The avian ‘prefrontal cortex’ and cognition
Onur Güntürkün

Both mammals and birds can flexibly organize their behavior over time. In mammals, the mental operations generating this ability are called executive functions and are associated with the prefrontal cortex. The corresponding structure in birds is the nidopallium caudolaterale. Anatomical, neurochemical, electrophysiological and behavioral studies show these structures to be highly similar. The avian forebrain displays no lamination that corresponds to the mammalian neocortex, hence lamination does not seem to be a requirement for higher cognitive functions. Because all other aspects of the neural architecture of the mammalian and the avian prefrontal areas are extremely comparable, the freedom to create different neural architectures that generate prefrontal functions seems to be very limited.

Addresses
Department of Biopsychology, Institute of Cognitive Neuroscience, Faculty of Psychology, Ruhr-University Bochum, 44780 Bochum, Germany

Corresponding author: Güntürkün, Onur (onur.guentuerkuen@rub.de)

Introduction
Mammals such as humans, macaques or rats can adjust their behavior to changing demands. They are capable of reversing learned behavioral choices, selecting appropriate responses according to contextual information, and withholding actions until a suitable situation occurs. In short, they optimally organize their behavior over time. The set of cognitive skills required for this behavioral optimization is called ‘executive functions’ (see glossary) and is associated with the operations of the prefrontal cortex (PFC). The phylogenetic success of the order of mammals is probably related to the extraordinary cognitive flexibility that is generated by prefrontal circuits. Birds represent a broadly equally successful vertebrate order and a vast literature on avian cognitive skills testifies that birds are able to generate the same set of executive functions as mammals [1*]. However, birds and mammals differ substantially with regard to the organization of their forebrains, with birds lacking a laminated cortex. So, which neural mechanisms do birds use to generate the cognitive functions for which the PFC is required in mammals?

Comparing brains
The most obvious difference between the forebrains of mammals and birds is the lack of a laminated cortex within the avian telencephalon. The mammalian cortex, including neo-, archi- and paleocortical components, together with the claustrum and lateral parts of the amygdala, constitutes the forebrain pallium [2]. Pallium, striatum and pallidum make up the cerebrum. The absence of a laminated component within the avian cerebrum has led previous authors to believe that birds have virtually no pallium but an enormously hypertrophied striatum instead. However recent work fostered a new understanding of the avian telencephalic organization and the assumed homologies between avian and mammalian brain components [3]. This paradigm shift enables different conclusions about telencephalic evolution in vertebrates. It is now apparent that the organization of the basal ganglia is highly conserved among birds and mammals, whereas the organization of the pallial domains is more varied. The conserved organization of striatum suggests that there are constraints on how the basal ganglia can be organized, whereas the different organization of the pallium suggests that there are more variations on how this forebrain entity can be structured. This view has important implications for understanding brain mechanisms of cognition.

Birds possess a large pallium that makes up most of their forebrain volume. Thus, the mammalian neocortex is homologous to these avian pallial domains in terms of its shared pallial identity deriving from common ancestry [4*]. This, however, does not imply that cortical areas are one-to-one homologous counterparts to pallial components in birds. As outlined below, different pallial constituents of birds and mammals can be extremely similar in terms of anatomical, physiological and cognitive characteristics but still represent the result of convergent evolution.

Anatomy of an avian ‘prefrontal’ circuit
The PFC of mammals is densely innervated by dopaminergic fibers from the ventral tegmental area and the substantia nigra [5]. This dopaminergic innervation was usually taken as a characteristic element of the PFC. Based on behavioral evidence, Divac and colleagues proposed that a region in the dorsolateral forebrain of pigeons (nidopallium caudolaterale: NCL) is comparable with the mammalian PFC [6]. Subsequently, they
showed that the NCL is densely innervated by catecholaminergic fibers of probably dopaminergic nature (Figure 1; [7,8]). Later studies demonstrated that the NCL is indeed one of the main termination areas of dopaminergic fibers from the ventral tegmental area and the substantia nigra [9,10]. Most dopaminergic terminals within the NCL terminate on dendritic shafts and spines in close apposition to unstained asymmetric (probably excitatory) synapses [11] and primarily activate dopamine D1 receptors [12,13]. This architecture is identical to the organization of the PFC, where dopamine is thought to modulate, pre- and postsynaptically, the excitatory afferents to pyramidal cells through this triadic synaptic arrangement [14,15]. What differs between the NCL and PFC, however, is the dopaminergic input onto GABAergic interneurons. Whereas dopaminergic fibers in PFC also act via D1 receptors on GABAergic interneurons [14], inhibitory interneurons within the NCL do not seem to be positive for D1 receptors [16].

Sensory input reaches the PFC via a set of interconnected pathways that show a considerable overlap of different modalities. The primary sensory area of each modality projects first to an adjacent area, which then projects not only to the next modality-specific association area in line but also to a discrete area of the frontal cortex, which in turn reciprocates by sending fibers back to the projecting area [17]. This is identical for the NCL, which receives afferents from secondary and tertiary sensory areas of all modalities and projects back onto them [18]. In addition, the NCL projects to most parts of the somatic and limbic striatum, as well as to motor output structures [19]. Thus, identical to PFC, the avian NCL is a convergence zone between the ascending sensory and the descending motor systems. In addition, the NCL and PFC resemble each other in terms of their connections with the amygdala, the accumbens, visceral structures [19,20] and diverse chemically defined afferent systems (Figure 2; [21–23]).

One difference between the NCL and PFC is, however, the thalamic input. The mammalian PFC receives afferents from the mediodorsal (MD) nucleus of the thalamus [24]. Thalamic afferents to the NCL arise mainly from the dorsolateral posterior nucleus [19], which is not homologous to the MD nucleus [25] but still seems to serve similar functions [26]. Taken together, a comparison of the anatomical networks defining the NCL and PFC shows a large number of similarities with only few differences. Like the PFC, the avian NCL is a multimodal forebrain area that is located at the transformation from sensation to action, is modulated by dopaminergic fibers, and is tightly interrelated with structures serving limbic, visceral and memory-related functions.

**The mental ability to bridge time**

The prefrontal areas of mammals contribute to goal-directed sequences of behavior along the temporal domain [27]. Central to this capacity is the ability to hold information currently attended online for later use. This is usually tested in delay tasks such as delayed alternation learning (see glossary) in which the animal is required to alternate between the two response sites with an enforced delay. 

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**Figure 1**

Side view of a human and of a pigeon brain. The PFC and NCL are depicted in green. The pigeon brain in the lower middle part of the figure is to the same scale as the human brain.
delay between responses. Beginning with the first study of Mogensen and Divac [6], several authors have shown that, similar to PFC lesions, NCL lesions also result in delayed alternation deficits [26,28,29]. To disentangle the delay and the spatial component of the delayed alternation task, Diekamp et al. [30] conducted a nonspatial object-related working memory experiment in which the color of sample stimuli had to be maintained over delay periods. The results show that the working memory performance of the pigeons was reduced proportional to NCL-lesion size without causing deficits in sensory discriminations.

During the waiting period of delay tasks, PFC neurons show elevated sustained activity levels during the physical absence of the sample stimulus. This activity pattern probably represents the relevant stimulus [31] and/or the attended location [32*]. Similarly, a class of neurons within the NCL show elevated activity levels during the delay period [33]. Whole-cell patch-clamp recordings in the NCL reveal a class of neurons with an initial tonic firing and a relatively hyperpolarized action potential threshold [34]. This possibly enables activation by weak excitatory inputs and produces a sustained firing mode as required for short-term memory episodes (see glossary). In pigeons, firing patterns of delay neurons are related to the success rate of maintaining the relevant event [33]. Additionally, the ability of these cells to differentiate between rewarded and unrewarded stimuli correlates with the overall discrimination performance of the animal [35].

In mammals, the release of dopamine (DA) within the PFC and the subsequent activation of D1 receptors [36] plays a major role in sustained activity levels of delay cells and the animals' performance in working memory tasks [37]. Likewise in pigeons, local blockade of D1 receptors within the NCL selectively disrupts working memory performance [38]. Modulation of various stimulus-driven prefrontal inputs requires DA release within the PFC to be less precise with respect to time and synaptic location [39]. Indeed, the effective duration of extracellular prefrontal DA is rather long as a result of slow reuptake by DA transporters [40]. This diffusion-mediated volume transmission of prefrontal DA contrasts with striatal conditions, which are characterized by a fast reuptake system. An in vivo microdialysis study of the extracellular values of DA and its metabolites within the pigeon's NCL and striatum revealed identical conditions and showed that DA utilization in the NCL also follows a volume transmission mode (see glossary) [41].

The mental ability to bridge a time span requires a cascade of events that includes prefrontal DA release, activation of D1 receptors in a volume transmission mode, and finally sustained activity patterns of goal-coding pre-
frontal neurons that enable the animal to mentally hold active relevant information and shelter it against interfering input. On neurochemical, cellular and behavioral levels these events seem to unfold in virtually identical ways in the mammalian PFC and the avian NCL.

The cognitive control of mental shifts
Besides the ability to hold active relevant information during a waiting time, delayed alternation tasks also require the animal to switch from one (just rewarded) alternative to the other. Prefrontal lesions interfere with this kind of cognitive flexibility, resulting in a tendency to perseverate on previously rewarded stimuli [42]. These perseverations become most obvious during reversal tasks in which the animal that was previously rewarded for responding to, say, the green key, is now rewarded for choosing red. Several authors showed that NCL lesions [43,44] or blockade of D1 [45] or N-methyl-D-aspartate

Figure 3

(a) Sequence of events on (i) remember trials, (ii) forget trials and (iii) forget-probe trials. On remember and forget-probe trials the birds were presented with a test period, whereas on forget trials the test period was absent. The three horizontally arranged circles represent pecking keys along the wall of a conditioning chamber. The animals were trained to peck on the central key during the sample period, to remember the stimulus during a subsequent delay and finally to peck on the matching side key during the comparison period. However, this sequence was only to be executed if a tone during the cue period signaled a remember trial (R). If the tone signaled a forget trial (F), the animals were usually not confronted with a comparison period and could forget the sample stimulus. Only on occasional forget-probe trials were the keys lit to test if the pigeons were indeed unable to recall the previous sample. (b) Response profile of all NCL neurons with excitatory delay activities. The cue and the delay periods are shaded in gray. The vertical dashed lines separate the different periods of the task. Delay activity persists during remember trials (blue), but vanishes when the cue signals the onset of a forget trial (red). Abbreviations: ITI, intertrial interval; R, remember cue; F, forget cue. Used with permission.
(NMDA) receptors [46] within the NCL reduce performance in reversal tasks.

One crucial component of reversal is extinction, because the animals have to extinguish the previously learned association between a stimulus–response component and a subsequent reinforcement. Usually, the extinction and the response inhibition components cannot be properly differentiated in reversal tasks. Lissek and Güntürkün [47] introduced a new experimental design that is able to differentiate these two constituents by forcing the animals to first wait during presentation of a red light and then to peck during a green light. Subsequently, the extinction period started in which the animals were no longer reinforced for pecking during the green light. Blocking NMDA receptors within the NCL did not increase responses to the red key (unimpaired response inhibition) but rendered the animals unable to stop their responding to the green key (absence of extinction learning). Thus, activation of the NMDA receptors of the NCL is required for extinction learning and, therefore, contributes to tasks that demand cognitive flexibility such as during reversal learning.

Executive control requires several further mental faculties such as response selection, proper scheduling of behavioral components and the ability to adjust one’s own responses to changing contextual requirements. Several lesional or NMDA-blockade experiments demonstrated that the NCL contributes to these cognitive operations [26,44,48,49]. A further component of cognitive flexibility is the ability to remember relevant information selectively and to discard irrelevant information. A recent elegant study [50] showed that neurons of the NCL evince sustained activation throughout the delay period of a memory task when pigeons were instructed to remember the stimulus. When instructed to forget, not only was the neuronal sustained activation abolished, but also the behavioral performance dropped to chance level (Figure 3). To sum up, these studies exploring the neural basis of avian executive functions not only show that birds are able to generate the same cognitive skills as mammals but also demonstrate that the PFC and NCL resemble each other in being a central component of these processes.

Making decisions in a complex world

Animals must continuously make decisions about, for example, where to feed, when to fight, and with whom to mate. Their decisions imply a constant weighing of the costs and benefits of their activities and ultimately deter-
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Outstanding questions

- What (if any) are the advantages of cortical lamination, if the same cognitive operations can be performed by the un laminated avian pallium?
- Is the avian pallium constituted by repetitions of canonical circuits, as is the case for the neocortex?
- What are the computational demands that define the core of executive functions? These demands probably constituted the first step of a convergent evolution of mammalian and avian brains that resulted in the high degree of similarity between PFC and NCL.

Conclusions

The mammalian PFC and the avian NCL show an astonishing degree of resemblance in terms of anatomical, neurochemical, electrophysiological and cognitive characteristics. Based on topographical and genetic arguments [2,58], however, they do not seem to be homologous as a telencephalic entity within the pallium but probably represent a case of evolutionary convergence (homoplasy). The discovery of this convergence in terms of neuronal circuits is paralleled by recent studies that clearly reveal that, in particular, corvids and parrots are able to generate cognitive abilities identical to apes [59–62]. Emery and Clayton [1] argue that these common cognitive operations derive from a shared cognitive tool kit consisting of causal reasoning, flexibility, imagination and prospection. Most of these shared cognitions thus depend on the PFC and the NCL.

Because the nonlaminated NCL is able to generate the same set of executive functions as the PFC, lamination cannot be a structural requirement for higher cognitive functions. Other anatomical and neurochemical conditions are, however, virtually identical between the NCL and PFC. This makes it likely that there exist only very limited neural solutions for the realization of higher cognitive functions. The freedom to create different neural architectures that are able to generate the same cognitive operations seems to be very restricted. As a consequence, a selection pressure for complex cognitive abilities probably resulted in the convergent evolution of highly similar associative forebrain structures within two classes of vertebrates that otherwise have vastly different brains.

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
- of outstanding interest


This review provides a new interpretation of the evolution of cognition. According to the authors, corvids and apes went through series of convergent evolutionary steps resulting in the constitution of the same set of higher cognitive functions. The existence of this common cognitive tool kit enables both corvids and apes to efficiently deal with the complexities of their physical and social world.


This paper represents a new perspective on the organization of the bird brain. It asserts that the century-old traditional nomenclature is outdated and does not reflect new molecular, genetic and behavioral studies that portray birds as comparable with mammals in their cognitive abilities and their telencephalic organization.


42. Alda-vence L, Costa-Miseraçs D, Divac I, Delius JD: Presumed ‘prefrontal cortex’ lesions in pigeons: effects on...


50. Rose J, Colombo M: Neural correlates of executive control in the avian brain. PLoS Biol 2005, 3:e190. A compelling study showing the involvement of NCL neurons in the decision either to actively remember or to forget visual stimuli. The authors interpret this as neural trace of the executive control of behavior, a hallmark of human frontal lobe function.


52. Machens CK, Romo R, Brody CD: Flexible control of mutual inhibition: a neural model of two-interval discrimination. Science 2005, 307:1121-1124. The authors conducted a task in which monkeys had to perceive a stimulus, maintain it for several seconds, and then compare it with a second stimulus, to decide immediately which of the two stimuli was larger. Single prefrontal neurons encoded the first stimulus and actively maintained it during delay. In the decision phase, however, they coded for the comparison between the two stimuli. Thus, this study demonstrates that prefrontal neurons adapt to task contingencies by dynamically switching between distinct behaviors.


In decision making, preference for a reward depends on the subjective value of the reward, which is a function of its amount and its delay-to-reward. In this paper, the authors provide evidence for a reward value signal of single NCL neurons reflecting the integration of the two crucial parameters ‘amount’ and ‘delay-to-reward’. This compound activation appeared to be modulated by the temporally discounted subjective value of the upcoming reward, and covaried with the animals' reward preference.


