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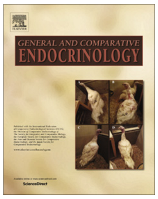

Review article

Mapping the brain of the chicken (*Gallus gallus*), with emphasis on the septal-hypothalamic region

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ABSTRACT

There has been remarkable progress in discoveries made in the avian brain, particularly over the past two decades. This review first highlights some of the discoveries made in the forebrain and credits the Avian Brain Nomenclature Forum, responsible for changing many of the terms found in the cerebrum and for stimulating collaborative research thereafter. The Forum facilitated communication among comparative neurobiologists by eliminating confusing and inaccurate names. The result over the past 15 years has been a standardized use of avian forebrain terms. Nonetheless, additional changes are needed. The goal of the paper is to encourage a continuing effort to unify the nomenclature throughout the entire avian brain. To emphasize the need for consensus for a single name for each neural structure, I have selected specific structures in the septum and hypothalamus that our laboratory has been investigating, to demonstrate a lack of uniformity in names applied to conservative brain regions compared to the forebrain. The specific areas reviewed include the distributions of gonadotropin-releasing hormone neurons and their terminal fields in circumventricular organs, deep-brain photoreceptors, gonadotropin inhibitory neurons and a complex structure and function of the nucleus of the hippocampal commissure.

1. Introduction

In 2002 a significant meeting, The Avian Brain Nomenclature Forum, was held with the goal of revising the terminology and thereby our understanding of all neural structures within the avian forebrain relative to that of other vertebrates. It was evident that many names that had been used in the avian brain were based upon false homology assumptions (Edinger, 1908; Ariëns-Kappers et al., 1960). Specifically, the telencephalon of birds was thought to be composed largely of highly developed basal ganglia (Reiner et al., 2004). Recent immunological, molecular and tract-tracing data documented that the avian basal ganglia occupied solely the ventromedial region of the anterior forebrain, as it does in mammals. The Forum members had discussions and conducted additional experiments for 2 years, from 2000 to 2002. With that information, 28 neurobiologists met at Duke University throughout a three-day period and changed most of the names in the telencephalon (Reiner et al., 2004; Jarvis et al., 2005). For the first time, the use of the terms published for the avian forebrain clearly indicated that the forebrain was not composed largely of basal ganglia and that birds possessed a substantial cortical-like brain region. The term cortex was not used for the substantial brain region covering the basal ganglia since by definition it did not have six layers of cells as displayed by mammals. The term pallium, meaning a cloak or covering, was used for cortical-like tissue. Since the 2004–05 publications, the suggested new terms have been adopted widely by the neuroscience community and more importantly, better communication has occurred among neuroscientists as well as among members of the very diverse avian research community.

The purpose of this paper is to address four objectives:

1) Review the progress made in structures mapped and named in the avian forebrain since the Avian Brain Nomenclature Forum.
2) Introduce an initiative to continue that effort throughout the avian brain.
3) Select a few septal and hypothalamic structures to demonstrate why consensus is needed even in the more conservative regions below the forebrain.
4) Emphasize a need to enhance the value of avian reference species for the ongoing

BRAIN initiative to map the human brain in more detail than ever before.

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2. Progress made in structures mapped and named in the avian forebrain

Despite the very different macro-structure of the mammalian 6-layered cortex compared to the avian grouping of cells throughout its pallium, a hypothesis was introduced nearly 50 years ago stating that on a cell-to-cell basis, the organization of this important brain region was not that different between birds and mammals. Specifically, it was proposed that there existed homology among avian pallial cells and the particular layered cells identified in each of the 6 layers characteristic of the mammalian cortex (Karten, 1969, 1991). During the past decade, data have supported that pioneering hypothesis. For example, a fundamental characteristic of the cortex of mammals was the presence of columns of neurons forming functional modules perpendicular to the cortical cell layers (Mountcastle, 1998). Although a column of neurons in the avian Wulst was documented (Pettigrew, 1979) and specific columns of neurons were proposed to exist within the avian pallium (Shimizu et al., 2010), the first solid evidence for the existence of functional columns was shown within field L (Wang et al., 2010), the pallial location of neurons in birds that respond to sound (Fig. 1) (Wang et al., 2010). Another laboratory independently showed that robust genetic mammalian markers that identify incoming sensory input into cortical-like tissue were highly conserved among vertebrates. They discovered that mammalian neocortical layer 4 neurons expressed the same set of markers from thalamic inputs as comparable pallial cell types in avian species that receive sensory thalamic inputs (Dugas-Ford et al., 2012). They also identified a conserved set of gene markers for output neurons from mammalian layer 5 functional columns in the cortex that likewise were found in a known output pallial region of birds, the arcopallium (Dugas-Ford et al., 2012). Input and output gene markers of the auditory and visual system in two different avian taxa (zebra finches and chicks) were identified. Regarding the avian visual system, layer 4-type sensory markers were found in the entopallium, the structure that receives thalamic visual input and the same conserved layer 5-type output markers were found in the avian arcopallium (Dugas-Ford et al., 2012). A recent study likewise documented detailed, functional columns within the avian visual system involving the entopallium (Fig. 2) (Ahumada-Galleguillos et al., 2015). The entopallium receives visual input from a major visual thalamic nucleus and neurons in those functional columns contain the same homologous genetic markers that signify layer 4-type mammalian input markers (Dugas-Ford et al., 2012). Functional columns were also shown for other sensory systems in birds (Fig. 3; Jarvis et al., 2013). An extensive gene analysis, particularly of the song system of birds and vocal learning system of mammals showed evidence that the avian nidopallium is similar to cortical layers 2/3 of mammals (Pfenning et al., 2014). For his seminal findings in avian neuroanatomy throughout his career and remarkable insight into the organization of the avian pallium, Dr. Harvey J. Karten was inducted into the National Academy of Sciences in 2015.

It is important to note that the cell-type homology hypothesis (Karten, 1969, 1997) is controversial. In a thoughtful paper (Medina et al., 2013), it was stated that the data of Dugas-Ford et al. (2012) supporting the cell-type homology hypothesis are inconclusive. The main reason was that the genes selected for comparison among mammalian, reptilian and avian species in the latter paper were not involved in early developmental events, rather were related to later maturational processes or functions of neurons. It therefore was emphasized that to identify specific homologies of adult structures, it is necessary to focus on early development as the processes are highly conserved. Utilizing sets of developmental regulatory genes that clearly differentiate dorsal pallium from its adjacent pallial regions was highly recommended (Medina et al., 2013). A competing hypothesis that has been proposed regarding the origin of cortical evolution is the tetrapartite pallium model (Puelles et al., 2017, 2007, 2016; Puelles, 2011). It has been developed utilizing genes expressed early in embryonic development in order to understand a fundamental Bauplan (body or brain plan of morphological features) shared by all vertebrates.

Other refinements in the nomenclature and new functional divisions have been suggested for the avian pallium. Specifically, a partial, mirror image organization of the avian cerebrum has been proposed (Jarvis et al., 2013). Primary sensory input into the pallium was shown to occur in two parallel avian locations: the intercalated hyperpallium and intercalated nidopallium (Fig. 3). Primary sensory neurons in the former project to secondary hyperpallium interneurons and to tertiary interneurons in the dorsal region of the mesopallium. Primary sensory neurons in the latter project to secondary nidopallium interneurons and to tertiary interneurons in the ventral region of the mesopallium. Output from the two parallel cerebral circuits in the pallium occurs within the arcopallium (Jarvis et al., 2013). Recently, the long-sought-after claustrum homology in avian species has been

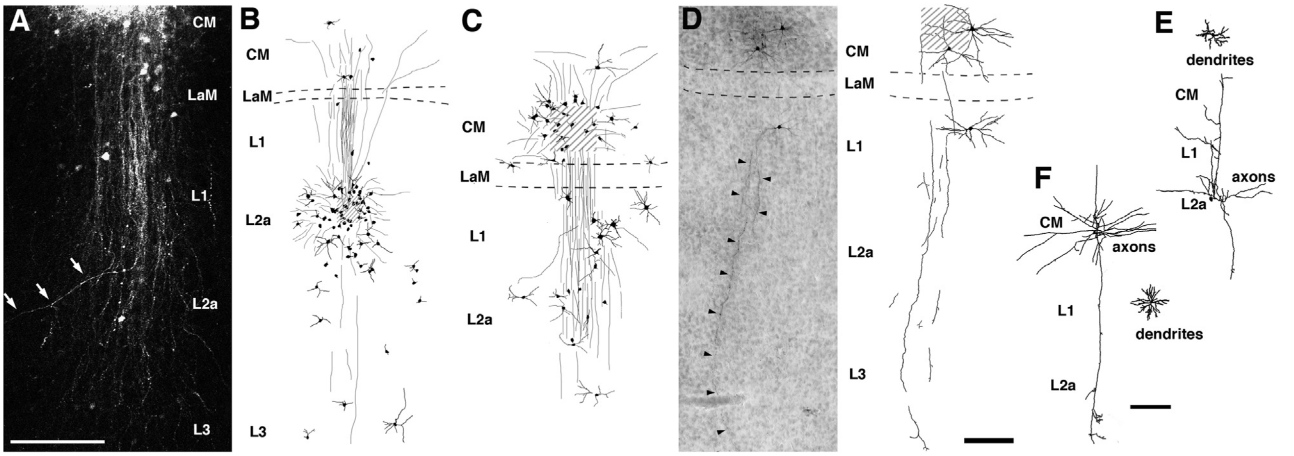

Fig. 1. Columnar organization of the Field L auditory complex in chicks. A. Confocal microscopic image of labeling following an injection of biotinylated dextran amine (BDA) conjugated with rhodamine into caudal mesopallium (CM). Labeled neurons were restricted within a column crossing four layers. B-D. Labeled neurons and fibers following a BDA injection into Field L2a (B) and CM (C and D). Dashed lines indicate location of a mesopallial lamina (LaM). E and F. Intracellularly filled neurons in L2a (E) and CM (F). [Scale bars: 200 µm in A-D, 200 µm (E, F)]. [Reproduced from Wang et al. (2010)].

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