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REVIEW

The convergent evolution of neural substrates for cognition

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Abstract This review describes a case of convergence in the evolution of brain and cognition. Both mammals and birds can organize their behavior flexibly over time and evolved similar cognitive skills. 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. In mammals, executive functions are associated with the prefrontal cortex. The corresponding structure in birds is the nidopallium caudolaterale. Anatomic, neurochemical, electrophysiologic and behavioral studies show these structures to be highly similar, but not homologous. Thus, despite the presence (mammals) or the absence (birds) of a laminated forebrain, 'prefrontal' areas in mammals and birds converged over evolutionary time into a highly similar neural architecture. The neuroarchitectonic degrees of freedom to create different neural architectures that generate identical prefrontal functions seem to be very limited.

Convergent evolution of brain and behavior

Organisms change during the process of evolution by modifications of already existing organisms. When a species splits into two new ones, the two groups of descendants share many common features. They usually can easily be recognized as being relatives due to common characteristics of their morphology and their behavior. Also the various groups of animals that are the further descendants of these two species retain a number of the shared features that reflect their common heritage. If a shared trait of two species can be traced back to a common ancestor without interruption, we have a case of *homology*. The eyes of vertebrates are such a case: Despite all differences that can be seen between the eyes of, say, a coral snake and a human, it is possible to show that indeed the eyes of snakes and humans derive from a common ancestor that lived nearly 300 million years ago and that already possessed a similar eye structure (Gehring, 2005). At first glance, the eyes of octopus might also look very similar to the human eye: it is constituted by a lens that functions identically to that of humans; it has a vitreous humor and a retina that resemble ours in several aspects. But human and octopus eyes share no common ancestor. Thus, the last common ancestor of humans and octopus had no eyes that are comparable with the condition in each of these lines of animals. The similarity of the eyes of octopus and humans is, therefore, due to *convergent evolution*. Convergent evolution describes the acquisition of the same biologic trait in unrelated lineages of organisms due to a similar selection pressure. Convergent evolution can explain how the selection pressure for excellent object vision in the lines leading to humans and octopus caused a similar series of changes that then resulted in a similar design of the eye (Wake, Wake, & Specht, 2011). Thus, in the two lineages of life which led to humans and octopus, a similar eye was invented twice because both lineages needed it.

During the evolutionary time not only bodies are subject to change, but also behavior and cognitive skills. Therefore, we can see convergent evolution also in the realm of behavioral traits. For example, some Tetragnatha spiders of the Hawaiian Archipelago have independently evolved similar web building behaviors due to a common selection pressure in comparable ecological niches (Blackledge &

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Gillespie, 2004). Since the behavior is organized by neural structures, it is possible that also the brains of these spider species have converged at certain levels. But what exactly happens in the brains when two groups of animals converge with respect to their cognitive skills? Do their brains then also assume a very similar neural architecture? Or are differently organized brains able to produce the same kind of cognitive output? In the following, a case of convergent evolution of cognitive skills between mammals and birds will be discussed. I will first show how similar the cognitive capabilities of these two classes of vertebrates are (Kirsch, Güntürkün, & Rose, 2008) and then outline the neural structures that enable these skills (Rose, Güntürkün, & Kirsch, 2009).

Behavioral skills of birds and mammals

The class of mammals to which we belong is phylogenetically very successful. Mammals spread over the whole world and captured most ecological niches. In virtually every niche, mammals represent top predators. This success story is, at least in part, due to the ability of mammals to adjust their behavior flexibly to changing demands. Mammals like humans, macaques or rats are quickly able to learn new behavioral choices and abandon old ones; they successfully select appropriate responses according to contextual information and withhold actions until a suitable situation occurs (Allen & Bekoff, 1997). In short, they optimally organize their behavior over time. Birds represent an about equally successful vertebrate class and a vast literature testifies that birds are able to generate many of the same cognitive functions as mammals (Emery & Clayton, 2004). Corvids like the European magpie are able to recognize themselves in the mirror (Prior et al., 2008; Fig. 1), and have an understanding of object permanence similar to humans (Pollok, Prior, & Güntürkün, 2000). Other corvids like blue jays display episodic-like memory (Clayton, Bussey, & Dickinson, 2003), and crows demonstrate behavior that resembles theory-of mind (Bugnyar & Heinrich, 2005), and show highly sophisticated ability for causal understanding in tool use (Bird & Emery, 2009). Even the lowly pigeon is able to memorize up to 725 different visual patterns (Fersen & Güntürkün, 1990), learns to categorize complex images (Yamazaki, Aust, Huber, & Güntürkün, 2007) or ranks patterns using transitive inference logics (Fersen von, Wynne, Delius, & Staddon, 1990). The evolution of these abilities is an example of convergent evolution 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 evolved independently (Jarvis et al., 2005).

Neuroarchitecture of birds and mammals

Although mammals and birds are highly similar at the behavioral level, their evolutionary lines separated nearly 300 million years ago. Due to this great evolutionary distance, the anatomic organizations of their forebrains differ substantially. The most notable difference is the lack of a laminated cortex in the avian telencephalon (Güntürkün, 2005).

In recent years, our understanding of the evolution of vertebrate brains and the homologies between the avian and the mammalian brains has advanced substantially. To reflect this new understanding, the Avian Brain Nomenclature Consortium, a group of leading experts in the field, has proposed a radically new view on the homologies

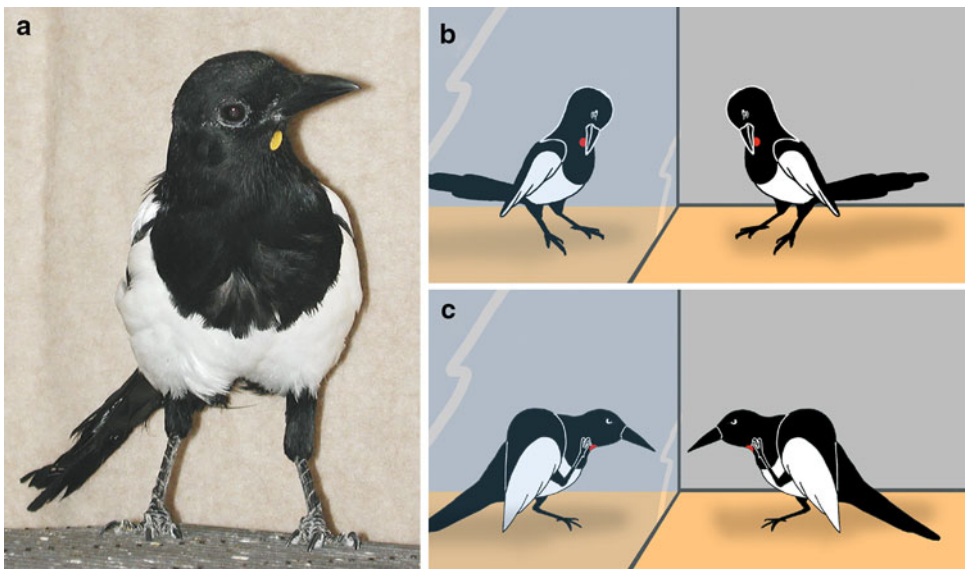

Fig. 1 Self-recognition in the mirror in magpies. **a** Magpie with a mark in the throat region; **b**, **c** schematic depictions of focus movements toward the throat which were counted as attempts to remove the mark. Based on Prior, Schwarz, and Güntürkün (2008)

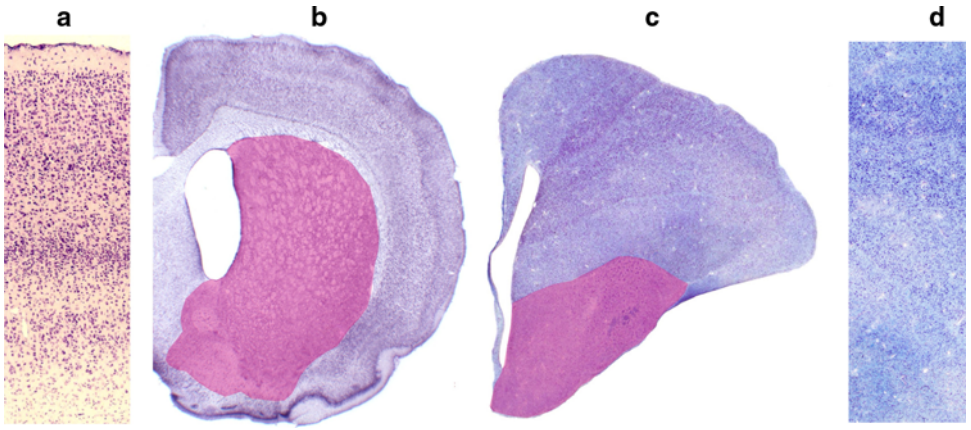

Fig. 2 Comparison of the forebrain organization of representatives of mammals and birds. **a** Magnification of the primary visual cortex of the macaque. The lamination is readily visible. **b** rat and **c** pigeon forebrain in frontal sections. The subpallial areas are highlighted to disambiguate them from the overlying pallium. In the rat brain, this pallium is mostly of neocortical nature. The pallium in the pigeon is not laminated, but consists of clusters of major brain areas. **d** Magnification of a slab through the pigeon brain that crosses through several clusters. Note the absence of a clear lamination

between the avian and the mammalian brains (Reiner et al., 2004). The classical view on the avian brain dated back to the 1900s and it was based on Edinger's model of brain evolution (Edinger, Wallenberg & Holmes, 1903). According to his formulation, the vertebrate brain evolution consisted of a series of additions of new brain entities, with the mammalian neocortex being the last and the most advanced step. In mammals, the cortex constitutes the largest part of the forebrain pallium. The mammalian pallium mainly follows a laminar organization, whereas the avian pallium is organized in nuclei. The absence of a laminated component within the avian forebrain led Ludwig Edinger to assume that birds have virtually no pallium, but an enormously hypertrophied striatum instead. Based on neurochemical, histologic, behavioral, embryological and genetic studies, this view is meanwhile rejected (Reiner et al., 2004). Birds do indeed possess a large pallium, but this pallium is not laminated. In Fig. 1, a monkey and a pigeon forebrains are shown with the subpallium (mostly basal ganglia) highlighted differently. It is obvious that pigeons have a large pallium that stretches above the subpallium (Fig. 2).

At first glance, we have a case of cognitive, but not of neural convergent evolution: birds and mammals have independently evolved highly similar cognitive skills, but achieve these abilities with vastly different forebrain architectures: while mammalian pallium is laminated that of birds is not. In the following, we will see that this is too simple a view. I will outline that the evolution of mammalian and avian forebrains differs in lamination, but shows remarkable similarities in their allometric properties, as well as in the microarchitecture of their associative pallial structures.

Allometry: big brains for smart animals

Allometry is the study of the relationship between the size of an animal and the size of any of its parts, for example its brain. Animals with bigger bodies have bigger brains (Jerison, 1979). A large number of studies also show that higher cognitive abilities correlate with relatively larger brain sizes in mammals (Harvey & Krebs, 1990). For example, social learning, innovation, and tool use are all positively correlated with large brain size across primate species (Reader & Laland, 2002). Similarly, Deaner, van Schaik, and Johnson (2006) also found a similar trend of positive correlations over primate genera for up to 30 different cognitive tests. The very same is true for birds. Here, innovation rate, tool use, and reversal learning are positively correlated with larger pallial brain sizes (Lefebvre, Reader, & Sol, 2004). Also, brain size facilitates survival in novel regions of the world in birds (Sol, Duncan, Blackburn, Cassey, & Lefebvre, 2005) and mammals (Lefebvre & Sol, 2008). Large brains can result from a mosaic-like pattern of selective relative growth of brain components (Iwaniuk, Dean, & Nelson, 2004). In song birds, brain growth is mainly driven by an increase of the pallium. Especially, corvids with their impressive cognitive skills possess much larger associative pallial areas than other birds (Rehkämper, Frahm, & Zilles, 1991).

Among corvids, especially New Caledonian crows display extraordinary skills in making and using an impressive range of tools (Hunt & Gray, 2003). They also are able to bend unfamiliar material like wire into functional tools (Weir, Chappell, & Kacelnik, 2002), can use one tool to get another (metatool use) (Taylor, Hunt, Holzhaider, & Gray, 2007), and solve complex physical cognition tasks that

require causal and analogic reasoning (Taylor, Hunt, Medina, & Gray, 2009) that rival those of apes (Emery & Clayton, 2004). New Caledonian crows have one of the largest avian brains for their body size (Cnotka, Güntürkün, Rehkämper, Gray & Hunt, 2008). In fact, their relative brain/body-ratio (not their encephalization) is higher than that of humans (Cnotka et al., 2008). More interestingly, the relative size of their associative forebrain and their striatopallidal complex is disproportionally enlarged (Mehlhorn, Rehkämper, Hunt, Gray, & Güntürkün, 2010). This is also the case for primates: they also display an over proportionally enlarged associative forebrain and striatum compared with other non-primate mammals (Stephan, Baron, & Frahm, 1988; Rehkämper et al., 1991; Keverne, Martel, & Nevison, 1996; Barton & Harvey, 2000; Sol, Bacher, Reader, & Lefebvre, 2008).

These data from corvids, in general, and New Caledonian crows, in special, reveal an important insight into the evolution of cognitive functions: despite a radically different structure of the pallium (laminated vs. non-laminated), an evolutionary increase of cognitive skills goes along with a volume increase of associative forebrain structures and their striatal termination fields. In other words, the enlargement of associative forebrain structures seems to be the default option in the evolution of high-cognitive skills like selective and sustained attention, categorization, episodic memory, spatial cognition, tool use, prospection, social cognition, problem solving, and self-recognition.

The avian "Prefrontal Cortex"

To date, I discussed the allometric properties of associative forebrain structures of mammals and birds with respect to differences of cognitive skills among taxa. In the following, I will focus on the microarchitecture of one of the associative forebrain areas. The focus structure in mammals will be the prefrontal cortex (PFC). The PFC is firmly associated with the generation of *executive functions*, a cluster of cognitive functions that describe the ability to spontaneously generate efficient strategies when relying on self-directed task-specific planning. The functional equivalent of the PFC is the avian nidopallium caudolaterale (NCL) Hartmann and Güntürkün (1998) (Güntürkün, 2005; Kirsch et al., 2008). As outlined below, NCL and PFC are the crucial structures in the mediation of executive functions and share a large number of anatomic, physiologic, and functional similarities (Fig. 3).

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; but the NCL is also densely innervated by dopaminergic fibers from the ventral tegmental area and the substantia nigra (Wynne & Güntürkün, 1995). Additionally, the architecture of the dopaminergic terminals within the NCL closely resembles that of the PFC (Schnabel et al., 1997; Durstewitz, Kröner, Hemmings Jr, & Güntürkün 1998; Metzger, Jiang, & Braun, 2002). The NCL is also comparable with 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 (Kröner & Güntürkün, 1999). In addition, the NCL projects to most parts of the somatic and limbic striatum, as well as to motor output structures that then project to brainstem areas that process incoming sensory information (Güntürkün & Remy, 1990). Thus, identically 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, nucleus accumbens, visceral structures, and diverse chemically defined afferent systems (Kröner & Güntürkün, 1999). Thus, a comparison of the anatomic network defining the NCL and PFC shows a large number of similarities with only a few differences. As the PFC, the avian NCL is a multimodal forebrain area, located at the convergence zone from sensation to action, is modulated by dopaminergic fibers and tightly interrelated with structures serving limbic, visceral, and memory-related functions (Rose et al., 2009).

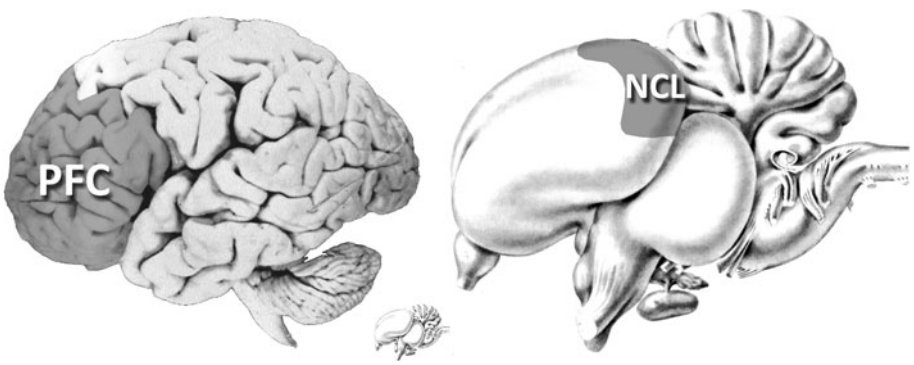

Fig. 3 Human (*left*) and pigeon brain (*right*) with the prefrontal cortex (PFC) and the nidopallium caudolaterale (NCL) being highlighted. The pigeon brain in the lower middle part of the figure is to the same scale as the human brain. Based on Güntürkün (2005)

The cellular machinery for working memory in birds and mammals

Working memory is a critical component of executive functions and it has been defined in parallel and rather independently in pigeons and humans. The 'human' (Baddeley & Hitch, 1974) and the 'pigeon' definitions of working memory (Honig, 1978) differ only with respect to the presence of a language-component in humans. Not only is working memory very similar between mammals and birds, but, as outlined below, also the neural processes generating working memory seem to be identical in both orders.

During delay periods of working memory tasks, a memory trace of the relevant information has to be held active. PFC neurons in macaques (Machens, Romo, & Brody, 2005) and NCL neurons in pigeons (Diekamp, Kalt, & Güntürkün, 2002a; Browning, Bruce Overmier, & Colombo, 2011) display a sustained activity during delay that possibly hold online a memory trace for the subsequent response or an expected outcome associated with each sample. If this activity within NCL breaks down, the animal is likely to err (Rose & Colombo, 2005). Consequently, PFC-lesions in rats (Dunnett, Nathwani, & Brasted, 1999) and NCL-lesions in pigeons (Güntürkün, 1997; Diekamp, Gagliardo, & Güntürkün, 2002b) always disrupt delay-task performance.

Delay time-specific activations of PFC neurons are modulated by the dopaminergic system via D1-receptors (Sawaguchi, 2001; Vijayraghavan, Wang, Birnbaum, Williams, & Arnsten, 2007). Consequently, blockade of dopaminergic D1-receptors in the NCL of pigeons (Güntürkün & Durstewitz, 2001) or the PFC of macaques (Sawaguchi & Goldman-Rakic, 1991) disrupts working memory performance. Possibly, dopamine stabilizes active prefrontal neural representations against interfering input (Durstewitz, Kelc, & Güntürkün, 1999) by altering ionic and synaptic conductances which enhance spike frequencies of preactivated assemblies (Durstewitz, Seamans, & Sejnowski, 2000; Seamans, Durstewitz, Christie, Stevens, & Sejnowski, 2001). Thus, dopamine release in PFC/NCL could result in self-sustained activity being more robust to distracting stimuli and keeping the system focused on a particular goal state (Durstewitz et al., 1999). The cellular properties for these effects were described in mammals (Seamans & Yang, 2004) and they are likely to also exist in a similar way in pigeons (Kröner, Gottmann, Hatt, & Güntürkün, 2002).

For dopamine to play a stabilizing role in working memory, it has to be released during delay tasks. Indeed, both in monkeys (Watanabe, Kodama, & Hikosaka, 1997) and pigeons (Karakuyu, Herold, Güntürkün, & Diekamp, 2007), an increase of dopamine efflux in PFC and NCL, respectively, has been observed in working memory tasks. Neurochemical studies show that dopamine release in the PFC favors a diffusion-mediated volume transmission. This characteristic sluggishness of dopamine-reuptake within the PFC probably plays a key role in integrating stimulus-driven input and dopamine release: when dopamine is only slowly removed from extracellular space and thus spreads far from its release site, its presence is less precise with respect to time and synaptic location. As a consequence, it enables associative forebrain structures to easily integrate stimulus-driven events and dopamine releases (Schultz, 1998). Thus, volume transmission represents a key feature of the dopaminergic control of prefrontal functions. An in vivo microdialysis study of the extracellular values of dopamine and its metabolites within the pigeon's NCL revealed indeed a volume transmission mode (Bast, Diekamp, Thiel, Schwarting, & Güntürkün, 2002): Dopamine release in the NCL was associated with a lower reuptake by the dopamine transporter and could correspondingly accumulate in extracellular space. Thus, the mode of dopamine-utilization was identical in the mammalian PFC and the avian NCL.

Taken together, the mammalian PFC and the avian NCL show an astonishing degree of structural, cellular, and biochemical resemblances in the neuronal mechanisms with which the working memory is generated. Since the whole pallium is homologous between mammals and birds (Reiner et al., 2004), does this mean that also the PFC and NCL are homologous pallial fields? Probably not. Based on topographic and genetic arguments (Puelles et al., 2000; Medina & Reiner, 2000), PFC and NCL are possibly not homologous as pallial fields, but represent a case of evolutionary convergence. Thus, non-homologous fields within a homologous pallium converged over 300 million years into a mammalian and an avian version of a prefrontal entity to subserve highly similar functions. In the end, both areas acquired highly similar cellular properties to generate working memory. This evolutionary scenario offers a sobering lesson: there seem to be the only limited degrees of freedom to generate neural structures for cognitive operations like working memory.

Concluding remarks

Function before form

Birds and mammals have independently evolved the highest cognitive skills. Within the class of mammals, it is the primate order that stands out in cognitive terms. Within the class of birds, corvids and parrots take a similar position. Comparative cognitive analyses show that especially corvids reach cognitive skills that are on par with apes.

Despite these similarities in cognitive terms, birds and mammals have vastly different organized forebrains. Although their pallia are homologous, the mammalian dorsal pallium (cortex) is laminated while that of birds is not. Thus, lamination cannot be a structural requirement for the highest cognitive abilities.

Big brains for smart creatures

Both for birds and mammals, cognitive skills go along with an increase in brain size. This increase is especially evident in the associative areas of the pallium and their striatal termination fields. Thus, cognition needs associative space, irrespective how the brain is organized otherwise. The more cognitive flexibility is required for an animal, the larger its associative pallium has to grow.

Limited degrees of freedom

Avian and mammalian pallia are homologous as a whole entity, but this does not necessarily hold for one-to-one comparisons between different pallial fields (areas). PFC and NCL of mammals and birds, respectively, are both key fields for the generation of executive functions, but PFC and NCL are very likely not homologous. But despite this evolutionary difference, these two structures show an astonishing degree of similarity in terms of connectivity, neurochemistry, function, and electrophysiology. These similarities are most evident in the case of stimulus maintenance, as required for the short-term memory component of working memory. Thus, the establishment of certain cognitive operations seems to require a certain neural microcircuit. Even in forebrains that importantly differ in terms of the presence or the absence of a laminated architecture, there seem to be very limited degrees of freedom in establishing different microcircuits for identical cognitive operations.

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References

Allen, C., & Bekoff, M. (1997). *Species of Mind*. Cambridge: MIT.

Baddeley, A. D., & Hitch, G. (1974). Working Memory. In G. H. Bower (Ed.), *The Psychology of Learning and Motivation* (pp. 47–90). San Diego: Academic Press.

Barton, R. A., & Harvey, P. H. (2000). Mosaic evolution of brain structure in mammals. *Nature, 405*, 1055–1058.

Bast, T., Diekamp, D., Thiel, C., Schwarting, R. K. W., & Güntürkün, O. (2002). Microdialysis in the 'Prefrontal Cortex' and the striatum of pigeons (Columba livia): Evidence for dopaminergic volume transmission in the avian associative forebrain. *The Journal of Comparative Neurology, 446*, 58–67.

Bird C. D., Emery N. J. (2009). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences*, *USA*, *106*, 10370–10375.

Blackledge, T.A., Gillespie, R. G. (2004). Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. *Proceedings of the National Academy of Sciences*, *USA*, *101*:16228–16332.

Browning, R., Bruce Overmier, J., & Colombo, M. (2011). Delay activity in avian prefrontal cortex—sample code or reward code? *European Journal of Neuroscience, 33*, 726–735.

Bugnyar, T., & Heinrich, B. (2005). Ravens, *Corvus corax*, differentiate between knowledgeable and ignorant competitors. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *272*, 1641–1646.

Clayton, N. S., Bussey, T. J., & Dickinson, A. (2003). Can animals recall the past and plan for the future? *Nature Reviews Neuroscience, 4*, 685–691.

Cnotka, J., Güntürkün, O., Rehkämper, G., Gray, R. D., & Hunt, G. R. (2008). Extraordinary large brains in tool-using New Caledonian Crows (*Corvus moneduloides*). *Neuroscience Letters, 433*, 241–245.

Deaner, R. O., van Schaik, C. P., & Johnson, V. (2006). Do some taxa have better domain-general cognition than others? A meta-analysis of non-human primate studies. *Evolutionary Psychology, 4*, 149–196.

Diekamp, B., Gagliardo, A., & Güntürkün, O. (2002a). Nonspatial and subdivision-specific working memory deficits after selective lesions of the avian 'prefrontal cortex'. *The Journal of Neuroscience, 22*, 9573–9580.

Diekamp, B., Kalt, T., Güntürkün, O. (2002a). Working memory neurons in pigeons. *The Journal of Neuroscience*, *22 RC210*, 1–5.

Dunnett, S. B., Nathwani, F., & Brasted, P. J. (1999). Medial prefrontal and neostriatal lesions disrupt performance in an operant delayed alternation task in rats. *Behavioural Brain Research, 106*, 13–28.

Durstewitz, D., Kelc, M., & Güntürkün, O. (1999). A neurocomputational theory of the dopaminergic modulation of working memory functions. *The Journal of Neuroscience, 19*, 2807–2822.

Durstewitz, D., Kröner, S., Hemmings, H. C., Jr, & Güntürkün, O. (1998). The dopaminergic innervation of the pigeon telencephalon: Distribution of DARPP-32 and cooccurrence with glutamate decarboxylase and tyrosine hydroxylase. *Neuroscience, 83*, 763–779.

Durstewitz, D., Seamans, J. K., & Sejnowski, T. J. (2000). Dopamine-mediated stabilization of delay-period activity in a network model of prefrontal cortex. *Journal of Neurophysiology, 83*, 1733–1750.

Edinger, L., Wallenberg, A., Holmes, G. M. (1903). Untersuchungen über die vergleichende Anatomie des Gehirns. 3. Das Vorderhirn der Vögel. *Abhandlungen der Senckenbergischen Gesellschaft*, *20*, 343–426.

Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science, 306*, 1903–1907.

Fersen von, L. & Güntürkün, O. (1990). Visual memory lateralization in pigeons. *Neuropsychologia*, *28*, 1–7.

Fersen von, L., Wynne, C. D., Delius, J. D., & Staddon, J. E. (1990). Deductive reasoning in pigeons. *Naturwissenschaften, 77*, 548–549.

Gehring, W. J. (2005). New perspectives on eye development and the evolution of eyes and photoreceptors. *Journal of Heredity, 96*, 171–184.

Güntürkün, O. (1997). Cognitive impairments after lesions of the neostriatum caudolaterale and its thalamic afferent: functional

similarities to the mammalian prefrontal system? *Journal of Brain Research, 38*, 133–143.

Güntürkün, O. (2005). The avian 'prefrontal cortex' and cognition. *Current Opinion in Neurobiology, 15*, 686–693.

Güntürkün, O., & Durstewitz, D. (2001). Multimodal areas of the avian forebrain—blueprints for cognition? In G. Roth & M. Wullimann (Eds.), *Brain Evolution and Cognition* (pp. 431–450). Heidelberg: Spektrum Akademischer Verlag.

Güntürkün, O., & Remy, M. (1990). The topographical projection of the nisthmi pars parvocellularis (Ipc) onto the tectum opticum in the pigeon. *Neuroscience Letters, 111*, 18–22.

Hartmann, B., & Güntürkün, O. (1998). Selective deficits in reversal learning after neostriatum caudolaterale lesions in pigeons—possible behavioral equivalencies to the mammalian prefrontal system. *Behavioural Brain Research, 96*, 125–133.

Harvey, P. H., & Krebs, J. R. (1990). Comparing brains. *Science, 249*, 140–146.

Honig, W. K. (1978). Studies of Working Memory in the Pigeon. In S. H. Hulse & W. K. Honig (Eds.), *Cognitive Processes in Animal Behavior* (pp. 211–248). New York: Hillsdale.

Hunt, G. R., & Gray, R. D. (2003). Diversification and cumulative evolution in new Caledonian crow tool manufacture. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *270*, 867–874.

Iwaniuk, A. N., Dean, K. M., Nelson, J. E. (2004). A mosaic pattern characterizes the evolution of the avian brain. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *271*, S148–S151.

Jarvis, E. D., Güntürkün, O., Bruce, L. L., Csillag, A., Karten, H., Kuenzel, W., et al. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Review Neuroscience, 6*, 151–159.

Jerison, H. J. (1979). The evolution of diversity in brain size. In M. E. Hahn (Ed.), *Development and Evolution of Brain Size* (pp. 29–57). New York: Academic Press.

Karakuyu, D., Herold, C., Güntürkün, O., & Diekamp, B. (2007). Differential increase of extracellular dopamine and serotonin in the 'prefrontal cortex' and striatum of pigeons during working memory. *European Journal of Neuroscience, 26*, 2293–2302.

Keverne, E. B., Martel, F. L., Nevison, C. M. (1996). Primate brain evolution: genetic and functional considerations, *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *262*, 689–696.

Kirsch, J., Güntürkün, O., & Rose, J. (2008). Insight without cortex: Lessons from the avian brain. *Consciousness and Cognition, 17*, 475–483.

Kröner, S., Gottmann, K., Hatt H., Güntürkün, O. (2002). Cell types within the neostriatum caudolaterale of the chick: Intrinsic electrophysiological and anatomical properties. *Neuroscience*, *110*, 495–473.

Kröner, S., & Güntürkün, O. (1999). Afferent and efferent connections of the caudolateral neostriatum in the pigeon (*Columba livia*): A retro- and anterograde pathway tracing study. *The Journal of Comparative Neurology, 407*, 228–260.

Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution, 63*, 233–246.

Lefebvre, L., & Sol, D. (2008). Brains, lifestyles and cognition: Are there general trends? *Brain, Behavior and Evolution, 72*, 135–144.

Machens, C. K., Romo, R., & Brody, C. D. (2005). Flexible control of mutual inhibition: a neural model of two-interval discrimination. *Science, 307*, 1121–1124.

Medina, L., & Reiner, A. (2000). Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends in Neuroscience, 23*, 1–12.

Mehlhorn, J., Rehkämper, G., Hunt, G. R., Gray, R., & Güntürkün, O. (2010). Tool making New Caledonian crows have larger associative brain areas. *Brain, Behavior Evolution, 75*, 63–70.

Metzger, M., Jiang, S., & Braun, K. (2002). A quantitative immuno-electron microscopic study of dopamine terminals in forebrain regions of the domestic chick involved in filial imprinting. *Neuroscience, 111*, 611–623.

Pollok, B., Prior, H., & Güntürkün, O. (2000). Development of object-permanence in the food-storing magpie (*Pica pica*). *Journal of Comparative Psychology, 114*, 148–157.

Prior, H., Schwarz, A., & Güntürkün, O. (2008). Mirror-induced behaviour in the magpie (*Pica pica*): Evidence for self-recognition. *PLoS Biology, 6*, e202.

Puelles, L., Kuwana, E., Puelles, E., Bulfone, A., Shimamura, K., Keleher, J., Smiga, S., et al. (2000). 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. *The Journal of Comparative Neurology*, *424*, 409–438.

Reader, S. M., Laland, K. N. (2002). Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, USA*, *99*, 4436–4441.

Rehkämper, G., Frahm, H. D., & Zilles, K. (1991). Quantitative development of brain and brain structures in birds (Galliformes und Passeriformis) compared to that in mammals (insectivores and primates). *Brain Behavior Evolution, 37*, 125–143.

Reiner, A., Perkel, D. J., Bruce, L. L., Butler, A. B., Csillag, A., Kuenzel, W., et al. (2004). Revised nomenclature for avian telencephalon and some related brainstem nuclei. *The Journal of Comparative Neurology, 473*, 377–414.

Rose, J., & Colombo, M. (2005). Neural correlates of executive control in the avian brain. *PLoS Biology, 3*, e190.

Rose, J., Güntürkün, O., Kirsch, J. (2009). Evolution of association pallial areas: in birds. In M. D. Binder, N. Hirokawa, & U. Windhorst (Eds.), *Encyclopedia in Neuroscience* (pp. 1215–1219). Springer: Berlin.

Sawaguchi, T. (2001). The effects of dopamine and its antagonists on directional delay-period activity of prefrontal neurons in monkeys during an oculomotor delayed-response task. *Neuroscience Research, 41*, 115–128.

Sawaguchi, T., & Goldman-Rakic, P. S. (1991). D1 dopamine receptors in prefrontal cortex: Involvement in working memory. *Science, 251*, 947–950.

Schnabel, R., Metzger, M., Jiang, S., Hemmings, H. C., Jr, Greengard, P., & Braun, K. (1997). Localization of dopamine D1 receptors and dopaminoceptive neurons in the chick forebrain. *The Journal of Comparative Neurology, 388*, 146–168.

Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of Neurophysiology, 80*, 1–27.

Seamans, J. K., Durstewitz, D., Christie, B.R., Stevens, C.F., Sejnowski, T.J. (2001). Dopamine D1/D5 receptor modulation of excitatory synaptic inputs to layer V prefrontal cortex neurons. *Proceedings of the National Academy of Sciences, USA*, *98*, 301–306.

Seamans, J. K., & Yang, C. R. (2004). The principal features and mechanisms of dopamine modulation in the prefrontal cortex. *Progress in Neurobiology, 74*, 1–58.

Sol, D., Bacher, S., Reader, S. M., & Lefebvre, L. (2008). Brain size predicts the success of mammal species introduced into novel environments. *American Naturalist, 172*, S63–S71.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., Lefebvre, L. (2005). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences, USA*, *102*, 5460–5465.

Stephan, H., Baron, G., Frahm, H. D. (1988). Comparative size of brains and brain components. In: H. D. Steklis, J. Erwin (Eds.),

Comparative Primate Biology (pp. 1–38). New York: Alan R. Liss.

Taylor, A. H., Hunt, G. R., Holzhaider, J. C., & Gray, R. D. (2007). Spontaneous metatool us by New Caledonian crows. *Current Biology, 17*, 1504–1507.

Taylor, A. H., Hunt, G. R., Medina, F. S., Gray, R. D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *276*, 247–254.

Vijayraghavan, S., Wang, M., Birnbaum, S. G., Williams, G. V., & Arnsten, A. F. (2007). Inverted-U dopamine D1 receptor actions on prefrontal neurons engaged in working memory. *Nature Neuroscience, 10*, 376–384.

Wake, D. B., Wake, M. H., & Specht, C. D. (2011). Homoplasy: From detecting pattern to determining process and mechanism of evolution. *Science, 331*, 1032–1035.

Watanabe, M., Kodama, T., & Hikosaka, K. (1997). Increase of extracellular dopamine in primate prefrontal cortex during a working memory task. *Journal of Neurophysiology, 78*, 2795–2798.

Weir, A. A. S., Chappell, J., & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science, 297*, 981.

Wynne, B., & Güntürkün, O. (1995). The dopaminergic innervation of the forebrain of the pigeon (*Columba livia*): A study with antibodies against tyrosine hydroxylase and dopamine. *The Journal of Comparative Neurology, 358*, 1–19.

Yamazaki, Y., Aust, U., Huber, L., & Güntürkün, O. (2007). Lateralized cognition: Asymmetrical and complementary strategies of pigeons during discrimination of the "human" concept. *Cognition, 104*, 315–344.