CellPress

Review

Cognition without Cortex

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Assumptions on the neural basis of cognition usually focus on cortical mechanisms. Birds have no cortex, but recent studies in parrots and corvids show that their cognitive skills are on par with primates. These cognitive findings are accompanied by neurobiological discoveries that reveal avian and mammalian forebrains are homologous, and show similarities in connectivity and function down to the cellular level. But because birds have a large pallium, but no cortex, a specific cortical architecture cannot be a requirement for advanced cognitive skills. During the long parallel evolution of mammals and birds, several neural mechanisms for cognition and complex behaviors may have converged despite an overall forebrain organization that is otherwise vastly different.

Trends

Cognition in corvids and parrots reaches the same level of excellence and diversity as in apes. Among others, bird cognition encompasses abilities such as delay of gratification, mental time travel, reasoning, metacognition, mirror self-recognition, theory of mind, and third-party intervention.

The cerebrum of birds and mammals is homologous but very differently organized.

Birds lack a neocortex but have instead several large pallial aggregations without apparent laminar structure. However, according to some scientists, these aggregations might correspond to cortical layers.

Independent from each other, birds and mammals have developed similar brain organizations that could constitute the neural basis of their cognitive skills. Birds have a functional analog to the prefrontal cortex that generates executive functions. Their telencephalic connectome is highly similar to that of diverse mammalian species and they show a 'hidden' lamination that resembles cortical canonical circuits in parts of their sensory pallial territories.

Convergent Evolution of Cognition and Brain

What happens at the neural level when two groups of animals converge during evolution with regard to their cognitive skills? Do their brains also assume a similar neural architecture? Or are differently organized nervous systems able to produce comparable cognitive abilities? This is a foundational question for the field of Cognitive Neuroscience. Recent discoveries in birds have yielded new insights and represent a promising direction for finding answers.

The class of mammals to which we humans belong is extremely successful. Mammals live in practically all ecological niches in which vertebrates can survive. And wherever mammals occur, they represent some of the top predators [1]. This phylogenetic success story is, at least in part, due to the ability of mammals to innovate novel behaviors in changing environments, incorporate contextual information into their decisions, and learn from various social situations, thereby increasing their survival rate [2]. These and other cognitive abilities are key to the spread of mammals into practically every corner of our planet. Birds represent an equally successful vertebrate class, and novel studies testify that they generate many of the same cognitive functions as mammals [2–5]. But the evolutionary lines of birds and mammals separated approximately 300 million years ago [4]. This extremely long period of **parallel evolution** (see Glossary) is readily visible in the organization of mammalian and bird brains. Both classes have a large **cerebrum** that makes up most of the brain and that can be subdivided into a pallial and a subpallial territory (in Latin '**pallium**' means mantle). The **subpallium**, in which the striatum is the largest component, has a strikingly similar organization in mammals and birds [6]. It is even likely that the basic circuitry of most of the subpallium is similar across animals from lampreys to humans, and can be traced back to a common ancestor that lived approximately 535 million years ago [7].

It is much more difficult to understand the evolutionary trajectories of the pallium in the different classes of vertebrates. In mammals, the pallium is dominated by the **neocortex** that covers most of the forebrain. There are meanwhile doubts on the evolutionary novelty of the 'neo'cortex [8]. But we will use this term for lack of a better one. The six-layered appearance of the neocortex is the hallmark of a mammalian brain. A highly maintained **laminar** and columnar architecture is apparent across all mammalian species. There is no comparable structure in the bird telencephalon. As visible in Figure 1, the avian pallium is characterized by several large nuclear aggregations without any laminar structure apparent. In the late 19th to early 20th century, this

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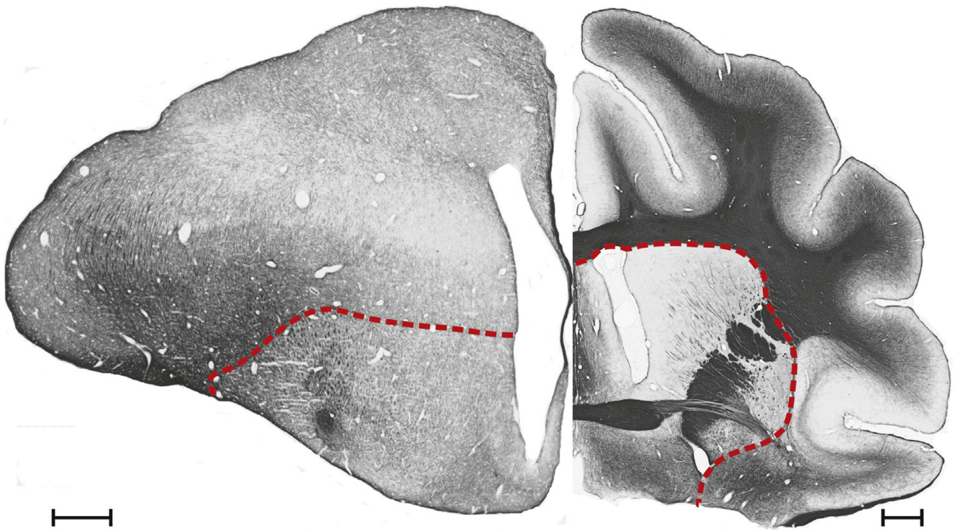

Trends in Cognitive Sciences

Figure 1. Anatomical Depiction of a Bird and a Mammal Brain. The frontal section shows the forebrain of a pigeon (left) and of a ferret (right), brought to the same height. In both cases a Gallyas staining of myelinated axons was used. The red dotted line depicts the border between the pallium (above) and the subpallium (below). In the ferret, the most ventral part of the section also encompasses parts of the diencephalon. Note the typical cortical morphology of the pallium in the ferret brain. Nothing comparable is discernible in the pigeon. Scale bars = 1 mm. Ferret brain section: courtesy of Claudia Distler.

glaring difference sparked the idea of a stair-step evolutionary development of the vertebrate brain: it was assumed that mammals were the last class to evolve, and with their emergence the six-layered cerebral cortex became a *de novo* brain area (ergo, 'neo-cortex'). Earlier neural structures were thereby all retained. It was assumed that higher cognitive abilities must depend on cortical processing, and because birds do not have a cortex, birds should be incapable of higher cognition [4,9].

We now know that this is wrong [4,10,11]. But how solid is the recent evidence for advanced cognitive abilities in birds? Could it be that cognition in birds is highly specialized in few domains such that we overestimate their mental prowess when testing them in their narrow areas of cognitive excellence? Moreover, if birds do indeed have broad and excellent cognitive capabilities, how do they generate these mental skills without cortex?

Bird Cognition Is Not Inferior to Mammalian Cognition

Traditionally, birds have been used as model systems for studying learning and memory, optimal foraging decisions, and song [12]. More recently, 'higher' cognitive abilities that are considered to underlie physical and social problem-solving abilities such as aspects of impulsive control, inferential reasoning, planning ahead, perspective taking, and role understanding were included. It has been argued that these skills, often subsumed under the term 'complex' cognition, form a cognitive tool-kit comparable to that of mammals [13]. Although also reptilian cognition should not be underestimated, nothing at the level and scope of bird cognition has been reported for this animal group so far [14]. Thus, it is likely that mammalian and avian complex cognition represent convergent developments.

Critiques have pointed out that most studies on bird cognition have tested these animals in narrowly defined domains with few paradigms [15,16]. Food-hoarding is a good example. Most **corvids** store food for later consumption and this behavior is very useful for asking cognitive questions under laboratory conditions, including sophisticated topics such as mental time travel,

Glossary

Cerebrum: those parts of the brain that contain the pallial and subpallial territories. In mammals this incorporates the cortex, the hippocampus, the claustrum, the amygdala, the basal ganglia, and the olfactory bulb.

Convergent evolution (or homoplasy): refers to the independent evolution of similar characters in species of different lineages due to comparable selection pressures. Convergent evolution results in analogous characters with similar appearances or functions, although these were not present in the last common ancestor of the two lineages.

Corvids: birds of the crow family, a relatively closely related group of oscine passerine birds that includes crows, ravens, rooks, magpies, choughs, jays, and nutcrackers, and is found worldwide. Most species are characterized by a high brain-to-body mass ratio, ecological flexibility, and a complex social life, featuring long-term partnerships and dynamic groups structured by social relationships.

Hodology: the study of pathways between brain areas. The term derives from the Greek word hodos which means 'road'.

Homology: describes cases in which a shared trait of two species can be traced back to a common ancestor without interruption.

Laminar: most of the neocortex has six cellular layers or laminae. Each layer is constituted by distinctive cell populations with unique connectivity patterns. At first glance, neocortical lamination looks uniform (and is therefore sometimes called 'isocortical'). But a closer look reveals multitudes of subtle differences between neocortical areas.

Neocortex: the usually six-layered sheet of gray matter that constitutes the outermost part of the cerebrum of the mammalian brain.

Pallium: refers to the upper surface of the cerebrum and incorporates cortex or cortex–homolog structures, hippocampus, pallial amygdala, claustrum, and olfactory bulb.

Parallel evolution: describes the evolution of a similar character starting from a comparable ancestral condition. Thus, during parallel evolution two taxa start by sharing a similar ancestral character and then

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