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Review

Cognition without Cortex

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Assumptions on the neural basis of cognition usually focus on cortical mechanisms. Birds have no cortex, but recent studies in parrots and corvids show that their cognitive skills are on par with primates. These cognitive findings are accompanied by neurobiological discoveries that reveal avian and mammalian forebrains are homologous, and show similarities in connectivity and function down to the cellular level. But because birds have a large pallium, but no cortex, a specific cortical architecture cannot be a requirement for advanced cognitive skills. During the long parallel evolution of mammals and birds, several neural mechanisms for cognition and complex behaviors may have converged despite an overall forebrain organization that is otherwise vastly different.

Convergent Evolution of Cognition and Brain

What happens at the neural level when two groups of animals converge during evolution with regard to their cognitive skills? Do their brains also assume a similar neural architecture? Or are differently organized nervous systems able to produce comparable cognitive abilities? This is a foundational question for the field of Cognitive Neuroscience. Recent discoveries in birds have yielded new insights and represent a promising direction for finding answers.

The class of mammals to which we humans belong is extremely successful. Mammals live in practically all ecological niches in which vertebrates can survive. And wherever mammals occur, they represent some of the top predators [1]. This phylogenetic success story is, at least in part, due to the ability of mammals to innovate novel behaviors in changing environments, incorporate contextual information into their decisions, and learn from various social situations, thereby increasing their survival rate [2]. These and other cognitive abilities are key to the spread of mammals into practically every corner of our planet. Birds represent an equally successful vertebrate class, and novel studies testify that they generate many of the same cognitive functions as mammals [2–5]. But the evolutionary lines of birds and mammals separated approximately 300 million years ago [4]. This extremely long period of **parallel evolution** (see Glossary) is readily visible in the organization of mammalian and bird brains. Both classes have a large **cerebrum** that makes up most of the brain and that can be subdivided into a pallial and a subpallial territory (in Latin '**pallium**' means mantle). The **subpallium**, in which the striatum is the largest component, has a strikingly similar organization in mammals and birds [6]. It is even likely that the basic circuitry of most of the subpallium is similar across animals from lampreys to humans, and can be traced back to a common ancestor that lived approximately 535 million years ago [7].

It is much more difficult to understand the evolutionary trajectories of the pallium in the different classes of vertebrates. In mammals, the pallium is dominated by the **neocortex** that covers most of the forebrain. There are meanwhile doubts on the evolutionary novelty of the 'neo'cortex [8]. But we will use this term for lack of a better one. The six-layered appearance of the neocortex is the hallmark of a mammalian brain. A highly maintained **laminar** and columnar architecture is apparent across all mammalian species. There is no comparable structure in the bird telencephalon. As visible in Figure 1, the avian pallium is characterized by several large nuclear aggregations without any laminar structure apparent. In the late 19th to early 20th century, this

Trends

Cognition in corvids and parrots reaches the same level of excellence and diversity as in apes. Among others, bird cognition encompasses abilities such as delay of gratification, mental time travel, reasoning, metacognition, mirror self-recognition, theory of mind, and third-party intervention.

The cerebrum of birds and mammals is homologous but very differently organized.

Birds lack a neocortex but have instead several large pallial aggregations without apparent laminar structure. However, according to some scientists, these aggregations might correspond to cortical layers.

Independent from each other, birds and mammals have developed similar brain organizations that could constitute the neural basis of their cognitive skills. Birds have a functional analog to the prefrontal cortex that generates executive functions. Their telencephalic connectome is highly similar to that of diverse mammalian species and they show a 'hidden' lamination that resembles cortical canonical circuits in parts of their sensory pallial territories.

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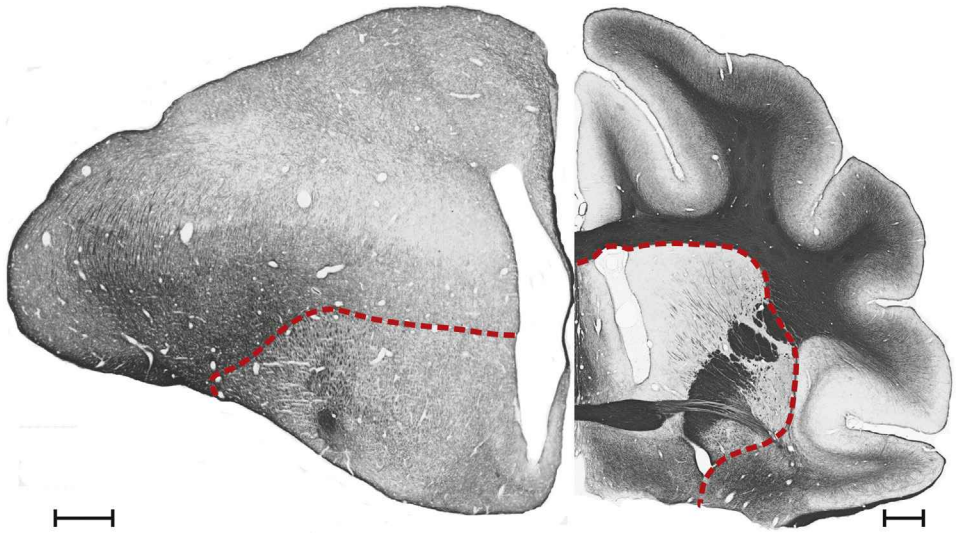

Trends in Cognitive Sciences

Figure 1. Anatomical Depiction of a Bird and a Mammal Brain. The frontal section shows the forebrain of a pigeon (left) and of a ferret (right), brought to the same height. In both cases a Gallyas staining of myelinated axons was used. The red dotted line depicts the border between the pallium (above) and the subpallium (below). In the ferret, the most ventral part of the section also encompasses parts of the diencephalon. Note the typical cortical morphology of the pallium in the ferret brain. Nothing comparable is discernible in the pigeon. Scale bars = 1 mm. Ferret brain section: courtesy of Claudia Distler.

glaring difference sparked the idea of a stair-step evolutionary development of the vertebrate brain: it was assumed that mammals were the last class to evolve, and with their emergence the six-layered cerebral cortex became a *de novo* brain area (ergo, 'neo-cortex'). Earlier neural structures were thereby all retained. It was assumed that higher cognitive abilities must depend on cortical processing, and because birds do not have a cortex, birds should be incapable of higher cognition [4,9].

We now know that this is wrong [4,10,11]. But how solid is the recent evidence for advanced cognitive abilities in birds? Could it be that cognition in birds is highly specialized in few domains such that we overestimate their mental prowess when testing them in their narrow areas of cognitive excellence? Moreover, if birds do indeed have broad and excellent cognitive capabilities, how do they generate these mental skills without cortex?

Bird Cognition Is Not Inferior to Mammalian Cognition

Traditionally, birds have been used as model systems for studying learning and memory, optimal foraging decisions, and song [12]. More recently, 'higher' cognitive abilities that are considered to underlie physical and social problem-solving abilities such as aspects of impulsive control, inferential reasoning, planning ahead, perspective taking, and role understanding were included. It has been argued that these skills, often subsumed under the term 'complex' cognition, form a cognitive tool-kit comparable to that of mammals [13]. Although also reptilian cognition should not be underestimated, nothing at the level and scope of bird cognition has been reported for this animal group so far [14]. Thus, it is likely that mammalian and avian complex cognition represent convergent developments.

Critiques have pointed out that most studies on bird cognition have tested these animals in narrowly defined domains with few paradigms [15,16]. Food-hoarding is a good example. Most **corvids** store food for later consumption and this behavior is very useful for asking cognitive questions under laboratory conditions, including sophisticated topics such as mental time travel,

Glossary

Cerebrum: those parts of the brain that contain the pallial and subpallial territories. In mammals this incorporates the cortex, the hippocampus, the claustrum, the amygdala, the basal ganglia, and the olfactory bulb.
Convergent evolution (or homoplasy): refers to the independent evolution of similar characters in species of different lineages due to comparable selection pressures. Convergent evolution results in analogous characters with similar appearances or functions, although these were not present in the last common ancestor of the two lineages.
Corvids: birds of the crow family, a relatively closely related group of oscine passerine birds that includes crows, ravens, rooks, magpies, choughs, jays, and nutcrackers, and is found worldwide. Most species are characterized by a high brain-to-body mass ratio, ecological flexibility, and a complex social life, featuring long-term partnerships and dynamic groups structured by social relationships.
Hodology: the study of pathways between brain areas. The term derives from the Greek word hodos which means 'road'.
Homology: describes cases in which a shared trait of two species can be traced back to a common ancestor without interruption.
Laminar: most of the neocortex has six cellular layers or laminae. Each layer is constituted by distinctive cell populations with unique connectivity patterns. At first glance, neocortical lamination looks uniform (and is therefore sometimes called 'isocortical'). But a closer look reveals multitudes of subtle differences between neocortical areas.
Neocortex: the usually six-layered sheet of gray matter that constitutes the outermost part of the cerebrum of the mammalian brain.
Pallium: refers to the upper surface of the cerebrum and incorporates cortex or cortex–homolog structures, hippocampus, pallial amygdala, claustrum, and olfactory bulb.
Parallel evolution: describes the evolution of a similar character starting from a comparable ancestral condition. Thus, during parallel evolution two taxa start by sharing a similar ancestral character and then

perspective taking, and attribution [17]. For instance, Western scrub jays were found to remember the what, where, and when details of a caching episode [18] and to plan ahead for positioning the caches on the next day [19]. These birds were also shown to protect their food caches from being pilfered by avoiding the view of conspecifics and to selectively re-cache items after being observed [20]. Likewise, ravens were reported to tactically deceive others in competition for food [21] and instantly discriminate between competitors that are knowledgeable or ignorant about the location of particular caches [22]. These findings on food-caching scrub jays and ravens may be interpreted as an indication for corvids having mental capacities that are on par with those of great apes [3]. By contrast, the corvid results may be seen as a special adaptation to the very context of food caching. The birds' mental capacities are thus thought to be highly domain-specific and not directly comparable with the flexibly used skills of primates (review in [23]). Recent studies indicate that such an interpretation is too restrictive: corvids have been found to show various primate-typical behaviors such as alliance formation, third-party intervention, postconflict reconciliation, and consolation (review in [24]), and they excel in a variety of experimental tasks and contexts other than caching (Figure 2A, Table 1).

Another illustrative case is the work on **parrots**. When it was shown that one African gray parrot called 'Alex' could not only learn to label items but also used his communication skills to solve various cognitive tasks, the findings caused suspicion [25]. Applying a same/different concept, for instance, was for a long time considered to be far beyond the capacities of birds [26]. One of the criticisms concerned the test procedure with Alex due to its possibility of cueing. In the meantime, aspects of reasoning abilities have been shown in different species of parrots [27,28] and corvids [29–31], each with representative sample sizes and by using a variety of methods, including touchscreen computers that prevent any form of cueing by experimenters (Figure 2B, Table 1).

Table 1 summarizes a selection of cognitive skills identified in the two most-studied bird groups for cognitive traits, corvids and parrots. When comparing the findings with those of primates as the most-studied mammalian group for cognitive traits, we see striking similarities of certain skills irrespective of the phylogenetic distance between groups, indicating high levels of cognitive convergence. For instance, whereas most birds and mammals are capable of solving visual displacement problems, only corvids, parrots, and apes tend to also solve invisible displacement problems. With regard to impulsive control, species of these groups produce better results when optimizing quality rather than quantity. Note that the skills listed in Table 1 are not exclusive to corvids, parrots, and primates as may be found in other species. Episodic-like memory, for instance, has been shown also in chickens, pigeons, and rodents (review in [3]); newborn chicks already show an intuitive sense of numerical magnitude, indicating that their brain is prewired in how it relates numbers to space [32]. These cases suggest that the possibility of mammals and birds may not only converge towards similar skills but may also inherit a set of cognitive skills from a common ancestor [33].

Taken together, there is little evidence for bird cognition being limited to a few specialized domains. Instead of overestimating their mental powers, we appear to underestimate the similarities between avian and mammalian skills. Recent studies on song birds reveal that species such as great tits are skilled problem solvers in the wild and readily establish experimentally induced foraging traditions [34]. However, similarity at the behavioral level does not need to reflect the same cognitive mechanism [23]. This may be particularly true for complex cognition: abilities such as tool use, cooperation, or deception are likely composed of different cognitive building blocks. For instance, cooperation may include aspects of learning, impulsive control, meta-memory, empathy, and theory of mind, but the degree to which each of the abilities has advanced may differ between species and taxonomic groups [35].

subsequently develop independent from each other a further similar character from this ancestral condition.

Parrots: are birds of the order Pscittaciformes that include 'true' parrots, cockatoos, and New Zealand parrots and are found in most tropical and subtropical regions. Similar to corvids, they are characterized by a high brain-to-body mass ratio and a complex social life, featuring long-term partnerships and dynamic groups structured by social relationships.

Subpallium: refers to the non-pallial part of the cerebrum and contains striatum, pallidum, striatal amygdala, and diagonal band of Broca.

Thalamorecipient layer: the neocortical layer IV receives sensory information from primary thalamic relay nuclei and is therefore called the thalamorecipient lamina. Other thalamic nuclei that do not participate in rapid unimodal sensory transfer project to neocortical laminae I–II and V–VI. Thus, lamina IV can be called thalamorecipient only with regard to fast unimodal thalamic sensory input.

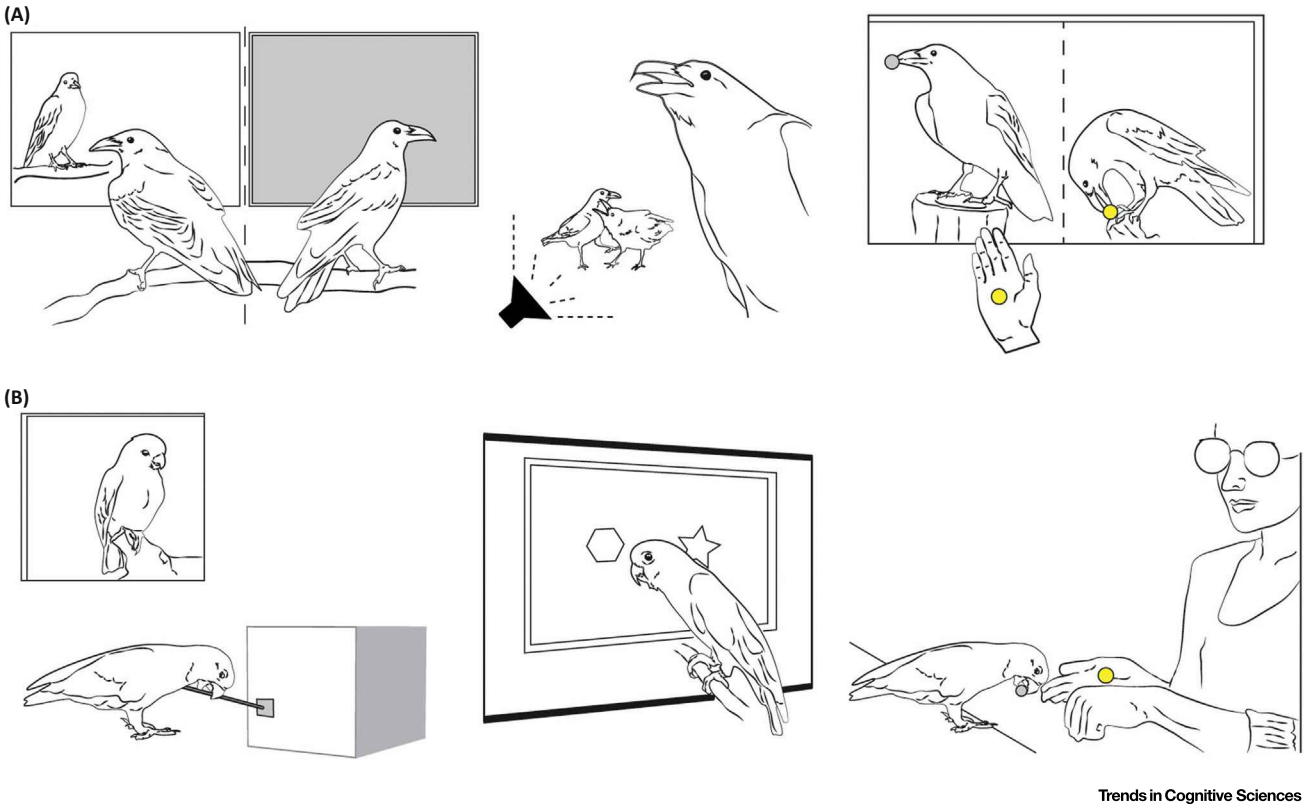

Figure 2. Examples of Breadth of Cognitive Skills Found in Corvids and Parrots. (A) Ravens differentiate knowers from guessers in a caching paradigm [22], they show third-party understanding in playback studies [67] and they respond to inequity in working effort by refusing to accept a preferred reward (yellow dot) in exchange for an initial reward if the neighbor has received the preferred reward for free [68]. (B) Goffin cockatoos learn tool use from a skilled demonstrator [69], they infer by exclusion correct solutions in a discrimination task on touchscreen computers [28] and they wait minutes for a better reward in an exchange task [70].

Mammalian and Avian Forebrains are Homologous

The broad and excellent cognitive abilities of birds are incompatible with the view that the avian brain lacks a functional equivalent to neocortex. But where is this avian equivalent? Classic neuroanatomical studies had proposed that birds and mammals have mainly subpallial structures in common. Of these, the avian striatum appeared spectacularly enlarged and to encompass most of the cerebrum (Figure 3) [36]. As such, bird brains were understood to be dominated by striatum, while having in addition only a small medial (hippocampus) and lateral (amygdala) pallium. A dorsal pallium (neocortex) was assumed to be absent in birds [4].

It was Harvey Karten's work beginning in the 1960s that sparked new insights [37]. He showed that the sensory and motor connectivity patterns of the avian cerebrum were similar to those of mammals. Based on these findings, he proposed that it was cortical neuron types, not brain areas, which were homologous and thus coinherited from the last common ancestor. But if avian and mammalian cortex neurons are homologous, then birds should consequently have a homolog to cortex, although with rather a different internal arrangement. Thus, an explanation was proposed that later was coined 'nuclear-to-layer' hypothesis [4]. This hypothesis suggests that the last common ancestor of birds and mammals possessed a nuclear dorsal pallium that already had all the connectivities that characterize modern avian and mammalian forebrains. When this ancestral entity was subsequently transformed into a mammalian layered neocortex, it maintained the connectivity of the ancestral nuclear network [38]. According to this line of

Table 1. Selection of Cognitive Operations Studied in Corvids, Parrots, and Primates

Realm/Skill	Birds Tested and Outcome	Comparison with Primates
Object permanence: memory for items that are temporary outside view	Most tested corvids (overview in [71–73]) and parrots [74,75] reach Piagetian Stage 6, that is, they track invisible displacements African gray parrots and Goffin cockatoos [74] solve transposition tasks, the latter also translocation and rotation tasks; carrion crows fail in transpositions but pass some rotation tasks [71]	Within primates, apes come up to Piagetian Stage 6 (e.g., [76]) and manage transpositions and rotation tasks [77]
Delay of gratification: ability to forgo an immediate reward to gain a better quality or quantity; control of impulsiveness	Time to wait depends on task, context, and value of expected reward: *Accumulation task:* African gray parrots wait only a few seconds [78], but carrion crows and ravens wait up to 5 min when tested for improving reward quality [79] *Exchange task:* crows and ravens wait up to 3–6 min for improving reward quality but hardly for improving reward quantity (maximum 20 s; [79]); Goffin cockatoos wait up to 1.5 min for improving reward quality and 20 s for improving reward quantity [70]; an African gray parrot responds to the label 'wait' up to 15 min for improving reward quality [80]	Time to wait depends on same factors as in birds: *Delay choice task:* most monkeys wait up to 30 s, some monkeys and apes 1–2 min (review in [81]; but see [82]) *Accumulation task:* macaques, capuchins, and apes wait up to 2–3 min [83]; chimpanzees wait up to 18 min when they can divert their attention to toys [84] *Exchange task:* capuchins wait up to 40 s for improving reward quality but usually only up to 20 s for improving reward quantity [85]; macaques and chimpanzees wait up to 3–4 min for improving quantity [83,86]
Mental time travel: episodic-like memory for past events and episodic-like planning of future events	*Memory:* Western scrub jays and magpies remember the what, where, and when of caching episodes (i.e., what food they hid in which locations at which points of time; review in [3]); scrub jays flexibly update their knowledge about the rate of perishability of food after the time of memory encoding [87] *Prospection:* Western scrub jays are capable of planning where to cache what food for the next morning [19], without reference to their current motivational state [88]; Eurasian jays overcome their current desire in anticipation of future events [88]	*Memory:* in caching–analog paradigms, apes and Rhesus monkeys (as well as rodents) remember the what, where, and when of past events (review in [89]) *Prospection:* apes select and save tools for future need [90], but chimpanzees fail to plan ahead in exchange paradigm [91]; squirrel monkeys but not Rhesus macaques alter behavior in anticipation of future thirst [92]
Reasoning: inferring solution on the basis of partial information (inference by exclusion, transitive inference) or by drawing on analogy (relational matching, same/different)	*Exclusion:* most corvids tested in object choice tasks show inference by exclusion in visual but not in auditory domain (overview in [93]; but see [94]); African gray parrots succeed in visual and in auditory domain [95] and flexibly use exclusion in Premack's 'apple–banana' task [27]; Goffin cockatoos tested in discrimination task on touchscreen computer use inference by exclusion, among different strategies [28] *Transitivity:* several corvids [96,97] are capable of inferring relations between stimuli based on shared relations with other stimuli *Analogy:* African gray parrots [25], orange-winged amazons [98], and a carrion crow [31] are capable of applying same/different concept using English labels (parrot) and relational matching to sample task in visual domain (amazons, crow), respectively	*Exclusion:* apes and most monkeys show inference by exclusion in object choice tasks but do so more readily in visual than in auditory domain [99,100]; some New World monkeys also have problems with inferring location of food in visual domain [101] *Transitivity:* chimpanzees, Rhesus and squirrel monkeys (overview in [102]) show transitive inference in overlapping stimuli discriminations *Analogy:* mixed results with relational matching to sample in visual domain in apes (overview in [103]); some capuchins [104] and baboons [105] succeed in this task, but only after intensive training; all apes succeed in spatial relational similarity paradigm when presented with logic–causal relations (tubes connecting cups [106]); bonobos and chimpanzees also master some reasoning by non-causal

Table 1. (continued)

Realm/Skill	Birds Tested and Outcome	Comparison with Primates
		relational similarity (lines connecting cups)
Meta-cognition: knowledge about own knowledge (monitor and control of own cognitive processes)	Large-billed crows succeed in retrospective but fail in prospective meta-memory task (how they did on a test as compared with how they will do on a test) using a delayed matching to sample paradigm with escape option [107]	Rhesus and capuchin monkeys succeed in prospective meta-memory tasks; the former also succeed in retrospective meta-memory task (overview in [108]); evaluating various alternative hypotheses about the underlying mechanism, Rhesus monkeys were shown to reliably use memory strength as discriminative cue for information seeking [109]; in support of this, a subject chooses uncertainty response when its memory is magnetically erased [110] Apes [111], Rhesus monkeys, but not capuchin monkeys (overview in [112]) seek information when they are ignorant about a food location before they make a choice
Mirror self-recognition: awareness of own body and (possibly) individual identity	Magpies [113] and jackdaws [114] show self-contingent behaviors in front of mirrors; two out of five magpies pass mark test New Caledonian crows [115], gray parrots [116], and keas [117] engage in social behaviors and mirror-directed exploratory behavior, but lack self-directed behavior in front of mirror; the former two species also use a mirror instrumentally to localize food	Most apes show self-contingent behavior and pass mark tests (overview in [118]); lesser apes fail mark test but may show mirror-guided self-inspection [119] Capuchin monkeys and macaques show social response but not self-contingent behavior and fail mark test (overview in [120]); Rhesus monkeys show mirror-guided self-directed behavior towards implant and pass mark test after intensive visual–somatosensory training [121]
Theory of mind: inferring others' mental states (perception, intention, knowledge, belief)	Ravens and rooks follow gaze into distant space and geometrically behind optical barriers (review in [29]); jackdaws are sensitive to human attention state in object choice and food retrieval paradigms [122] Ravens [22] and Western scrub jays [20] differentiate between conspecifics that are knowledgeable and ignorant about food caches; both species seem capable of experience projection [123,124]; Eurasian jays attribute desire for particular food types to their partner [125]	Several primates follow gaze into distant space, apes and some monkeys also geometrically behind barriers (review in [126]) Chimpanzees and Rhesus monkeys differentiate knowers from guessers in food-retrieval paradigms, but not in helping paradigm (review in [127]); capuchin monkeys may learn to do so in helping paradigm [128]; chimpanzees seem capable of attributing goals, intentions, perception, and knowledge to others, but not beliefs (review in [127]); Rhesus monkeys also fail in belief attribution task [129]
Vocal learning: sound production learning in the vocal domain	Many corvids and parrots show an open-ended learning capacity for conspecific and heterospecific sounds [130]; learned vocalizations tend to reflect particular social relationships, resulting in shared sounds used in communication within pairs/groups as well as between pairs/groups [131]; when appropriately trained, gray parrots use learned calls not only to attract others' attention but come to understand the communicative content [25]	For most non-human primates, vocal production learning plays a relatively minor role in communication; in contrast, primates' comprehension of vocalizations is highly developed and flexible [132]

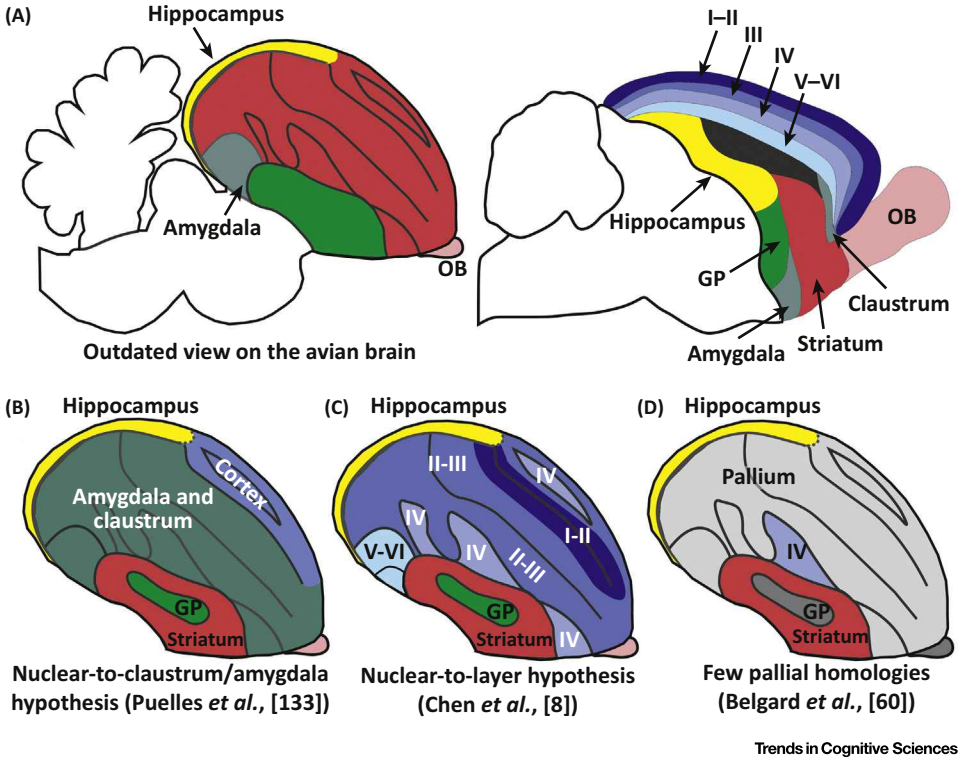

Figure 3. Different Hypotheses on Homologies between Avian and Mammalian Telencephalia. (A) According to the classic and now outdated view, most of the bird telencephalon was supposedly homologous to the mammalian striatum. Only small pallial territories were seen as comparable to amygdala, hippocampus, and olfactory bulb. See the color-coded labels in the rat brain (right side) for comparisons. (B) The nuclear-to-claustrum/amygdala hypothesis assumes that the majority of the avian pallium is homologous as a field to the amygdala and claustrum. Only a small dorsal aspect is homologous to the cortex [133,134]. (C) The latest version of the nuclear-to-layer hypothesis posits that individual layers plus the amygdala and claustrum are homologous as fields to certain bird pallial nuclei [8,53]. (D) A recent transcriptomic analysis revealed only a few pallial homologies between bird and mammalian pallia [60]. Dark gray areas were not analyzed. Abbreviations: GP, globus pallidus; OB, olfactory bulb; I–VI, cortical layers.

reasoning, individual mammalian neocortical layers should be homologous to individual bird forebrain nuclei.

An important step towards answering this question was the Duke Avian Nomenclature Forum of 2002. Based on an overwhelming body of data from genetics, neurochemistry, anatomy, and physiology, a consortium of neuroscientists at the conference concluded that most of the large dorsal territory of the avian cerebrum is pallial. This pallial territory was seen as homologous to regions of the mammalian brain that includes neocortex, hippocampus, claustrum, and pallial amygdala [35]. The smaller ventral part of the avian cerebrum was identified as subpallial, and highly comparable with its mammalian counterpart in all developmental and anatomical details [6]. Thus, bird brains are not dominated by striatum. But how much of the avian pallium is equivalent or even homologous to neocortex?

Do Birds Have an Equivalent to Cortex?

An astonishing number of similarities between avian pallium and mammalian neocortex have now been discovered. Some of them are discussed in the following sections. But are these similarities due to **homology** or **convergent evolution**? Surprisingly, this question has become increasingly difficult to answer (Box 1). As such, it is likely that each of the avian parallels to mammalian neocortex constitute a mixture of basic homologous elements and convergent patterns.

Box 1. Hunt for an Avian Homolog to Cortex

The fact that the avian cerebrum is mostly pallial does not imply that it is has to be all cortical since not all pallial component give rise to cortex. Indeed, it was proposed that most of the avian pallium is homologous to amygdala [135]. This idea was later extended to the nuclear-to-claustrum/amygdala hypothesis [4] that posits that only a small part of the avian cerebrum is cortical, while the rest is homologous to amygdala, endopiriform nucleus, and/or claustrum [55,133] (Figure 3). One weakness of this hypothesis is the small number of genetic expression patterns yet analyzed of which some even contradicts this claim [54,60]. The lack of fate-mapping data on relevant taxa [136] is another weak point. In addition, amygdala-projecting thalamic neurons have different identities to those that project to cortex-equivalent areas [136].

Dugas-Ford *et al.* [59] discovered that gene expressions of mouse cortical neurons from granular (layer IV) and infragranular (layer V) layers correspond to those of avian pallial nuclei that receive thalamic sensory input ('granular') or have descending projections ('infragranular'). This perfectly fits to the nuclear-to-layer hypothesis. These results were recently extended by research that suggests that most of the avian pallial nuclei are homologous to cortical layers as well to amygdala and claustrum [8,53]. Given that pallial amygdala and claustrum are possible derivatives of cortical layers, most of the avian pallium would have a 'hidden' laminated architecture that corresponds in several aspects to cortical layers. The main weaknesses of this hypothesis are: firstly, the dataset could be explained by convergent developmental molecular programs; secondly, the as-of-yet undiscovered major developmental cellular migrations that it postulates [56].

The most sobering news about the avian cortex came from a study in which a transcriptomic analysis of over 5000 genes in the cerebrum of chickens and mice was conducted [60]. The only significant similarities discovered were between striatal, hippocampal, and layer IV/nidopallial samples. In light of this, transcriptome-based homologies between avian and mammalian pallia appear unexpectedly weak. However, this is different for a more recent study that could identify broader homologous brain regions also with >7000 genes [54].

Why is it so difficult to find generally accepted homologies between neural fields of avian and mammalian pallia? It could be that homology arguments that rest only on developmental genetics are insufficient. Brains are characterized by complex, dynamic reciprocities within subsystems that change over developmental time and thereby constantly modify genetic expression patterns. Meaningful analyses therefore require that relevant genes, comparable developmental time points, and correct neural subsystems are identified and used for comparisons. This is tremendously difficult. Thus, further meaningful criteria for homologies should be incorporated similar to, for example, those from connectivity analyses [137].

The Avian 'Prefrontal Cortex'

The mammalian prefrontal cortex (PFC) is associated with the generation of executive functions, that is, a cluster of diverse cognition functions that reach from working memory to planning. The functional equivalent of the PFC is the avian nidopallium caudolaterale (NCL), an associative area in the caudalmost part of the bird forebrain [10,11,39]. Similar to the PFC, also the NCL is a center of multimodal integration [40] and connects the higher-order sensory input to limbic and motor structures [41]. Thus, identical to the PFC, the avian NCL is a convergence zone between the ascending sensory and the descending motor systems [42]. Also similar to the PFC, the NCL is densely innervated by dopaminergic fibers. These fibers release dopamine, in particular during the delay period of working memory tasks in volume transmission mode [43,44]. They also modulate the mental maintenance component of working memory via D1 receptors [45]. As neurons in the PFC of monkeys do, the NCL neurons also temporarily maintain information by sustained delay activity in working memory tasks [46]. NCL lesions not only interfere with working memory but also with all further cognitive tasks that are known to depend on the mammalian PFC [47]. NCL neurons encode cognitive operations such as decision making [48], rule tracking [49], encoding of subjective values [50], and the association of outcomes to actions [51]. Some differences in thalamo-pallial connectivity [41] and neuronal coding properties [52] exist between the PFC and NCL. But for the absolute majority of findings in neurochemistry, connections, and functions, the NCL and PFC are highly similar. However, given that their locations are on opposing ends of the cerebrum, and that at least some genetic expression patterns might contradict a homology as a field, the NCL and PFC possibly represent a spectacular case of evolutionary convergence [8,53–56]. Thus, non-homologous fields within a homologous pallium converged over the course of 300 million years into mammalian and avian prefrontal areas that serve highly similar functions. In doing so, both areas gained the ability to generate the same cognitive functions using similar cellular properties.

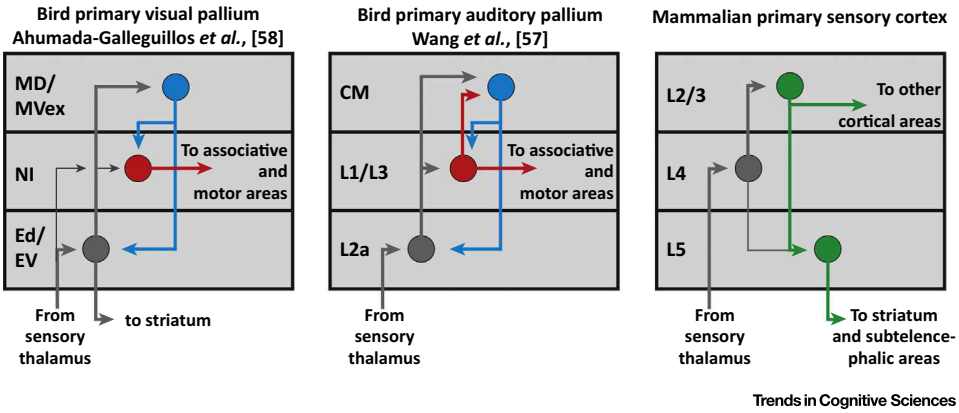

Figure 4. Highly Schematized Overview of the Connectivity Patterns in the 'Layered' Primary Visual and Auditory Bird Pallium [57,58] and the Mammalian Primary Sensory Cortex. For the bird data some layers were collapsed into one. The cortex schema represents only the main connections [138]. Thin lines represent weaker connections. The left two panels represent results from *in vitro* tracing experiments. The horizontal arrow that leads to associative and motor areas depicts connections that are known from the literature [62], but of which we do not know if they originate from the depicted cell types. Abbreviations: CM, mesopallium caudale; Ed, entopallium dorsale; EV, entopallium ventrale; L1/L2a/L3, Field L1, L2a, L3; MD, mesopallium dorsale; MVex, mesopallium ventrale, external layer; NI, nidopallium intermedium.

Layers in a Non-Laminated Forebrain

The absence of a layered pallium was one of the reasons why neuroanatomists concluded a century ago that bird forebrains could not harbor a cortex [36]. In the years since, evidence has accumulated in support of an 'invisibly layered' bird pallium. Some genetic expression patterns already suggested a three-layered composition of avian cell nuclei (Box 1). But the most spectacular evidence for a layered bird pallium comes from *in vitro* tracing studies of primary auditory and visual forebrain areas [57,58]. These and further studies [53] demonstrate the existence of three main layer-like entities that can be further subdivided into several sublayers. Axonal columns are positioned orthogonally to these layers and reciprocally connect the sensory recipient territories with an overlaying nidopallial and mesopallial column (Figure 4). The entry point to this system is the **thalamorecipient layer**, which shares genetic expression profiles and morphological features with the cortical granular layer IV [8,59,60]. From there, columnar point-to-point projections lead to two overlying layers that reciprocate with the thalamorecipient lamina and also project horizontally to associative and motor structures. To some extent, this avian circuitry resembles the cortical canonical circuit that is defined by repetitive topographic interlaminar circuits [61]. In the neocortex, these canonical circuits provide the computational properties that characterize cortical dynamics. Mammalian and avian pallial layers are similar, but not identical (Figure 3). If their similarity is due to convergence, a laminated forebrain based on repetitive columnar interlaminar circuits could represent a computational necessity for flexible sensorimotor integration. At this point it is important to note that cascades of interconnected pallial territories do not necessarily imply a layer-like organization but could simply reflect sequences of sensory integration along neighboring areas. But the orthogonal arrangement of the cellular columns as well as the cortical lamina-specific genetic expression patterns makes the hypothesis of the 'invisibly layered' bird pallium conceivable.

The Avian Connectome

It is a futile enterprise to try to understand the cognitive functions of a brain without analyzing information flow within its neural network. Connectomes are comprehensive maps of the neural connections of a brain and help to reconstruct the organization of this flow. The reconstruction of the connectome of the pigeon cerebrum demonstrated that the pigeon connectome is

organized similarly to that of primates [62]. Both are modular, small-world networks with a connective core of hub nodes that include prefrontal-like and hippocampal structures. Most interestingly, similar to the 'prefrontal module' the top-level modules were highly comparable to those of the human structural connectome [63]. This finding is even more exciting when we realize that the NCL of birds and the PFC of primates are functionally analogs rather than homologs. Thus, these two structures do not derive from common ancestry but represent the outcomes of two completely independent and convergent evolutionary trajectories. The fact that these two structures constitute such highly similar topological centralities of their respective connectomes suggests the following: if two neural structures of different animals share the same function, they may also share the same connectivity blueprint.

Concluding Remarks

We started with a simple question: when two groups of animals converge during evolution with regard to their cognitive skills, do their brains also converge? The animals that we are comparing are birds and mammals; members of two vertebrate classes that have evolved in parallel for approximately 300 million years. By reviewing the literature of several different realms of cognitive operation, we were able to show that the cognitive skills of parrots and corvids are truly on par with primates. The implication of this finding cannot be overestimated. It implies that in diverse areas of cognition, birds with small, non-cortical brains of 5–20 g can show identical capabilities to apes with large cortices and brain weights of between 275 and 500 g. Two bold implications can be deduced from these findings: first, complex cognition does not require a layered cortex. Second, absolute brain weight is no relevant variable when judging cognitive prowess between differently organized brains.

The question of to what degree avian and mammalian brains converged during the evolution of similar cognitive abilities is difficult to answer as it forces us to first differentiate between neural characters that are similar due to homology (common ancestor) or **homoplasy** (functional convergence). Thereby, homologous characters can have very different appearances. For example, the pallium of birds and mammals is homologous but very different in its overall architecture [4]. Some neurogenetic studies suggest that even single cortical laminae are homologous to some bird cerebrum nuclei (Box 1). However, the genetic literature on homology is currently far from settled and full of discrepant findings. It is therefore conceivable that some of the discovered similarities represent a deep homology of brain and cognition that is based on a small set of homologous neuroregulatory elements such as neurogenetic, cellular, and hodological (**hodology**) characters [64]. From this shared point of departure, it is conceivable that birds and mammals independently went through a parallel evolution that was shaped by two forces: first, similar cognitive selection pressures that resulted in comparable neural functions; second, evolutionary constrains due to homologous neuroregulatory elements that amplified the similarities in the details of these neural functions (Box 1).

The result is two groups of animals with cerebra that look very different at first glance (Figure 1), but in actuality display a large number of correspondences upon closer examination. Three examples give evidence for these 'hidden' similarities: first, despite their different overall appearances, avian and mammalian cerebra possess connectomes that are comparable small worlds with equivalent hubs and modules [62]. Second, birds and mammals independently evolved highly similar prefrontal entities that generate comparable executive functions [47]. As with the connectome, it is likely that these similarities are generated by brain structures that are not homologous as fields. Third, layered, columnar wiring arrangements of neurons are visible in the primary sensory fields of the bird pallium and resemble canonical cortical circuits [57,58].

These findings offer a sobering lesson: there seem to be only limited degrees of freedom in generating neural structures that support complex cognition. As a result, birds and mammals

Outstanding Questions

Which characters of avian and mammalian pallia are truly homologous and which result from convergent or parallel evolution? It is conceivable that only few basic elements represent truly homologous traits. However, these elements could constrain degrees of freedom of subsequent evolution such that high levels of comparable neural and cognitive features emerge.

Do birds and mammals utilize highly similar small neuronal circuits to compute building blocks of cognitive operations? Such a comparison at the level of microcognition could reveal that the mechanistic emergence of computational dynamics in cognitive operations requires a certain design – such as that identical in these two taxa that have developed in parallel since 300 million years.

convergently evolved similar neural mechanisms. These similarities are disguised by the dissimilar general appearance of the avian and mammalian cerebrum. Currently, the resemblances discovered are related to the anatomical and functional organization of brain areas, or to overall connectivity patterns. The next frontier will be the area of microcognition, that is, the ability of very small circuits of neurons to compute building blocks of cognitive operations. Indeed, highly similar cellular properties have already been discovered in both birds and mammals for working memory [46,65], encoding of subjective value [50], as well as rule [49] and numerosity representation [66]. Future studies will show if birds and mammals are comparable in many more realms of microcognition and if these similarities are due to evolutionary convergence (see Outstanding Questions).

Acknowledgments

This work is supported by grants from the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) (SFB 874, FOR1581, and Gu 227/16-1) and the Fonds zur Förderung der wissenschaftlichen Forschung (FWF, Austrian Science Fund) (Y366-B17 and W1234).

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