Diane Lee, Loreta Medina, Claudio V. Mello, George Paxinos, David J. Perkel, Alice Powers, Anton Reiner, Toru Shimizu, Georg Striedter, Stephanie White, and Martin Wild), four postdoctoral fellows (Gerald Hough, Lubica Kubikova, Tom V. Smulders, and Kazuhiro Wada), five graduate students (Jennifer Dugas-Ford, Haruhito Horita, Scott Husband, Keiko Yamamoto, and Jing Yu), and one undergraduate student (Connie Siang). All Forum attendees are co-authors of this and the companion paper (Reiner et al., 2004). Attendance at the meeting was open to all who wished to attend, and travel and lodging costs, as well as the costs of the meeting itself, were supported by awards from NSF and NIH for the Forum. An additional 12 individuals assisted in technical aspects of the Forum, including computer network specialists, audio-visual specialists, a web specialist, microscopy specialists, administrators, and graduate and undergraduate student assistants. These persons are listed in the acknowledgments. Erich Jarvis and Anton Reiner served as co-organizers of the meeting.

Voting—The planning committee had decided prior to the meeting that any nomenclature change needed a high degree of concurrence among Forum attendees if it was to be widely accepted by the field as a replacement for any existing term. We therefore decided changes on a structure-by-structure basis, with 80% approval required for acceptance of each new term. Each faculty member attending was accorded a full vote and each postdoctoral fellow a half vote. Graduate and undergraduate students did not vote, but their input was considered. The limits on student voting were put in place because of the perception that students were not yet adequately conversant with the issues of relevance to the terminology revision, whereas postdoctoral fellows were considered at least partly familiar. For pallial structures, it proved necessary to eliminate some of the proposed options by simple majority votes, before a final vote of approval for a given name change could be conducted. The final set of approved new names for pallial structures was largely an amalgam of the most highly favored choices from the different sets of proposals.

Guiding principles—In adopting a new terminology, several guiding principles were embraced. The overall goals were to remove inaccurate implications of homology where they existed (notably for the pallium) and to recognize homology where it was amply demonstrated (notably for brainstem and subpallial structures). Because our intent was to improve communication among avian and mammalian brain specialists, in the case of instances in which one-to-one homology (also termed discrete homology by Smith, 1967) had been clearly demonstrated, we believed it highly advantageous to adopt for birds the same name as used for that structure in mammals (e.g., globus pallidus instead of paleostriatum primitivum). The gain in communication and the already established familiarity of the new avian term (because of its use in mammals) were thought to far outweigh any disadvantages inherent in abandoning the old name and old abbreviation. For the pallium, we confronted the issue of whether sufficient data were available to conclude safely and unequivocally that given structures possessed one-to-one homology with specific structures in mammals. In the end, we concluded that sufficient evidence did not exist for such one-to-one equivalences at the pallial level, other than for the piriform cortex (Karten, 1969, 1991; Bruce and Neary, 1995; Striedter, 1997; Smith-Fernandez et al., 1998; Medina and Reiner, 2000; Puelles et al., 2000; Reiner, 2000; Butler and Molnár, 2002; Butler et al., 2002; Wada et al., 2001).

The goal then became to remove any incorrect connotation of homology to the basal ganglia in the case of those pallial structures with the term “striatum” in the name. Although it was agreed by all that the new names for these structures should have pallium in the name, 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 developing new names that allowed retention of existing abbreviations was desirable and could be achieved with esthetically pleasing new terms. Alternatively, consideration needed to be given to the possibility that a new and simple descriptive terminology that did not retain abbreviations could make avian brain structures easy to learn and more broadly accessible to neuroscientists. As is clear from the region-by-region commentary in the companion paper (Reiner et al., 2004), in the end, retention of abbreviations was found to be highly desirable for the most intensely studied structures of avian pallium, so there would be easy linkage and clear continuity between the literature using old and new terms. Further information and avian brain images depicting this new nomenclature are available in Reiner et al. (2004) and on the Avian Brain Nomenclature Exchange website: <http://avianbrain.org>. Further details on the terminology options discussed during the Forum meeting by its attendees will be presented in a later publication, in a special edition of *Brain, Behavior and Evolution* dedicated to the nomenclature revision.

Final comments

The Avian Brain Nomenclature Forum was the result of growing awareness of the communication problems caused by the faulty and outdated avian brain terminology. The Forum sought to devise a new terminology that is free of errors and promotes accurate understanding of avian brain organization and evolution. We have been scrupulous to use only names implying homology that we are certain would not themselves later prove to be in error. We believe that the nomenclature changes we have devised can serve the field well, and we urge all investigators to use this new terminology. In making its recommendations for terminology change for specific structures, the Forum does not mean to imply that the names for all other structures in the avian brain are adequate and suitable. Nonetheless, we believe that the names changed by the Forum are those that were in greatest need of change and were the greatest hindrance to accurate understanding of avian brain organization.

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