Opinion piece

Avian evolution: from Darwin's finches to a new way of thinking about avian forebrain organization and behavioural capabilities

The study of birds, especially the Galapagos finches, was important to Darwin in the development of the theory of evolution by natural selection. Birds have also been at the centre of a recent reformulation in understanding cerebral evolution and the substrates for higher cognition. While it was once thought that birds possess a simple cerebrum and were thus limited to instinctive behaviours, it is now clear that birds possess a well-developed cerebrum that looks very different from the mammalian cerebrum but can support a cognitive ability that for some avian species rivals that in primates.

Keywords: Darwin's finches; basal ganglia; cerebrum; pallium; avian intelligence; telencephalic evolution

1. INTRODUCTION

The 13 different species of Galapagos finches that came to be known as Darwin's finches played an important role in Darwin's theory of evolution by natural selection (Lack 1947). These finches are similar in body size but differ in beak size. Although Darwin collected these and other birds during the layover of the HMS Beagle at the Galapagos Islands, the finches were so different in beak size from common finches that Darwin at first did not realize they were all finches. Upon his return to England, Darwin gave his collected specimens to the British ornithologist John Gould for identification. Gould came to realize that the disparate birds that Darwin had regarded as blackbirds, grosbeaks and finches were in fact 13 new species of ground finches. This helped Darwin form the idea that the different finch species had evolved from common ancestors that had flown from the mainland and adapted diversely to the foods on the different Galapagos Islands (Desmond & Moore 1991). While Darwin did not specifically refer to the finches in *On the Origin of Species*, he did mention the divergence of island avian species as evidence for evolution by natural selection (Darwin 1859). The finches were, however, described by him in the 1845 edition of *The Voyage of the Beagle*. He ended his

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One contribution of 10 to a Special Feature on 'Brain evolution'.

discussion of the finches in *The Voyage* by stating, 'Seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends' (Darwin 1845).

The study of birds has also been central to a more recent event in evolutionary thought, in this case a shift in how neuroscientists view brain evolution and the neural underpinnings of complex cognitive abilities. As with Darwin's finches, superficial appearance at first deceived scientists, but only with closer scrutiny was the reality grasped.

2. OLD IDEAS ABOUT VERTEBRATE BRAIN EVOLUTION

The older ideas about vertebrate brain evolution had their origins in the early twentieth century. The German neuroanatomist Ludwig Edinger was at the forefront, followed by his student Ariëns-Kappers (Edinger *et al.* 1903; Ariëns-Kappers 1909). They studied variation in the structure of brain among living species, because nervous system does not ossify, and they used simple stains of neuronal cell bodies and fibre tracts. Because of these limitations, their conclusions about homologies among brain regions were based on the general shape of the regions and the appearance and distribution of cells within them. For example, the telencephalon in mammals possesses two distinct regions that were evident to neuroanatomists of the early twentieth century: (i) the outer rind, whose neurons are arrayed into six layers that are spanned by the ascending dendrites of the neurons making up the layers, and (ii) a more centrally and basally located region whose neurons are uniformly distributed and possess radially symmetrical dendritic trees (electronic supplementary material, figure 1). Owing to its uniqueness to mammals and its lamination, the former region was named the neocortex, and due to its basal position and nuclear configuration the latter was termed the basal ganglia. Since most of the avian telencephalon resembled mammalian basal ganglia in its appearance, Edinger and Ariëns-Kappers concluded that birds lacked a neocortex and instead possessed a basal ganglia-dominated cerebrum (electronic supplementary material, figure 1).

Edinger and Ariëns-Kappers studied other vertebrate groups using the same approach, and developed a theory of vertebrate brain evolution. They concluded that while hindbrain, midbrain and diencephalon had been conservative, telencephalon had expanded by stepwise addition of new parts, beginning with a cerebrum devoted to olfaction in ancestral jawless fishes. In their view, a globus pallidus (called the paleostriatum owing to its presumed antiquity) was added in jawed fishes, a neostriatum was added in amphibians and a simple cerebral cortex in stem amniotes. Birds were thought to have elaborated the basal ganglia of stem amniotes and mammals have evolved neocortex from primitive stem amniote cerebral cortex. This *scala naturae* view of brain evolution became the dogma (Ariëns-Kappers *et al.* 1936), and it underpinned the flawed neuroanatomical terminology

for avian telencephalon employed throughout the twentieth century.

The theory of Edinger and Ariëns-Kappers implied that birds are intellectually inferior to mammals. Three scientific *Zeitgeists* reinforced this idea. First was the view that a neocortex was essential for a flexible behavioural repertoire (Elliot-Smith 1901). Consequently, since avian telencephalon was regarded as large basal ganglia, birds were presumed to lack the neural substrate for complex learning and cognition. Second, the basal ganglia were thought to be the repository for instinctive behaviours (Elliot-Smith 1901). Thus, any sophisticated avian behaviour was interpreted as a complex instinctive behaviour. Finally, behaviourism interpreted avian behaviour as the automatic execution of stimulus–response sequences, since it eschewed cognitive explanations of behaviour (Watson 1924).

3. NEW IDEAS EMERGE

Evidence rebutting this classical view began to accumulate in the 1960s with the advent of hodological and neurochemical methods. These methods revealed that only a limited basal part of avian telencephalon had the traits of mammalian basal ganglia (electronic supplementary material, figure 1) (Karten 1969; Reiner *et al.* 2005). Later studies revealed that the basal ganglia in both birds and mammals develop from a basal cerebral territory called the subpallium, and the circuitry, cell types and function of the basal ganglia are very similar in the two groups (Puelles *et al.* 2000; Reiner *et al.* 2005). Thus, it became clear that the basal ganglia occupy a smaller territory in the avian telencephalon than once realized.

The nature of the extensive territory above the true basal ganglia in birds began to be revealed by the pathway tracing and behavioural studies of Karten and colleagues, beginning in the mid-1960s (Karten 1969; Nauta & Karten 1970). They showed that the structures which were thought to be part of the striatal part of the basal ganglia in birds and had thus been called the neostriatum and hyperstriatum receive visual, auditory and somatosensory input from thalamus, and play a role in sensory information processing resembling that of neocortex in mammals. Additionally, the upper part of the hyperstriatum and the region then termed the archistriatum in birds were found to give rise to major descending projections to the brainstem and spinal cord reminiscent of the outputs of mammalian motor cortex. Karten concluded that the hyperstriatum and neostriatum were pallial territories functionally akin to mammalian neocortex, as later confirmed by others (reviewed in Reiner *et al.* 2005). Moreover, avian pallium was found to be organized into modality-specific nuclei that resemble the layers of mammalian neocortex and possess inter-region connections reminiscent of those between neocortical layers. Owing to these realizations, the terminology for the avian telencephalon was recently revised to be consistent with accurate understanding of avian telencephalic organization (Reiner *et al.* 2004).

4. SIMILAR COMPLEX PROBLEM SOLVING: DIFFERENT FOREBRAIN SUBSTRATES

It is also now appreciated that many avian species are capable of sophisticated foraging strategies, elaborate parental and social behaviour, challenging homing and migratory behaviour, and/or complex vocal learning, with some avian groups even showing behavioural and cognitive skills comparable with those of primates (Marler 1996; Doupe & Kuhl 1999; Emery & Clayton 2004). The studies of Pepperberg (1999) with African grey parrots, in particular, showed that these parrots can meaningfully use human words, and grasp simple numerical and relational concepts. Similarly, New Caledonian crows can make tools out of twigs to retrieve inaccessible food, and pass this skill to other crows (Hunt 2000; Weir *et al.* 2002).

5. HOW DID AVIAN PALLIUM DIVERGE FROM MAMMALIAN PALLIUM?

Did mammalian neocortex and what are now called avian hyperpallium–mesopallium–nidopallium derive from the same antecedent within the telencephalon of stem amniotes (electronic supplementary material, figure 2)? Recent opinions are divided into two camps. Both accept that stem amniotes possessed a simple dorsal cortex that was the forerunner of the superior part of mammalian neocortex, and the hyperpallium in birds (Medina & Reiner 2000). The two camps diverge on the origin of mammalian temporal neocortex and the avian mesopallium–nidopallium. One viewpoint posits that temporal neocortex arose *de novo* after the divergence of the lineages leading to modern mammals on one hand and to living reptiles and birds on the other (Bruce & Neary 1995; Striedter 1997; Puelles *et al.* 2000). This perspective further proposes that the mesopallium–nidopallium of birds derives from a pallial region in stem amniotes that in the mammalian lineage gave rise to the claustrum, endopiriform region and/or pallial amygdala (electronic supplementary material, figure 2). As evidence, proponents point to the common location of avian mesopallium–nidopallium and mammalian claustrum–endopiriform–pallial amygdala deep to piriform cortex and a similarity in the expression of some developmentally regulated genes. This hypothesis has the difficulty that the thalamic projections to claustrum–endopiriform–pallial amygdala are either meagre or do not resemble those to avian nidopallium (Reiner *et al.* 2005). The other explanation proposes that a region ventrolateral to dorsal cortex in stem amniotes gave rise to temporal neocortex and mesopallium–nidopallium (Karten 1969; Nauta & Karten 1970; Butler 1994; Reiner 2000). Evidence offered for this view includes the observation that the continuity of dorsal cortex and mesopallium–nidopallium in primitive reptiles (i.e. *Sphenodon*) resembles that of mammalian superior and temporal neocortices, and the great similarity in connectivity and neurochemistry of the thalamus with specific visual and auditory pallial regions.

So, is avian mesopallium–nidopallium a highly functionally transformed version of structures that in mammals are also non-laminated but perform visceral

and affective functions (e.g. amygdala)? Or is much of avian pallium a structure that looks different from its mammalian homologue (neocortex) but performs similar functions? In either case, study of birds has revealed that higher order cognition can be carried out without a laminated cerebral cortex, which earlier generations of neuroscientists had regarded as impossible.

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