9. Jerison HJ (2001) The evolution of neural complexity. In: Roth G, Wullimann ME (eds) Brain evolution and cognition. Wiley, New York, pp 521–553
10. Carroll RL (1988) Vertebrate paleontology and evolution. Freeman, New York
11. Ayala EJ (1988) Can "progress" be defined as a biological concept? In: Nitecki MH (ed) Evolutionary progress. University of Chicago Press, Chicago Press, IL, pp 75–96
12. Gould SJ (1988) On replacing the idea of progress with an operational notion of directionality. In: Nitecki MH (ed) Evolutionary progress. University of Chicago Press, Chicago, IL, pp 319–338
13. Campbell CBG, Hodos W (1991) The *scala naturae* revisited: anagenesis and evolutionary scales in comparative psychology. J Comp Psych 105:211–221

Evolution of Association Pallial Areas: In Birds

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Definition

This essay describes a case of ▶homoplasy of mammalian and avian brains. Both mammals and birds can organize their behavior flexibly 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.

Characteristics

Behavior defines the frontier along which animals interact with evolutionary selection pressures. Therefore, neural architectures are shaped during evolution to produce certain behavioral traits that are required to stand the race for fitness. If species from different lineages are faced with the same selection pressure they might react with the same solution at the behavioral level. But how many degrees of freedom are there on the neural level to achieve the same behavioral solutions? In other words, can differently organized brains implement the same set of behaviors? In the following, a case of ▶homoplasy between mammals and birds will be discussed, contrasting the behavioral skills employed by both orders as well as the neural structures that enable these skills.

Behavioral Skills of Birds and Mammals

The order of mammals is phylogenetically very successful. Mammals like humans, macaques or rats are able to adjust their behavior flexibly to changing demands. They are able to reverse-learn behavioral choices, select appropriate responses according to contextual information and withhold actions until a suitable situation occurs. In short, they optimally organize their behavior with time [1,2]. Birds represent an about equally successful vertebrate order and a vast literature testifies that birds are able to generate many of the same cognitive functions [1,2]. Pigeons, for example, are able to memorize up to 725 different visual patterns, reverse-learn contingencies, learn to categorize images as "human-made" or "natural" or rank patterns using transitive inference [3]. The evolution of these abilities is an example of ▶homoplasy that enables birds and mammals to utilize a very similar repertoire of behavioral skills. These skills were not inherited from a common ancestor, however, but rather were evolved independently [3]. Furthermore, corvids in particular have developed cognitive skills to a degree that can only otherwise be found in primates. The level of corvid cognitive abilities is indicated by feats such as causal reasoning, prospection and the ability to use experience in predicting the behavior of conspecifics. Another domain in which birds stand out is the use of tools. New Caledonian crows use different types of tools for different purposes; they manufacture specific tools to standardized patterns and carry them while foraging. In the laboratory they are reported to use analogy with previous experience when using unknown materials to manufacture novel tools [4]. Another example of the vast behavioral repertoire of birds is ▶episodic-like memory. Many corvids store food items and recover them often months later for consumption. In caching food items, corvids are known to show ▶episodic-like memory; they remember *where* and *when* they stored *what* food item. This enables the birds to retrieve perishable food earlier, while non-perishable items can be left in storage or to recache food that might be pilfered by another bird. In sum, these abilities place corvids amongst the cognitively most developed species, finding a match only in a very few primate species [4].

Neuroarchitecture of Birds and Mammals

A sharp contrast to the numerous similarities of mammals and birds on the behavioral level is the great evolutionary distance and therefore the substantially different organization of avian and mammalian forebrains. The lines of

birds and mammals separated about 300 million years ago. This evolutionary distance resulted in a number of crucial organizational differences on the neural level, the most notable being the lack of a laminated cortex in the avian telencephalon [1,2].

In recent years our understanding of the evolution of vertebrate brains and the homologies between avian and mammalian brains has advanced substantially. To reflect this new understanding, The Avian Brain Consortium, a group of leading experts in the field, has proposed changes to the avian brain nomenclature and renamed many avian telencephalic structures [3,5]. The classical avian brain nomenclature dated back to 1900 and was based on Edinger's model of brain evolution. According to his formulation, vertebrate brain evolution consisted of a series of additions of new brain entities, with the mammalian neocortex being the last and most advanced step. In mammals, the cortex, including neo- archi- and paleo-cortical components, together with the claustrum and lateral parts of the amygdala, constitutes the forebrain pallium. Pallium and subpallial structures, including the striatum and pallidum, make up the cerebrum. While the organization of the striatum is highly conserved among birds and mammals, pallial organization is rather different. The mammalian pallium mainly follows a laminar organization, while the avian pallium is organized in nuclei. The absence of a laminated component within the avian cerebrum led Edinger to assume that birds have virtually no pallium but an enormously hypertrophied striatum instead. Based on neurochemical, histological, behavioral, embryological and genetic studies, this view had to be rejected. Birds do indeed possess a large pallium, which consists of four main subdivisions, the hyper-, meso-, nido- and arco-pallium (Fig. 1).

The field homologies between these different subdivisions and corresponding mammalian structures are a topic of active research. For most divisions, consensus, if ever possible, has not yet been reached.

It is well known that the cognitive skills of mammals depend on their pallial association structures. These areas are organized following a general principle. Primary sensory structures project to the surrounding unimodal association areas, which in turn project to polysensory association structures. The sensory projections of the avian pallium are organized according to the same principle (Fig. 2).

Within the visual system, the afferent fibers entering the pallium project either to the visual Wulst, a subdivision of the hyperpallium or to the entopallium, a subdivision of the nidopallium. The thalamofugal (Wulst) and the tectofugal (entopallium) systems correspond to the mammalian geniculo-cortical and extrageniculate pathways, respectively. The visual Wulst shows a pseudo-lamination, with a primary visual layer located ventrally and a unimodal association layer located dorsally. The entopallium is organized in a primary visual core and a surrounding belt, which is a unimodal association structure called the perientopallium [6]. This organization into primary sensory core and surrounding unimodal associative belt is shared by the somatosensory Wulst, the auditory field L and the trigeminal-recipient nucleus basorostralis pallii of the nidopallium. The primary sensory areas project to the corresponding unimodal association areas that, in turn, send afferents to poly-sensory association structures. In birds, until now only the ▶nidopallium caudolaterale (NCL) has been described as receiving polysensory input and participating in cognitive functions.

Functions of the Avian and Mammalian "Prefrontal Cortex"

In the following the focus will be on the NCL, the functional equivalent of the mammalian prefrontal cortex (PFC) for two reasons. First, the NCL is one of the best-understood avian pallial structures and analogy to the mammalian PFC has been established satisfactorily; second, NCL and PFC are the crucial structures in mediation of many of the behaviors mentioned above [2]. The function of the PFC is commonly described with the terms "executive functions" and "▶working memory." ▶Working memory (WM) has been defined in parallel and rather independently in pigeons and humans. The non-human and the human definitions of ▶working memory differ only with respect to the presence of a language-component in humans. Not only is WM behavior very similar between mammals and birds but the neural processes generating WM also seem to be identical in both orders. WM is based on the active maintenance and manipulation of stimulus information. These processes are mediated by neurons that show an elevated firing rate during delay periods of WM tasks. In other words, the representation of a physically absent stimulus is actively maintained over a delay. Disruption of this activation leads to a loss of the information, i.e. to forgetting. In mammals, this activation was first described in the PFC. Lesions to the PFC result in a disruption of WM. The same type of neuronal activity has been reported in the avian equivalent of the PFC, the NCL [7]. As in the case of the PFC, lesions to NCL lead to a decrease in WM-performance. In mammals, the release of ▶dopamine (DA) within PFC and the subsequent activation of D1-receptors play a major role in sustained activity levels of delay cells and the animals' performance in ▶working memory tasks. In pigeons, the local blockade of D1-receptors within NCL selectively disrupts ▶working memory performance [2].

Apart from stimulus maintenance, the PFC takes part in the selection of behavioral goals. In reversal tasks, for instance, animals learn to associate the response to one stimulus with reward and the response to an alternative stimulus with punishment. When the animals have
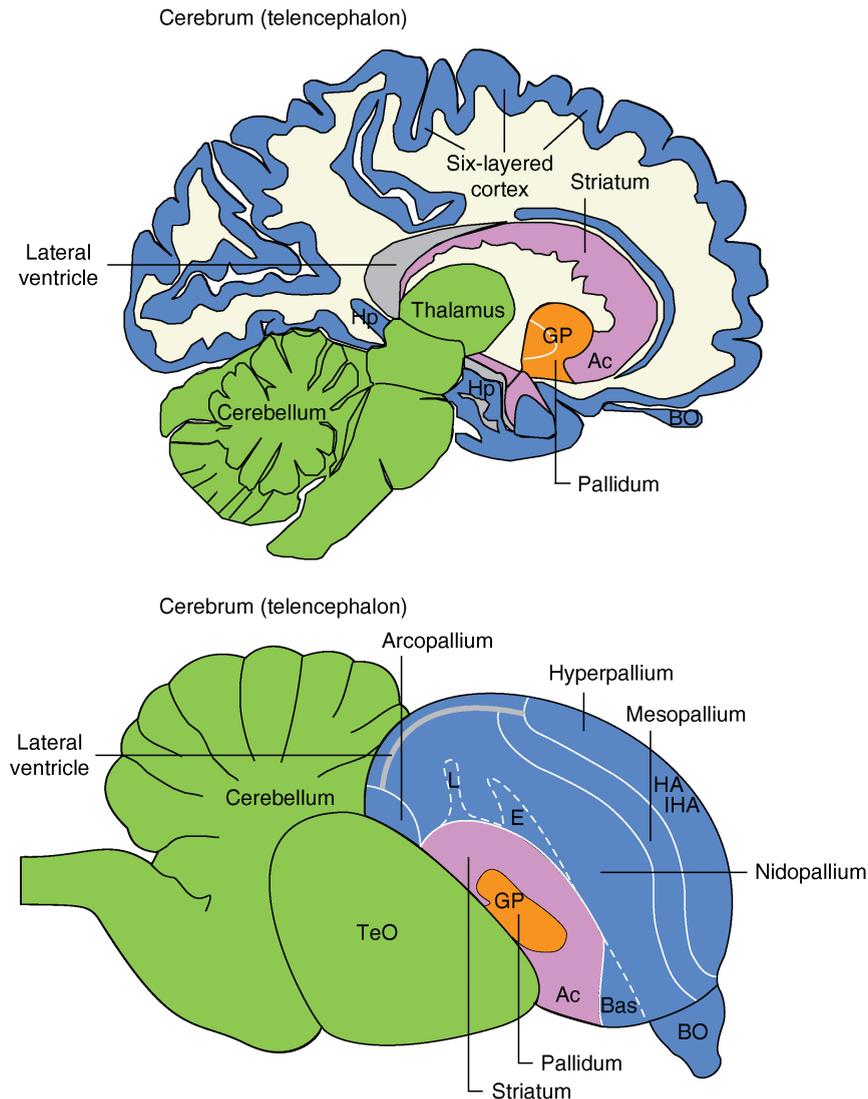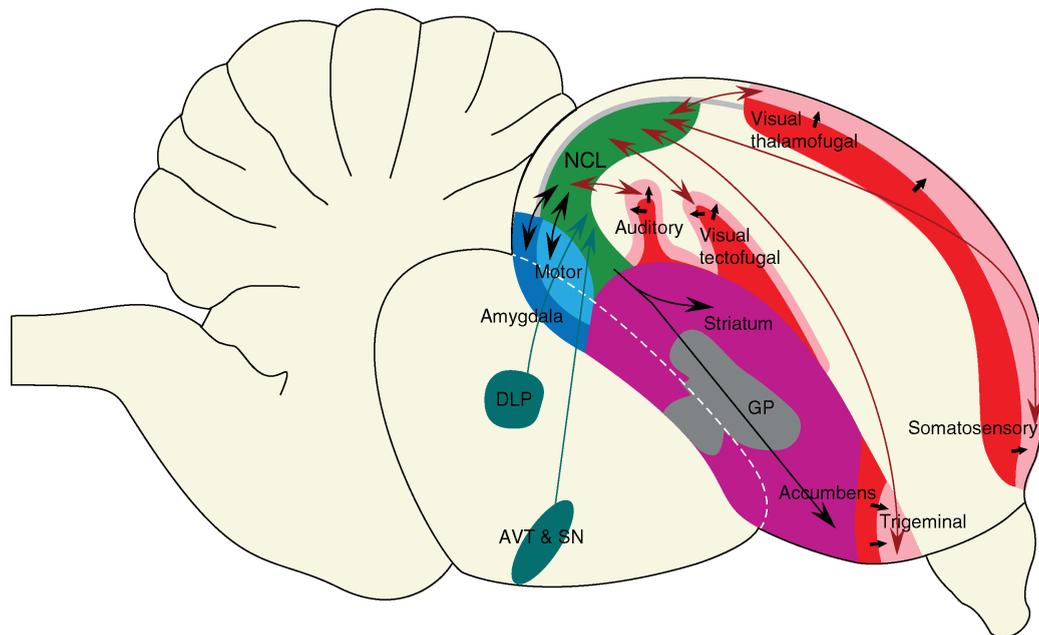
Evolution of Association Pallial Areas: In Birds. Figure 1 The new understanding of avian and mammalian brain relationships. Sagittal view of a human *(top)* and a pigeon *(bottom)* brain. Pallial structures are marked in blue, striatal structures in pink and pallidal structures in orange. Abbreviations: *Ac* nucleus accumbens; *Bas* nucleus basorostralis pallii; *BO* bulbus olfactorius; *E* entopallium; *GP* globus pallidus; *HA* hyperpallium apicale; *IHA* interstitial hyperpallium apicale; *Hp* hippocampus; *L* field L; *TeO* tectum opticum,NCL nidopallium caudolaterale.

established these associations, the contingencies are reversed, responses to the previously rewarded stimulus are now punished and vice versa. In order to master this task the animal has to monitor the success of its actions and reverse its behavior if the actions are unsuccessful. This flexibility in adapting to changing demands is severely disrupted in mammals with lesions to the PFC and the same holds for birds with NCL lesions or blockade of D1- [1] or NMDA-receptors in this area [8].

In order to plan goal-directed actions effectively and to decide between alternative strategies, it is crucial to integrate information about the costs and benefits of different actions. In other words, it is crucial to adjust

the effort to obtain a reward to the value of that reward. Transient pharmacological lesions to the NCL disrupt this ability and such animals will put as much effort into obtaining a small reward as into obtaining a large reward [9]. In line with this data, a recent study showed that neurons in the NCL reflect an animal's preference for a reward, based not only on the features of the reward but also on the delay until the reward is obtained [10].

The most straightforward example of a neural correlate of executive control reported in any species thus far has recently been provided by a single-cell study in pigeons. Pigeons were trained on a WM task during which the animals were informed that

Evolution of Association Pallial Areas: In Birds. Figure 2 Afferent and efferent connections of the ▶nidopallium caudolaterale. Primary sensory areas are depicted in red, secondary and tertiary areas in pink. The primary sensory areas project to secondary and tertiary structures (*small black arrows*), which have reciprocal connections with the ncl (*red arrows*). The visual thalamofugal and tectofugal systems correspond to the geniculocortical and colliculo-pulvino-extrastriate systems of mammals, respectively. The area labeled "motor" is the arcopallium, which has descending projections to various motor and premotor structures. Thalamic afferents arise from the nucleus dorsolateralis posterior thalami. Dopaminergic afferents stem from the area ventralis tegmentalis and the substantia nigra. Abbreviations: *AVT* area ventralis tegmenti; *DLP* nucleus dorsolateralis posterior thalami; *GP* globus pallidus; *SN* substantia nigra.

remembering a stimulus was necessary in order to obtain a reward. The animals were able to use this information, memorizing only relevant stimuli. Most importantly, this selectivity was reflected in the memory-period activity of NCL neurons. The vast majority of neurons showed memory related activity when the birds chose to remember; however, this activity was suppressed as soon as the birds knew that memorizing a stimulus was not required. This decision process, controlling the neural mechanisms that govern ▶working memory, is a prime example of executive functions as attributed to the mammalian PFC [11]. In spite of the great phylogenetical distance, the avian NCL and the mammalian PFC generate the same set of behaviors.

Connectivity of the "Prefrontal Cortex"

Returning to the initial question, how many degrees of freedom are there on the neural level to generate the same set of behaviors, structural differences and similarities between PFC and NCL will now be described. The PFC of mammals is densely innervated by dopaminergic fibers from the ventral tegmental area and the substantia nigra. This dopaminergic innervation

was usually taken as a characterizing element of the PFC. Ivan Divac and colleagues showed that the NCL is densely innervated by catecholaminergic fibers of probably dopaminergic nature. Subsequent studies demonstrated that NCL is indeed one of the main termination areas of dopaminergic fibers from the ventral tegmental area and the substantia nigra. The architecture of the dopaminergic terminals within the NCL closely resembles that of the PFC [1,2].

The NCL is comparable to the PFC in that it is a center of higher-order sensory integration. Sensory input reaches the NCL via a set of interconnected pathways that show a considerable overlap of different modalities (Fig. 2). The primary sensory area of each modality projects first to an adjacent area that then projects not only to the next modality-specific association area in line but also to the NCL, which in turn reciprocates by sending fibers back to the projecting area. In addition, NCL projects to most parts of the somatic and limbic striatum, as well as to motor output structures. Thus, identically to PFC, the avian NCL is a convergence zone between the ascending sensory and the descending motor systems. In addition, NCL and PFC resemble each other in terms of their

connections with the amygdala, nucleus accumbens, visceral structures and diverse chemically defined afferent systems. One difference between the connectivity of NCL and PFC is, however, the thalamic input. The mammalian PFC receives afferents from the mediodorsal (MD) nucleus of the thalamus. Thalamic afferents to the NCL arise mainly from the dorsolateral posterior nucleus, which is not homologous to MD but still seems to serve similar functions [1,2].

A comparison of the anatomical network defining NCL and PFC shows a large number of similarities with only a few differences. Like the PFC, the avian NCL is a multimodal forebrain area that is located at the convergence zone from sensation to action, is modulated by dopaminergic fibers and is tightly interrelated with structures serving limbic, visceral and memory-related functions.

Concluding Remarks

We have shown that birds are capable of generating complex behaviors that, in some cases, outperform the skills of most mammals. Given the phylogenetic distance between birds and mammals, it can be assumed that a number of these skills have evolved independently. On the neural level, it can be said that the avian and mammalian pallium seem to be homologous with respect to their phylogenetic continuity, but this does not necessarily hold for the different pallial domains, which could also be a product of ▶homoplasy. Discussion focused on the equivalence between PFC and NCL and showed that both structures generate the same set of cognitive functions using surprisingly similar systems. These structural similarities are most evident in the case of stimulus maintenance, as discussed in detail by Güntürkün [2]. Among the few obvious differences between avian and mammalian pallia is the lack of lamination, but this is evidently not a prerequisite in generating higher cognitive functions.

References

1. Güntürkün O (2005) The avian 'prefrontal cortex' and cognition. Curr Opin Neurobiol 15:686–693
2. Güntürkün O (2005) Avian and mammalian "prefrontal cortices": limited degrees of freedom in the evolution of the neural mechanisms of goal-state maintenance. Brain Res Bull 66:311–316
3. Jarvis ED, Güntürkün O, Bruce LL, Csillag A, Karten H, Kuenzel W, Medina L, Paxinos G, Perkel DJ, Shimizu T, Striedter GF, Wild JM, Ball GF, Douglas-Ford J, Durand SE, Hough G, Husband S, Kubikova L, Lee DW, Mello CV, Powers A, Siang C, Smulders TV, Wada K, White SA, Yamamoto K, Yu J, Reiner A, Butler AB (2005) Avian brains and a new understanding of vertebrate brain evolution. Nat Rev Neurosci 6:151–159
4. Emery NJ, Clayton NS (2004) The mentality of crows: convergent evolution of intelligence in corvids and apes. Science 306:1903–1907
5. Reiner A, Perkel DJ, Bruce LL, Butler AB, Csillag A, Kuenzel W, Medina L, Paxinos G, Shimizu T, Striedter GF, Wild M, Ball G, Durand S, Güntürkün O, Lee DW, Mello CV, Powers A, White SA, Hough G, Kubikova L, Smulders TV, Wada K, Douglas-Ford J, Husband S, Yamamoto K, Yu J, Siang C, Jarvis ED (2004) Revised nomenclature for avian telencephalon and some related brainstem nuclei. J Comp Neurol 473: 377–414
6. Krützfeldt NO, Wild JM (2004) Definition and connections of the entopallium in the zebra finch (*Taeniopygia guttata*). J Comp Neurol 468:452–465
7. Kalt T, Diekamp B, Güntürkün O (1999) Single unit activity during a Go/NoGo task in the "prefrontal cortex" of pigeons. Brain Res 839:263–278
8. Lissek S, Diekamp B, Güntürkün O (2002) Impaired learning of a color reversal task after NMDA receptor blockade in the pigeon (*Columba livia*) associative forebrain (neostriatum caudolaterale). Behav Neurosci 116:523–529
9. Kalenscher T, Diekamp B, Güntürkün O (2003) Neural architecture of choice behaviour in a concurrent interval schedule. Eur J Neurosci 18:2627–2637
10. Kalenscher T, Windmann S, Rose J, Diekamp B, Güntürkün O, Colombo M (2005) Single units in the pigeon brain integrate reward amount and time-to-reward in an impulsive choice task. Curr Biol 15:594–602
11. Rose J, Colombo M (2005) Neural correlates of executive control in the avian brain. PLoS Biol 3:e190

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Evolution of Association Pallial Areas: In Reptiles

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Synonyms

Association = Multimodal or polymodal sensory convergence; Pallium = Dorsal part of telencephalon

Definition
Associative Pallium

The adult ▶pallium includes areas that receive inputs from nuclei in the dorsal thalamus relaying unimodal sensory information, namely visual, auditory or somatosensory (and gustatory-visceroceptive). In most vertebrates, intrapallial connections allow multimodal convergence in some areas that constitute the associative pallial areas. Multimodal convergence might also occur at lower levels in the *neuroaxis*. For instance, some thalamic areas receive convergent afferents from