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The avian 'prefrontal cortex' and cognition

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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.

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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

Glossary

Executive functions: a small cluster of functions that are associated with the prefrontal area and that control and manage cognitive processes such as planning, cognitive flexibility, decision-making, and inhibiting inappropriate actions.

Delayed alternation learning: an experimental paradigm in which the subject or the animal is confronted with two response keys that both can provide reward. The task consists of a continuous alternation between the two keys with an enforced delay between responses. Prefrontal lesions interfere with the ability to switch from one rewarded side to the other while keeping in mind which side is to be chosen next.

Short-term memory episodes: the limited amount of time in which a limited amount of information is temporarily and actively stored.

Volume transmission: neurochemical transmission mode which is characterized by a slow and/or less extensive reuptake of extracellular neurotransmitters. The volume transmission mode of prefrontal dopamine results in an enhanced life time and a diffusion over longer distances of this transmitter.

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

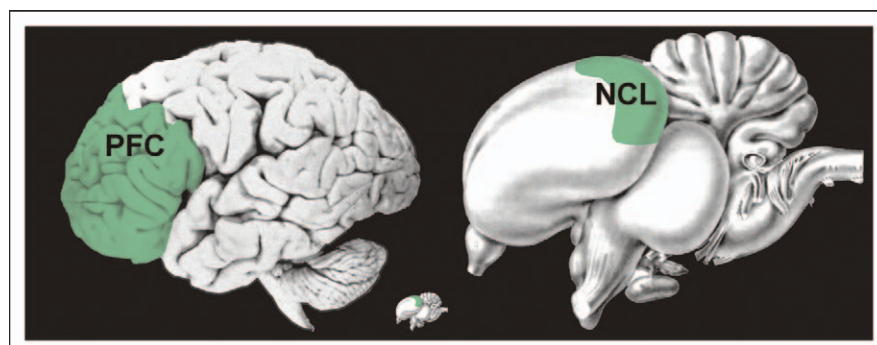
modalities. The primary sensory area of each modality projects first to an adjacent area, which then projects not only to the next modality-specific association area in line but also to a discrete area of the frontal cortex, which in turn reciprocates by sending fibers back to the projecting area [17]. 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

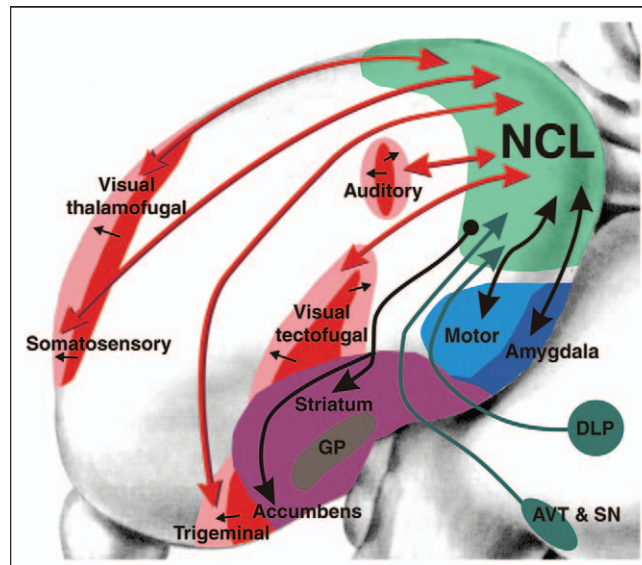
The prefrontal areas of mammals contribute to goal-directed sequences of behavior along the temporal domain [27]. Central to this capacity is the ability to hold information currently attended online for later use. This is usually tested in delay tasks such as delayed alternation learning (see glossary)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

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.

Figure 2



Simplified schematic diagram showing some of the connections of the NCL. The reciprocal connections with the sensory systems are depicted in red (primary sensory areas) and pink (surrounding secondary and tertiary sensory areas). The primary sensory areas project to secondary and tertiary structures (small black arrows), which then have reciprocal projections to and from the NCL (large red arrows). The visual thalamofugal and tectofugal systems correspond to the geniculocortical and colliculo-pulvino-extrastrate systems of mammals, respectively. The area labelled 'motor' is the arcopallium, which has descending projections to various motor and premotor structures. Thalamic afferents arise from the nucleus dorsolateralis posterior thalami (DLP). Dopaminergic afferents stem from the area ventralis tegmentalis (AVT) and the substantia nigra (SN). Abbreviations: GP, globus pallidus.

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-

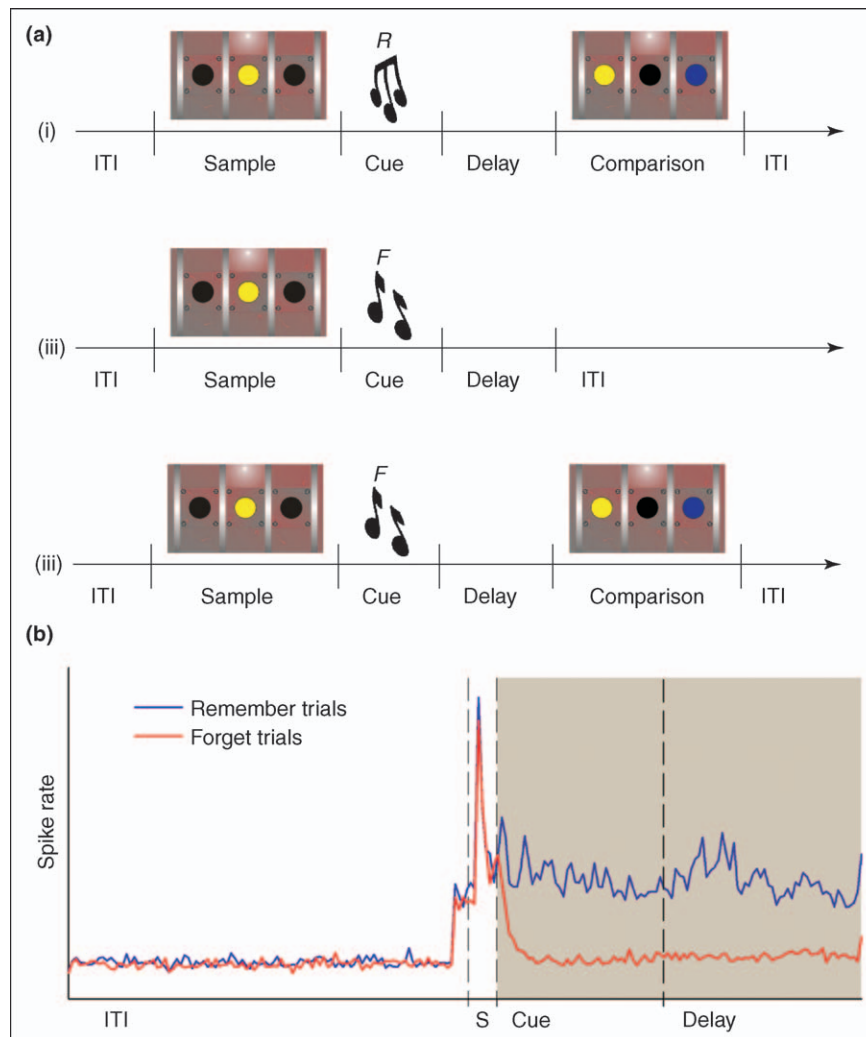
frontal neurons that enable the animal to mentally hold active relevant information and shelter it against interfering input. On neurochemical, cellular and behavioral levels these events seem to unfold in virtually identical ways in the mammalian PFC and the avian NCL.

The cognitive control of mental shifts

Besides the ability to hold active relevant information during a waiting time, delayed alternation tasks also

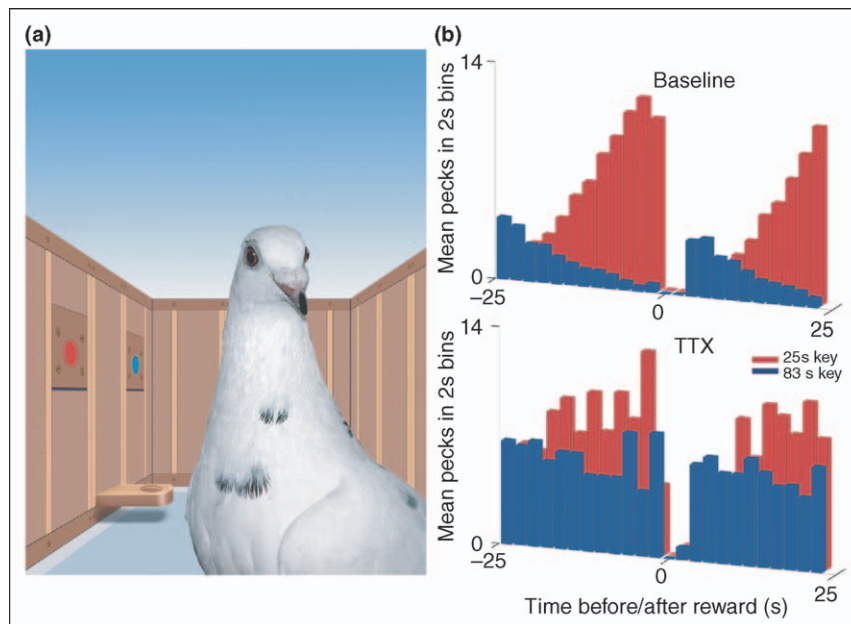
require the animal to switch from one (just rewarded) alternative to the other. Prefrontal lesions interfere with this kind of cognitive flexibility, resulting in a tendency to perseverate on previously rewarded stimuli [42]. These perseverations become most obvious during reversal tasks in which the 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



Neuronal activity patterns of NCL neurons and task design of the study of Rose and Colombo [50**]. This study shows that NCL neurons play a role in executive control – what to remember and what to forget – by linking the presence or absence of neuronal activity with remembering and forgetting. **(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.

Figure 4



Testing condition and distribution of pecks along the time axis in the study of Kalenscher *et al.* [53]. **(a)** This study tested the hypothesis that the NCL participates in the systematic allocation of behavioral resources during repetitive decisions. Pigeons were tested with a concurrent fixed interval schedule during which animals must continuously decide between two keys that are associated with distinct waiting times. The first peck on the red key after an interval of 25 s resulted in reward; the interval for the blue key was 83 s. Usually, the animals distribute their pecks between the two keys in a manner directly proportional to the relative frequency of rewards and, thus, inversely to the interval length of a key. **(b)** The distribution of pecks centered around rewards delivered by pecking the fast red key. As clearly apparent, the frequency of pecks on the red key increases systematically when approaching the expected reward time, whereas the number of pecks on the slow blue key decreases during this period. This systematic and appropriate allocation of pecks is lost when the activity patterns of NCL neurons are transiently blocked by tetrodotoxin (TTX). 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-

mine if they will outperform their competitors. Studies with patients [51] and single unit recordings with monkeys [52^{*}] show that the PFC participates in the representation and comparison of values to encode the appropriate decision. A straightforward way to analyze these functions is a concurrent fixed interval schedule in which animals must repeatedly decide between two keys that are associated with distinct reward frequencies (Figure 4). Usually, the animals distribute their pecks between the two keys in a manner directly proportional to the relative amount of rewards. Selective inactivation of the NCL during such a matching task did not affect pecking activity *per se*, but interfered with the process of continuous feedback-based selection of the momentarily most appropriate alternative [53].

To perform such tasks, animals have to consider reward amount and time-to-reward. Neurons in the monkey PFC represent each of these information categories [54,55], but it is unclear if their combination is integrated at single-cell level. In pigeons that had to decide between small, immediate rewards and large, delayed rewards, single NCL cells did indeed integrate information about reward amount and waiting time. The activity of these neurons reflected the current reward preference and thus the time point of the shift between reward alternatives [56^{**}]. Interestingly, in these neurons the subjective reward function decreased hyperbolically with waiting time, just as expected from various studies in humans and other animals [57].

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

Outstanding questions

- What (if any) are the advantages of cortical lamination, if the same cognitive operations can be performed by the unlaminated 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

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

1. Emery NJ, Clayton NS: **The mentality of crows: Convergent evolution of intelligence in corvids and crows.** *Science* 2004, **306**:1903-1907.

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.

2. Puelles L, Kuwana E, Puelles E, Bulfone A, Shimamura K, Keleher J, Smiga S, Rubenstein J: **Pallial and subpallial derivatives in the embryonic chick and mouse telencephalon, traced by the expression of the genes *Dlx-2*, *Emx-1*, *Nkx-2.1*, *Pax-6*, and *Tbr-1*.** *J Comp Neurol* 2000, **424**:409-438.
3. Reiner A, Bruce L, Butler A, Csillag A, Kuenzel W, Medina L, Paxinos G, Perkel D, Powers A, Shimizu T *et al.*: **Revised nomenclature for avian telencephalon and some related brainstem nuclei.** *J Comp Neurol* 2004, **473**:377-414.
4. Jarvis ED, Güntürkün O, Bruce L, Csillag A, Karten HJ, Kuenzel W, Medina L, Paxinos G, Perkel DJ, Shimizu T *et al.*: **Avian brains and a new understanding of vertebrate brain evolution.** *Nat Rev Neurosci* 2005, **6**:151-159.

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.

5. Gaspar P, Stepniewska I, Kaas JH: **Topography and collateralization of the dopaminergic projections to motor and lateral prefrontal cortex in owl monkeys.** *J Comp Neurol* 1992, **325**:1-21.
6. Mogensen J, Divac I: **The prefrontal 'cortex' in the pigeon. Behavioral evidence.** *Brain Behav Evol* 1982, **21**:60-66.
7. Divac I, Mogensen J: **The prefrontal "cortex" in the pigeon - catecholamine histofluorescence.** *Neuroscience* 1985, **15**:677-682.

8. Divac I, Mogensen J, Björklund A: **The prefrontal 'cortex' in the pigeon. Biochemical evidence.** *Brain Res* 1985, **332**:365-368.
9. Wynne B, Güntürkün O: **The dopaminergic innervation of the forebrain of the pigeon (*Columba livia*): a study with antibodies against tyrosine hydroxylase and dopamine.** *J Comp Neurol* 1995, **358**:1-19.
10. Metzger M, Jiang S, Wang J, Braun K: **Organization of the dopaminergic innervation of forebrain areas relevant to learning: A combined immunohistochemical/retrograde tracing study in the domestic chick.** *J Comp Neurol* 1996, **376**:1-27.
11. Metzger M, Jiang S, Braun K: **A quantitative immuno-electron microscopic study of dopamine terminals in forebrain regions of the domestic chick involved in filial imprinting.** *Neuroscience* 2002, **111**:611-623.
12. Schnabel R, Metzger M, Jiang S, Hemmings HC Jr, Greengard P, Braun K: **Localization of dopamine D1 receptors and dopaminergic neurons in the chick forebrain.** *J Comp Neurol* 1997, **388**:146-168.
13. Durstewitz D, Kröner S, Güntürkün O: **The dopaminergic innervation of the avian telencephalon.** *Prog Neurobiol* 1999, **59**:161-195.
14. Smiley JF, Goldman-Rakic PS: **Heterogeneous targets of dopamine synapses in monkey prefrontal cortex demonstrated by serial section electron microscopy: a laminar analysis using the silver-enhanced diaminobenzidine sulfide (SEDS) immunolabeling technique.** *Cereb Cortex* 1993, **3**:223-238.
15. Bandyopadhyay S, Gonzalez-Islas C, Hablitz JJ: **Dopamine enhances spatiotemporal spread of activity in rat prefrontal cortex.** *J Neurophysiol* 2005, **93**:864-872.
16. Durstewitz D, Kröner S, Hemmings HC Jr, Güntürkün O: **The dopaminergic innervation of the pigeon telencephalon: distribution of DARPP-32 and cooccurrence with glutamate decarboxylase and tyrosine hydroxylase.** *Neuroscience* 1998, **83**:763-779.
17. Pandya DN, Yeterian EH: **Prefrontal cortex in relation to other cortical areas in rhesus monkey: Architecture and connections.** In *The Prefrontal Cortex: Its Structure, Function, and Pathology*. Edited by Uylings HBM, van Eden CG, de Bruin JPC, Corner MA, Feenstra MGP. *Prog Brain Res* 1990, **85**:63-94.
18. Leutgeb S, Husband S, Ritters LV, Shimizu T, Bingman VP: **Telencephalic afferents to the caudolateral neostriatum of the pigeon.** *Brain Res* 1996, **730**:173-181.
19. Kröner S, Güntürkün O: **Afferent and efferent connections of the caudolateral neostriatum in the pigeon (*Columba livia*): A retro- and anterograde pathway tracing study.** *J Comp Neurol* 1999, **407**:228-260.
20. Kuenzel WJ, Blähsler S: **The visceral forebrain system in birds: Its proposed anatomical components and functions.** *Poultry Sci Rev* 1993/1994, **5**:29-36.
21. Dubbeldam JL, den Boer-Visser AM: **Distribution of gastrin-releasing peptide immunoreactivity in the brain of the collared dove (*Streptopelia decaocto*).** *Cell Tissue Res* 2000, **300**:139-151.
22. Lanuza E, Davies DC, Landete JM, Novejarque A, Martinez-Garcia F: **Distribution of CGRP-like immunoreactivity in the chick and quail brain.** *J Comp Neurol* 2000, **421**:515-532.
23. Metzger M, Toledo C, Braun K: **Serotonergic innervations of the telencephalon in the domestic chick.** *Brain Res Bull* 2002, **57**:547-551.
24. Preuss TM: **Do rats have prefrontal cortex? The Rose-Woolsey-Akert program reconsidered.** *J Cogn Neurosci* 1995, **7**:1-24.
25. Veenman CL, Medina L, Reiner A: **Avian homologue of mammalian intralaminar, mediodorsal and midline thalamic nuclei: immunohistochemical and hodological evidence.** *Brain Behav Evol* 1997, **49**:78-98.
26. Güntürkün O: **Cognitive impairments after lesions of the neostriatum caudolaterale and its thalamic afferent: functional similarities to the mammalian prefrontal system?** *J Hirnforsch* 1997, **38**:133-143.
27. McAlonan K, Brown VJ: **Orbital prefrontal cortex mediates reversal learning and not attentional set shifting in the rat.** *Behav Brain Res* 2003, **146**:97-103.
28. Mogensen J, Divac I: **Behavioural effects of ablation of the pigeon-equivalent of the mammalian prefrontal cortex.** *Behav Brain Res* 1993, **55**:101-107.
29. Gagliardo A, Bonadonna F, Divac I: **Behavioural effects of ablations of the presumed "prefrontal cortex" or the corticoid in pigeons.** *Behav Brain Res* 1996, **78**:155-162.
30. Diekamp B, Gagliardo A, Güntürkün O: **Nonspatial and subdivision-specific working memory deficits after selective lesions of the avian 'prefrontal cortex'.** *J Neurosci* 2002, **22**:9573-9580.
31. Constantinidis C, Franowicz MN, Goldman-Rakic P: **The sensory nature of mnemonic representation in the primate prefrontal cortex.** *Nat Neurosci* 2001, **4**:311-316.
32. Lebedev MA, Messinger A, Kralik JD, Wise SP: **Representation of attended versus remembered locations in prefrontal cortex.** *PLoS Biol* 2004, **2**:e365.
Using an ingenious behavioral paradigm, the authors showed that most prefrontal neurons were closely tied not to the sensory information maintained in working memory but to the spatial focus of attention. These results do not refute the idea that the prefrontal cortex processes working memory, but show that the maintenance of a perceived stimulus is just one of several prefrontal functions.
33. Diekamp B, Kalt T, Güntürkün O: **Working memory neurons in pigeons.** *J Neurosci* 2002, **22**:RC210, 1-5.
34. Kröner S, Gottmann K, Hatt H, Güntürkün O: **Cell types within the neostriatum caudolaterale of the chick: Intrinsic electrophysiological and anatomical properties.** *Neuroscience* 2002, **110**:459-473.
35. Kalt T, Diekamp B, Güntürkün O: **Single unit activity during a Go/NoGo task in the 'prefrontal cortex' of pigeons.** *Brain Res* 1999, **839**:263-278.
36. Tseng KY, O'Donnell P: **Post-pubertal emergence of prefrontal cortical up states induced by D1-NMDA co-activation.** *Cereb Cortex* 2005, **15**:49-57.
37. Chudasama Y, Robbins TW: **Dopaminergic modulation of visual attention and working memory in the rodent prefrontal cortex.** *Neuropsychopharmacology* 2004, **29**:1628-1636.
38. Güntürkün O, Durstewitz D: **Multimodal areas of the avian forebrain – blueprints for cognition?** In *Brain Evolution and Cognition*. Edited by Roth G, Wullimann M. Spektrum Akademischer Verlag; 2001:431-450.
39. Schultz W: **Predictive reward signal of dopamine neurons.** *J Neurophysiol* 1998, **80**:1-27.
40. Montague PR, McClure SM, Baldwin PR, Phillips PE, Budygin EA, Stuber GD, Kilpatrick MR, Wightman RM: **Dynamic gain control of dopamine delivery in freely moving animals.** *J Neurosci* 2004, **24**:1754-1759.
41. Bast T, Diekamp D, Thiel C, Schwarting RKW, Güntürkün O: **Microdialysis in the 'prefrontal cortex' and the striatum of pigeons (*Columba livia*): Evidence for dopaminergic volume transmission in the avian associative forebrain.** *J Comp Neurol* 2002, **446**:58-67.
42. Clarke HF, Walker SC, Crofts HS, Dalley JW, Robbins TW, Roberts AC: **Prefrontal serotonin depletion affects reversal learning but not attentional set shifting.** *J Neurosci* 2005, **25**:532-538.
43. Hartmann B, Güntürkün O: **Selective deficits in reversal learning after neostriatum caudolaterale lesions in pigeons – possible behavioral equivalencies to the mammalian prefrontal system.** *Behav Brain Res* 1998, **96**:125-133.
44. Aldavert-Vera L, Costa-Miserachs D, Divac I, Delius JD: **Presumed 'prefrontal cortex' lesions in pigeons: effects on**

- visual discrimination performance.** *Behav Brain Res* 1999, **102**:165-170.
45. Diekamp B, Kalt T, Ruhm A, Koch M, Güntürkün O: **Impairment in a discrimination reversal task after D1-receptor blockade in the pigeon 'prefrontal cortex'.** *Behav Neurosci* 2000, **114**:1145-1155.
 46. Lissek S, Diekamp B, Güntürkün O: **Impaired learning of a color reversal task after NMDA-receptor blockade in the pigeon 'prefrontal cortex'.** *Behav Neurosci* 2002, **116**:523-529.
 47. Lissek S, Güntürkün O: **Dissociation of extinction and behavioral disinhibition – functions of NMDA receptors in the pigeon associative forebrain during extinction.** *J Neurosci* 2003, **23**:8119-8124.
 48. Lissek S, Güntürkün O: **Maintenance in working memory or response selection – functions of NMDA receptors in the pigeon 'prefrontal cortex'.** *Behav Brain Res* 2004, **153**:497-506.
 49. Lissek S, Güntürkün O: **Out of context – NMDA receptor antagonism in the avian "prefrontal cortex" impairs context processing in a conditional discrimination task.** *Behav Neurosci* 2005, **119**:797-805.
 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.
 51. Oya H, Adolphs R, Kawasaki H, Bechara A, Damasio A, Howard MA III: **Electrophysiological correlates of reward prediction error recorded in the human prefrontal cortex.** *Proc Natl Acad Sci U. S. A.* 2005, **102**:8351-8356.
 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.
 53. Kalenscher T, Diekamp B, Güntürkün O: **A neural network for choice behaviour in a concurrent fixed interval schedule.** *Eur J Neurosci* 2003, **8**:2627-2637.
 54. Brody CD, Hernandez A, Zainos A, Romo R: **Timing and neural encoding of somatosensory parametric working memory in macaque prefrontal cortex.** *Cereb Cortex* 2003, **13**:1196-1207.
 55. Wallis JD, Miller EK: **Neuronal activity in primate dorsolateral and orbital prefrontal cortex during performance of a reward preference task.** *Eur J Neurosci* 2003, **18**:2069-2081.
 56. Kalenscher T, Windmann S, Rose J, Diekamp B, Güntürkün O, Colombo M: **Single units in the pigeon brain integrate reward amount and time-to-reward in an impulsive choice task.** *Curr Biol* 2005, **15**:594-602.
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.
 57. Green L, Myerson J: **A discounting framework for choice with delayed and probabilistic rewards.** *Psychol Bull* 2004, **130**:769-792.
 58. Medina L, Reiner A: **Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices?** *Trends Neurosci* 2000, **23**:1-12.
 59. Hunt GR, Gray RD: **Diversification and cumulative evolution in New Caledonian crow tool manufacture.** *Proc Biol Sci* 2003, **270**:867-874.
 60. Kenward B, Weir AA, Rutz C, Kacelnik AA: **Behavioural ecology: tool manufacture by naive juvenile crows.** *Nature* 2005, **433**:121.
 61. Clayton NS, Bussey TJ, Dickinson A: **Can animals recall the past and plan for the future?** *Nat Rev Neurosci* 2003, **4**:685-691.
 62. Pepperberg IM, Gordon JD: **Number comprehension by a grey parrot (*Psittacus erithacus*), including a zero-like concept.** *J Comp Psychol* 2005, **119**:197-209.