



Insight without cortex: Lessons from the avian brain

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ARTICLE INFO

Article history:

Received 6 March 2008

Available online 25 April 2008

Keywords:

Insight
Convergent evolution
Object permanence
Episodic memory
Theory of mind
Causal reasoning
Birds

ABSTRACT

Insight is a cognitive feature that is usually regarded as being generated by the neocortex and being present only in humans and possibly some closely related primates. In this essay we show that especially corvids display behavioral skills within the domains of object permanence, episodic memory, theory of mind, and tool use/causal reasoning that are insightful. These similarities between humans and corvids at the behavioral level are probably the result of a convergent evolution. Similarly, the telencephalic structures involved in higher cognitive functions in both species show a high degree of similarity, although the forebrain of birds has no cortex-like lamination. The neural substrate for insight-related cognitive functions in mammals and birds is thus not necessarily based on a laminated cortical structure but can be generated by differently organized forebrains. Hence, neither is insight restricted to mammals, as predicted from a “*scala naturae*”, nor is the laminated cortex a prerequisite for the highest cognitive functions.

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1. Introduction

Consciousness is a characteristic of the mind generally regarded to comprise qualities such as subjectivity and self-awareness. Additionally, it is thought to involve cognitive capabilities like insight and the ability to perceive the relationship between oneself and one's environment. Consciousness is a subject of much research in the philosophy of mind, psychology, neuroscience, and cognitive science. There is no doubt that humans are conscious, but only little is known about the evolution of consciousness. Evolutionary arguments always involve a comparative approach under which a variable of interest is analyzed in different species sharing varying degrees of similarity in their geno- or ecotype. To employ such a comparative approach, consciousness needs to be measurable or, at least, its presence or absence needs to be provable. Since consciousness involves elements of subjectivity and self-awareness, it is extremely difficult to study it experimentally in human subjects. This endeavor is even more difficult with animals. It therefore remains an open question whether it is even in principle possible to reconstruct the evolutionary history of consciousness.

Two intuitively appealing approaches to circumvent this problem involve the usage of either taxonomic and/or structural arguments. The taxonomic argument implies that lineages that are close to *Homo* are more likely to have higher cognitive abilities and, possibly, even consciousness. Following this assumption, the probability of being conscious decreases from apes to monkeys to non-primate mammals to birds. We will call this the “*scala naturae*” approach. Despite being attacked as having no theoretical substance (Hodos & Campbell, 1969), it still enjoys a broad appeal. This is nicely illustrated in (Humphrey, 1984): “Somewhere along the evolutionary path that led from fish to chimpanzee a change occurred in the nervous system which transformed an animal which simply “behaved” into an animal which at the same time informed its mind of the reason of its behavior.” The second intuitive account trying to reconstruct the evolutionary past of consciousness involves structural arguments. Here, consciousness is usually associated with the occurrence of the neocortex. Since humans

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have an especially large encephalization quotient (Van Dongen, 1998) and since we have little doubt that the majority of human cognitive skills are generated by neocortical processes (Deaner, Isler, Burkart, & van Schaik, 2007) the occurrence of this neural structure might be the critical evolutionary event that made consciousness possible. Thus, consciousness might require certain computations that can only be provided by the special architecture of the neocortex (Humphrey, 1984; Montagnini & Treves, 2003). We will call this the “*cortex is special*” argument.

In this essay we want to confute both, the “*scala naturae*” and the “*cortex is special*” arguments. Since, as outlined in the beginning, consciousness involves processes that are extremely difficult to analyze experimentally in a comparative context, we will focus instead on some cognitive capacities that are thought to be tightly associated with the presence of a conscious mind. Thus, we will focus this discussion on cognitive experiments studying insight. We will do this by reviewing the behavioral evidence for insight in birds. Birds and mammals are two taxonomic classes which separated at least 300 million years ago (Fig. 1). Thus, birds are very distant from humans in evolutionary terms and should therefore have a low chance to produce cognitive feats relevant for consciousness (the “*scala naturae*” argument). Additionally, birds have no neocortex and should therefore lack the neural machinery to produce mental skills that are closely related to conscious thought (the “*neo-cortex is special*” argument). Our aim is to show that at least some birds are on par with apes with regards to insight-related cognition. Additionally, we will show that birds produce these mental skills with neural structures that are not laminated and thus not cortical, but are otherwise functionally similar to the prefrontal cortex.

2. Behavioral skills of birds and mammals

The order of mammals is phylogenetically very successful. Mammals like humans, macaques, or rats are able to flexibly adjust their behavior 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 through time. 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 as mammals (Güntürkün, 2005a, 2005b). Pigeons, for example, are able to memorize up to 725 different visual patterns (von Fersen & Delius, 1989), learn to categorize images into ‘human’ vs. ‘non-human’ (Yamazaki, Aust, Huber, Hausmann, & Güntürkün, 2007) or ‘human-made’ vs. ‘natural’ (Lubow, 1974), or rank patterns using transitive inference (Jarvis et al., 2005). Transitive inference abilities have also been reported to be present in the Great Tit (Peake, Terry, McGregor, & Dabelsteen, 2002) and in Pinyon jays (Paz-y-Miño, Bond, Kamil, & Balda, 2004). With respects to auditory and vocal capacities, songbirds have been shown to display a high degree of flexibility in acquisition of new vocal sequences (Marler, 1997). Grey parrots are highly proficient in verbal communication (Pepperberg, 1999) and exhibit numerical understanding (Pepperberg & Gordon, 2005). Finally, birds have working memory (Honig, 1978), which has been proposed to require consciousness (Baars, 2003).

In addition to these more general cognitive abilities, birds are also able to generate insight-related cognition. According to Merriam-Webster’s Dictionary, “insight” is defined as “the power of seeing into a situation.” Examples for such processes are object permanence, mental time travel, theory of mind, and tool use/causal reasoning. In former times these cognitive skills were thought to be a domain solely of primates. However, recent studies have shown that corvids are able to display these abilities (Emery & Clayton, 2004). In the following we will discuss each of the specific aspects of insight.

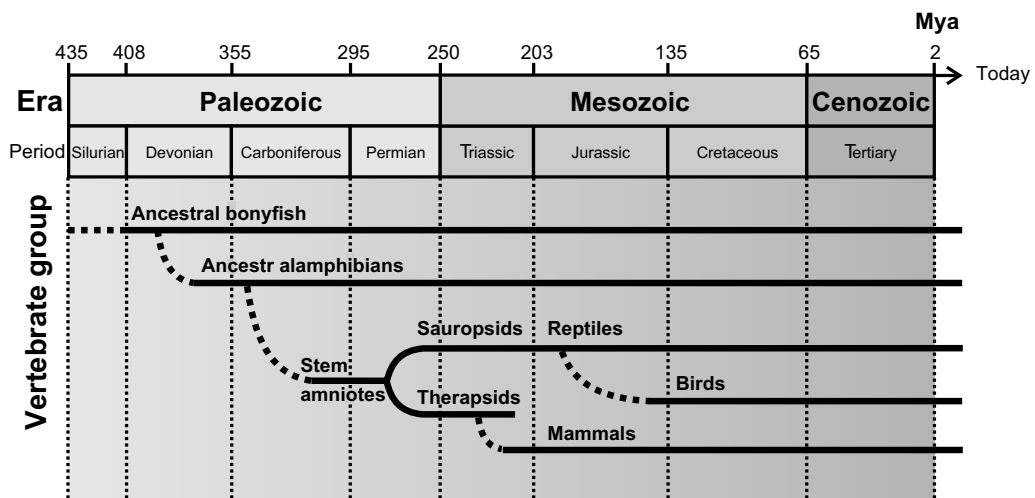


Fig. 1. Simplified modern view of vertebrate evolution. The diagram begins with the fish group that contains the most recent ancestors of land vertebrates. The ancestral amphibians are thought to have given rise to stem amniotes. Stem amniotes then split into at least two groups: the sauropsids, which gave rise to all modern reptiles; and the therapsids, which evolved into mammals. Many sauropsids (reptiles) are currently living. Solid horizontal lines indicate temporal fossil evidence. Dashed lines indicate proposed ancestral links based. Mya, million years ago.

2.1. Object permanence

Object permanence is the awareness that objects continue to exist when they are out of sight. To date, object permanence has been reported in avian species of different orders (ring doves: (Dumas & Wilkie, 1995); kakariki: (Funk, 1996); grey parrot: (Pepperberg, Willner, & Gravit, 1997)). One study (Pollok, Prior, & Güntürkün, 2000) demonstrated the presence and development of object permanence in magpies, a corvid species (Fig. 2A). In this study, object permanence was operationalized by presenting tasks 1–15 from Scale 1 (Uzgiris & Hunt, 1975). These tasks have proved to be suitable for interspecies comparisons and have been used successfully in earlier studies on object permanence in birds (Pepperberg et al., 1997). Pollok et al. (2000) reported that the tested animals reach Piagetian stages 4 and 5 very early and well before independence from parents. To test Piagetian stage 4 an object was completely hidden under a cover and the criterion performance was removing the cover and picking up the object. For testing Piagetian stage 5 the object was hidden either three times under one screen and then under another screen, or it was hidden alternately under two or three different coverings; the criterion performance was searching under the site of the last hiding. Additionally, the object was presented in the experimenter's hand and was passed successively under each of three screens and finally hidden under the screen where it disappeared last. Immediate search under the last screen demonstrated object permanence during successive visible displacements. In the last task testing stage 5 an object was hidden under three superimposed covers and criterion performance was indicated by obtaining the object after removing all covers. Magpies also mastered five of six simple successive invisible displacement tasks, making it very likely that they would also reach the highest Piagetian stage 6. This finding has recently been confirmed in Eurasian jays (Zucca, Milos, & Vallortigara, 2007). Thus, with respects to object permanence corvids leave most mammalian species behind and are on par with apes (Gómez, 2005).

2.2. Theory of mind

Theory of mind involves the attribution of one's own mental state and possible future behavior to another organism. This cognitive ability has been shown in scrub-jays (Clayton, Bussey, & Dickinson, 2003; Emery & Clayton, 2001) and ravens (Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2002, 2004) during food caching behavior (Fig. 2B). Caching food is com-

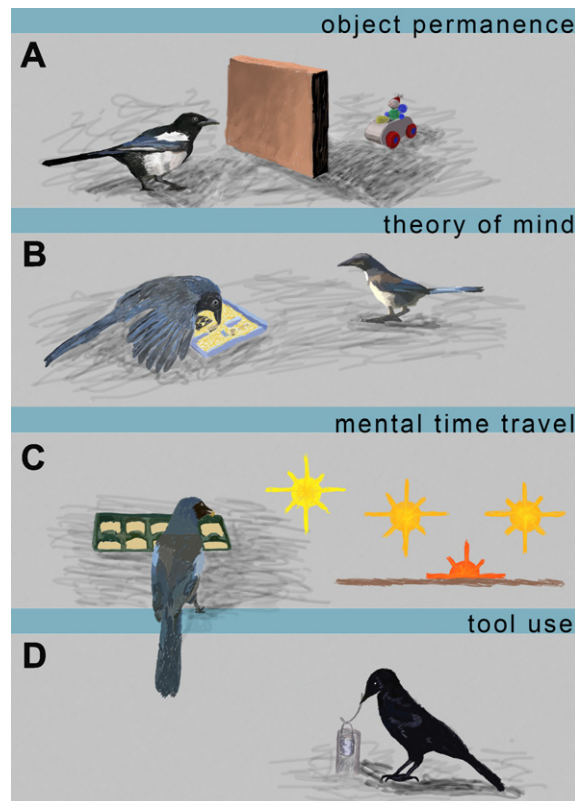


Fig. 2. The components of insight reported in corvids. The four cognitive abilities that contribute to insightful behavior: (A) object permanence: the awareness that objects continue to exist when they are out of sight; (B) theory of mind: the attribution of one's own mental state and possible future behavior to another organism; (C) mental time travel: the ability to recollect specific past episodes and to anticipate future needs and motivational states and (D) tool use/causal reasoning: the ability to select and manipulate objects in the environment as tools to achieve a goal.

petitive and costly, because another individual might steal the caches. In an experiment (Emery & Clayton, 2001) the birds were allowed to cache either in private or while a conspecific was watching, and afterwards to recover their caches in private. Scrub-jays that had previously stolen another bird's cache subsequently re-cached food when they had been observed during caching. Birds without the experience of stealing did not recache their food when they were observed during caching. These results indicate that the re-caching in sites unknown to the observer depends on the previous experience of having stolen food caches (Clayton et al., 2003). As the re-caching depends on the individual experience of stealing caches, the birds must project their own experience onto the observer inferring that what they can do a conspecific can do as well.

2.3. Mental time travel

Mental time travel refers to the ability to recollect specific past episodes (retrospective cognition/episodic memory) and to anticipate future needs and motivational states (prospective cognition). Episodic memory is marked by combined auto-epic (self-centered) memories for *what* happened *where* and *when* and allows the recall of unique past experiences (Tulving, 1983; Tulving & Markowitsch, 1998). While the auto-epic character of episodic memory is difficult to approach experimentally, episodic-like memory has been demonstrated in western scrub-jays (Fig. 2C), corvids that store food items and recover them for consumption, often months later. In recovering food items, they show memory for *what* food item was cached *where* and *when*. This enables the birds to retrieve perishable food earlier, while non-perishable items can be left in storage (Clayton et al., 2003; Clayton & Dickinson, 1998, 1999). Recently, Raby et al. demonstrated that corvids are also capable of prospective cognition (Raby, Alexis, Dickinson, & Clayton, 2007). The birds plan their breakfast, caching food at places where they previously learned to be hungry in the morning, furthermore preferentially caching those food items that they know to be missing at a given location.

2.4. Tool use/causal reasoning

Tool use/causal reasoning is the ability to select and manipulate objects in the environment to utilize them to achieve a goal, e.g. to access food that is normally out of reach. The New Caledonian crow stands out among corvids because of its impressive tool manufacturing skills. Their tool manufacture in the wild has features previously only observed in humans: these include

- (1) Diversification and standardization (Hunt, 2000): The authors observed New Caledonian crows cutting tools out of pandanus leaves which are well suited for pulling larvae out of tree holes. Although the tools differed in terms of length and number of cutting-steps, the general design and fashion was highly standardized over several populations of crows.
- (2) The use and crafting of hooks (Hunt, 1996; Hunt & Gray, 2004): The authors describe hooked-twig tools that crows manufactured from living secondary twigs. All were stripped of leaves and bark and had a hook on their wide ends. All birds used the hook end of those tools and by rapid back and forth movements picked up prey under detritus. Hook use suggests an appreciation of tool functionality, and the existence of a tool kit suggests the use of varying tools for different tasks.
- (3) Lateralization (Hunt, 2000; Hunt, Corballis, & Gray, 2001): The authors observed that most crows which manufactured the stepped-cut tool described in (1) started cutting this tool from the left side which demonstrates a functional lateralization or 'handedness' in pandanus tool-making. There were no obvious physical environmental factors, e.g. variation in habitat characteristics, number of counterparts on trees, or leaf-spiral direction, which could explain this preference.
- (4) Metatool use—the ability to use one tool on another (Taylor, Hunt, Holzhaider, & Gray, 2007): Under laboratory conditions New Caledonian crows were confronted with food that was placed in a 15 cm deep horizontal hole and a toolbox, which contained a 18 cm long stick which could be used to extract the food from the hole. Unfortunately, the long stick was out of reach of a crow's bill. In front of the toolbox a 5 cm long tool was placed. This tool was too short to extract the meat but could be used to extract the long tool from the tool box. Six out of seven crows initially attempted to extract the long tool with the short tool and four of them successfully obtained the meat on the first trial. This experiment shows that the crows did not solve the metatool task by trial-and-error learning, but based on analogical reasoning.
- (5) Cumulative changes in tool design (Hunt & Gray, 2003): The authors found three distinct pandanus tool designs: wide tools, narrow tools and stepped tools. The lack of ecological correlates of the three tool designs and their different, continuous and overlapping geographical distributions make it unlikely that they evolved independently. The similarities in the manufacture method of all designs further suggest that pandanus tools have gone through a process of cumulative change from a common historical origin.

Furthermore, New Caledonian crows are also able to modify unfamiliar material-like wire and aluminum into functional tools (Fig. 2D) (Weir, Chappell, & Kacelnik, 2002; Weir & Kacelnik, 2006).

In sum, higher cognitive functions that once were thought to be special to humans, or at least to our closest relatives, can be found in corvids. Corvids are only remotely related to us and species belonging to the intermediate taxa are unable to

demonstrate the cognitive abilities reviewed above. Thus, the advanced cognitive abilities of corvids are probably the result of convergent evolution (Emery & Clayton, 2004). This implies that we cannot assume a linear evolutionary increase of mental complexity, finally culminating in humans. Instead, high mental abilities were discovered several times in different branches of the evolutionary tree. These conclusions are not compatible with a “*scala naturae*” view of the evolution of insight-related cognition.

This leads to the question what neuronal features birds and mammals share. If species of different taxonomic classes share aspects of higher cognition, they might be expected to share the neuronal features that generate those capacities (Butler & Cotterill, 2006). Therefore, we will examine the similarities and differences in the neuroarchitecture of birds and mammals by interrogating the argument that the mammalian “*cortex is special*.”

3. Neuroarchitecture of higher cognition in birds and mammals

The drastically different organization of avian and mammalian forebrains stands in sharp contrast to the numerous similarities between these vertebrate classes at the behavioral level. Birds and mammals separated at least 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 (Güntürkün, 2005a, 2005b). Lamination is commonly seen as an evolutionary new and computationally advantageous type of neural architecture (Montagnini & Treves, 2003). Speaking in the words of Humprey (1984, p. 35): “My guess is that the relevant evolutionary change involved the development of a new brain—the ‘conscious brain’ parallel to the older ‘executive brain’.” Is that really the case?

In the last years our understandings of the evolution of vertebrate brains and the homologies between the avian and the mammalian brain have advanced substantially. To reflect this new understanding, The Avian Brain Consortium, a group of leading experts in the field, has reviewed the cumulated evidence for the slowly emerging paradigm shift and proposed a new avian brain nomenclature to address the newly evolving view (Jarvis et al., 2005; Reiner et al., 2004). The classical avian brain nomenclature dated back to the turn of the 19th to the 20th century and was based on Edinger’s model of brain evolution (Edinger, Wallenberg, & Holmes, 1903). 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 paleocortical components, together with the claustrum and lateral parts of the amygdala, constitute 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, the 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 et al. (1903) to assume that birds have virtually no pallium but an enormously hypertrophied striatum instead. It was concluded that birds were not capable of higher cognition but followed an instinct-based behavioral repertoire (Edinger et al., 1903). Based on neurochemical, histological, behavioral, embryological, and genetic studies this view had to be rejected (Reiner et al., 2004). Birds do indeed possess a large pallium, consisting of several main subdivisions (Fig. 3). Two conclusions from this paradigm shift are important for the present review: (1) The avian striatum is not hypertrophied but takes about the same proportion of the cerebrum as in mammals. Thus, birds are not bound to instinct-based behavior; (2) The avian pallium is about as large as the mammalian pallium and most of its subcomponents are similar to neocortical fields with regards to their connectivity and histochemistry (Reiner, Yamamoto, & Karten, 2005). Thus, avian and mammalian pallia resemble each other, even though they do not share the architectural feature of lamination.

In addition, it is conceivable that cortical lamination is not an evolutionary new invention that happened only in the line leading to modern mammals, but is instead an old feature, which was abandoned to some extent by modern reptiles and birds. This suggestion is based on observations of the forebrain organization of tuatara. Tuatara are lizard-like reptiles that have retained primitive traits making them *living fossils* from an early period of vertebrate development at the division between birds and reptiles. Tuatara have a three-layered forebrain that resembles the cortical neuronal cell plate (Reiner & Northcutt, 2002). This finding might imply that a laminated forebrain was already inherited by sauropsids (that later gave rise to birds and reptiles) but was later partly abandoned for a non-laminated forebrain organization. In sum, the ‘neo’cortex is not necessarily a new invention. Since birds do not have a laminated forebrain but are able to show high mental capabilities, the process of insightful behavior needs no lamination. The neuronal circuits for insightful behavior have probably evolved several times and do not necessarily require the architecture of our neocortex. These conclusions are not compatible with a “*cortex is special*” view of the evolution of insight-related cognition. In the following we will further argue that an area of the human brain commonly associated with insightful behavior, the prefrontal cortex, also has a functional analog in birds. The presence of a functionally similar area in the avian pallium that is, however, not laminated, calls the assumption of a laminated cortex as a requirement for higher cognition into serious question.

4. Functions of the avian and mammalian ‘prefrontal cortex’

Complex cognitive abilities are not generated by single cortical areas but are instead orchestrated by a pattern of activities spanning many cortical fields. Among these, the prefrontal cortex (PFC) probably plays the most important role since it monitors and organizes cortical activity patterns according to goal-directed cognition. Thus, the PFC is probably most crucially

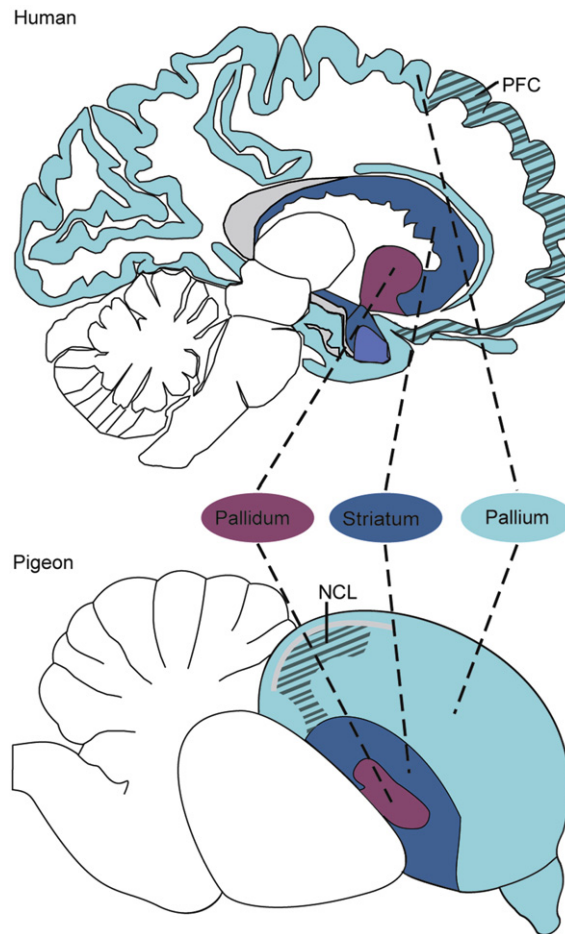


Fig. 3. The new understanding of avian and mammalian brain relations. Sagittal view of a human (top) and a pigeon (bottom) brain. Abbreviations: PFC, prefrontal cortex; NCL, nidopallium caudolaterale.

involved in insight-related cognition in humans and some other mammals (Gómez, 2005). The functions of the PFC were mostly studied in relation to so-called “executive function”, a cluster of cognitive functions underlying the ability to spontaneously generate efficient strategies when relying on self-directed task-specific planning (Taylor, Saint-Cyr, & Lang, 1986). As will be shown below, the nidopallium caudolaterale (NCL), an area in the avian pallium, shows important neural similarities to the PFC and generates executive functions without displaying any visible lamination.

4.1. Anatomy

Like the PFC, NCL is a higher order association area and is closely tied to all secondary sensory and motor structures (Güntürkün & Durstewitz, 2001; Kröner & Güntürkün, 1999; Leutgeb, Husband, Ritters, Shimizu, & Bingman, 1996; Metzger, Jiang, & Brain, 1998). Two anatomical properties of the PFC were thought to be characteristic for this structure; first, a rich dopaminergic innervation from tegmental cell groups A9 and A10; second, strong afferent connections from the dorsomedial nucleus of thalamus (Divac, Bjorklung, Lindvall, & Passingham, 1978; Reiner, 1986). In 1985, Divac and Mogensen were the first to show a dopaminergic innervation of the NCL and proposed that this avian structure might be equivalent to the mammalian PFC (Divac & Mogensen, 1985; Divac, Mogensen, & Björklund, 1985). More recent results substantiated this claim (Durstewitz, Kelc, & Güntürkün, 1999; Durstewitz, Kröner, & Güntürkün, 1999; Mogensen & Divac, 1993).

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 sends fibers back to the projecting area (Pandya & Yeterian, 1990). This is found identically for the NCL which receives afferents from secondary and tertiary sensory areas of all modalities and projects back onto these (Leutgeb et al., 1996). In addition, NCL projects to most parts of the somatic and limbic striatum, as well as to motor output structures (Kröner & Güntürkün, 1999). Thus, identical 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, the nucleus accumbens, visceral structures (Kröner & Güntürkün, 1999; Kuenzel & Blähser, 1993) and diverse chemically defined afferent systems (Dubbeldam & den Boer-Visser, 2000; Lanuza, Davies, Landete, Novejarque, & Martínez-García, 2000; Metzger, Toledo, & Braun, 2002).

In summary, PFC and NCL share many important anatomical features; however, their architecture differs grossly. The PFC shows the typical cortical lamination while the NCL is not laminated. In the following we will review behavioral evidence and compare the functional role of PFC and NCL, thus questioning the relevance of lamination for the generation of insightful behavior.

4.2. Behavior

The PFC serves complex functions, usually subsumed under the terms ‘working memory’ and ‘executive control of behavior’. Functional equivalence of PFC and NCL was initially proposed by Divac and Mogensen, based on findings that ablation of the NCL led to a disruption of performance on a working memory task, while performance on a visual discrimination task was unaffected (Güntürkün, 1997; Mogensen & Divac, 1982). The involvement of NCL in working memory has later been confirmed when delay activity, the neural correlate of stimulus maintenance, was described in NCL neurons (Diekamp, Kalt, & Güntürkün, 2001; Rose & Colombo, 2005).

Initial evidence suggesting an involvement in executive control of behavior has been reported more recently. An important component of executive control is the ability to adjust the effort to obtain a reward to the value of that reward. Transient pharmacological lesions to the NCL disrupt this ability, lesioned animals will put as much effort into obtaining a small reward as into obtaining a large reward (Kalenscher, Diekamp, & Güntürkün, 2003). 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 (Kalenscher et al., 2005). Another component of executive control is the ability to rapidly adjust to changing environmental demands. A frequently used paradigm to assess this flexibility is reversal learning (Lissek, Diekamp, & Güntürkün, 2002). In this procedure a learned stimulus-reward contingency is reversed, so that the S– now predicts the reward while the S+ does not. In solving this task animals go through three distinct stages; persistency on the previously learned association, randomized responding and acquisition of the new contingency. Lesions to the NCL and blockade of dopamine- (Güntürkün, 2005b) or NMDA-receptors (Lissek et al., 2002) in this area lead to extended persistency and hence to a severe disruption of behavioral flexibility.

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 (Rose & Colombo, 2005). The authors trained pigeons on a working memory task during which the animals learned that 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 activity of NCL neurons during the memory phase. The vast majority of neurons showed activity when the birds chose to memorize a stimulus; however, this activity was suppressed as soon as the birds knew that remembering 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 (Rose & Colombo, 2005).

Taken together, the evidence summarized here shows that the NCL is functionally equivalent to the PFC and hence that the NCL corresponds to the mammalian brain structure that is most probably critical for the generation of insightful behavior. Conclusively, we must refute the “*cortex is special*” argument and conclude that higher cognitive functions, such as insight, can arise from neural structures that do not share the architecture of the mammalian neocortex.

5. Concluding remarks

We have shown that birds are capable of generating complex behavior. Especially corvids seem to be on par with apes in most aspects studied. Given the phylogenetic distance between birds and mammals, we may assume that a number of these skills have evolved independently. Thus, concerning the evolution of insight and possibly consciousness, taxonomic proximity to Homo is not a condition sine qua non. We can therefore refute the “*scala naturae*” argument for insightful behavior.

Brainwise, the avian and mammalian pallia are homologous with respect to their phylogenetic continuity. However, the avian pallium shows no lamination similar to the mammalian neocortex. Despite this structural difference, both mammals and birds have evolved an associative pallial structure that subserves similar functions. Since this area is associated with executive function in both birds and mammals, complex cognitive functions in terms of “insight” are not necessarily bound to the presence of a laminated forebrain. We can therefore also refute the “*cortex is special*” argument for insightful behavior.

The considerable difficulty to experimentally assess the evolution of consciousness opens the doors to intuitively appealing rationales like the “*scala naturae*” and “*cortex is special*” arguments. While we do not know if it is in principle possible to reconstruct the evolution of consciousness, much can be learned by the comparative investigation of higher cognitive functions, such as insight, and their neural substrates. Insight is a cognitive ability that provides an important advantage for every species living and foraging under complex social and ecological conditions. This adaptive advantage very likely forced some taxonomic groups of mammals and birds to convergently develop similar insightful behavior along with ‘prefrontal’ neural functions. If insight and prefrontal function are indeed related to consciousness, it might be conceivable that consciousness was invented independently several times during evolution.

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