

Opinion

Why birds are smart

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Many cognitive neuroscientists believe that both a large brain and an isocortex are crucial for complex cognition. Yet corvids and parrots possess non-cortical brains of just 1–25 g, and these birds exhibit cognitive abilities comparable with those of great apes such as chimpanzees, which have brains of about 400 g. This opinion explores how this cognitive equivalence is possible. We propose four features that may be required for complex cognition: a large number of associative pallial neurons, a prefrontal cortex (PFC)-like area, a dense dopaminergic innervation of association areas, and dynamic neurophysiological fundaments for working memory. These four neural features have convergently evolved and may therefore represent ‘hard to replace’ mechanisms enabling complex cognition.

Tales of cortical superiority

Many comparative cognitive neuroscientists subscribe to the idea that complex cognitive abilities like those found in primates require at least two key neural features. The first is a large brain. A wealth of data show that, within taxa, large-brained animals display more cognitive skills than those with smaller brains [1]. This is visible in primates [2], Cetacea [3], and birds [4,5], but has also been shown in insects [6]. Although details about relative or absolute brain size and similar variables are debated [5], the idea that larger brains can in principle provide more neurons and thus more computing power is generally accepted [5,7]. The second common prerequisite for complex cognition is the mammalian cerebral cortex (Box 1). The isocortical component of the cerebral cortex is considered particularly important given its unique topographical organization. In the **isocortex** (see Glossary), vertical input and output systems closely interact with long-distance horizontal fibers such that neurons across cortical areas can be associated to represent and memorize multiple objects’ features through Hebbian learning [8]. This design allows the various attributes of a currently perceived object to be linked with each other to form a single percept that can be associated with an internal representation [9].

When compared with large mammals, birds have very small brains that comprise seemingly homogeneous nuclear clusters. These glaring anatomical differences should cast a dim prospect on avian cognition. However, across an array of cognitive tasks, several avian taxa perform similarly to great apes and appear to rely on similar cognitive algorithms. How is that possible? Our inability to answer this question shows that we are still far from a generic understanding of the link between brain structure and cognition.

This opinion attempts to partially solve this riddle by identifying features that characterize the brains of both ‘smart’ mammals and ‘smart’ birds. Such an approach might show which neural mechanisms are necessary for complex cognition. To this end, we start by first characterizing avian cognition by providing several examples. Then, we question the assumption that big brains are a useful measure of processing capacity, proceed to provide a novel view on the organization of the bird forebrain, and review the first studies on large-scale neural networks that could constitute the substrate for avian cognition. In the end, we argue that four features are currently excellent candidates for complex cognition in corvids, parrots, and great apes. These are: (i) large

Highlights

Corvids and parrots with brains of 5–20 g show cognitive properties similar to those of great apes like chimpanzees with brains of about 400 g.

An isocortex is ideal to represent and process sensory information but is not a necessity for complex cognition.

We identified four convergently evolved neural features of smart birds and mammals: many associative pallial neurons, a pallial area that overtakes functions of the mammalian prefrontal cortex, dense dopaminergic innervation of associative pallial areas, and flexible neural fundaments of working memory.

As in mammals, avian cognition emerges from transiently activated forebrain networks.

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Box 1. The many names of the cerebral cortex

The word 'cortex' refers to several laminated brain structures like the (mostly) six-layered cerebral cortex, the three-layered cerebellar cortex, or the three-layered reptilian cortex of the dorsal pallium. To be more specific, it is important to use the term 'cerebral cortex' that in humans constitutes 82% of the brain mass but contains only 19% of all neurons of the human brain [108]. In primates, about 90% of the cerebral cortex comprises the six-layered isocortex. The Ancient Greek term 'isos' means 'equal' or 'same'. All areas of the isocortex have a similar appearance, although detailed analyses uncover regional differences that are used to subdivide the isocortex into different areas. The isocortex is sometimes also called the 'neocortex' because it is an evolutionary novelty of mammals. The remaining 10% of the cerebral cortex comprises the 'allocortex', with the Ancient Greek term 'allos' meaning 'all others' or 'rest'. These others are traditionally subdivided into the 'archicortex', with the Ancient Greek term 'arche' meaning 'origin', and the 'paleocortex', from the Ancient Greek 'palaios' meaning 'old'. The archicortex contains, among others, the hippocampal formation, the entorhinal cortex, and the retrosplenial cortex. The paleocortex contains many structures, some of which have six layers while others are hardly layered at all. To list a few, the paleocortex contains the olfactory bulb and tubercle, the cortical nucleus of the amygdala, the septum, and the prepiriform cortex [109]. Previously, it was assumed that paleo-, archi-, and isocortex constitute a phylogenetic sequence that moves from old to novel. This view is no longer accepted.

quantities of associative pallial neurons; (ii) a PFC-like area; (iii) dense dopaminergic innervation of association areas; and (iv) dynamic neurophysiological properties of neuron groups that hold information in working memory. There are strong arguments that these have evolved independently in birds and mammals and thus could constitute 'hard to replace' mechanisms for brains that perform complex cognition.

Smart birds

When Irene Pepperberg started her studies on cognitive feats in African gray parrots (Figure 1A) in the late 1970s, the concept of small, non-cortical bird brains was so dominant that she sometimes received unusual reviewer comments like 'What are you smoking?' ([10], p. 72). This has changed. Especially in the past few years, studies have shown that some birds, particularly corvids and parrots, have cognitive abilities that rival those of great apes. For example, ravens plan for different kinds of future events. They will refuse an immediately available small reward and instead select a tool or a token. The next day they either use the tool or barter the token to obtain a larger reward [11]. When New Caledonian crows use tools (Figure 1B), they can mentally represent each step, thereby minding the identity and location of an apparatus and out-of-sight tools while planning sequences of behaviors [12]. In Australia, sulfur-crested cockatoos learned to open household waste bins with individual style and site-specific differences (Figure 1C). This culture rapidly spread via social learning to 44 Sydney suburbs, thereby forcing people to develop a counterculture of technical measures to prevent pilfering [13]. However, could it be that birds excel in only a few cognitive domains, while primates demonstrate sophisticated domain-general cognition? A detailed comparison of studies in eight cognitive domains concluded that corvids, parrots, and non-human primates possess similar domain-general cognitive capacities. [14]. A subsequent review of the results of 28 different cognitive domains tested on corvids, parrots, and primates came to a similar conclusion [15]. Using the Primate Cognition Test Battery to study cognitive development, it could be demonstrated that ravens perform on par with orangutans and chimps, except for spatial skills [16].

Thus, corvids, parrots, and primates reach similarly high levels of performance. However, do they rely on the same algorithms (i.e., the selection and sequence of necessary mental processes) to solve a task? Here, it seems that all avian species tested to date use mental algorithms similar to mammals, whether corvid, parrot, chicken, or pigeon. For example, pigeons not only discriminate between stimuli differing in numerosity but, like monkeys, display distance effects and are constrained by Weber's law [17]. Corvids go through cognitive developmental steps of object permanence identical to those of children and make the same errors when tested before they have reached a certain stage [18–20]. Similarly, the development of sensorimotor skills and

Glossary

Connectome: a network of connections between synapses, neurons, brain areas, or axonal fiber systems.

Convergent evolution: describes a case in which two species share a feature of similar appearance or function that has evolved independently due to similar selection pressures. It is important to note that this feature was not present in the last common ancestor of these two species.

Homology: defines a case in which a shared attribute of two species can be traced back to a common ancestor without interruption.

Hub node: a densely interconnected node that has an above average amount of connections to other nodes.

Isocortex: the six-layered sheet of gray matter with mostly similar cytoarchitecture that creates the outermost part of the cerebrum of the mammalian brain and constitutes in primates more than 90% of the cerebral cortex.

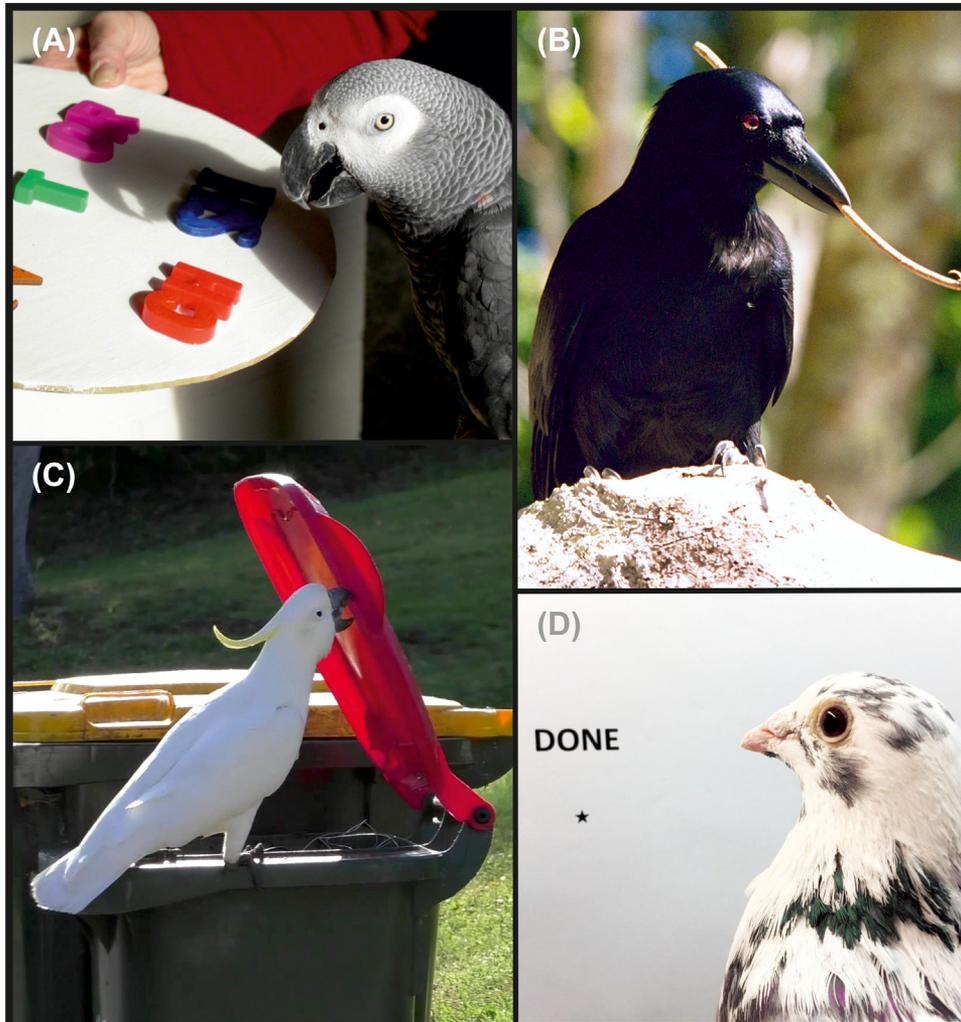
Local field potential (LFP): an electrical potential that is recorded with electrodes within the brain and that shows the transient summed cellular activity of nearby neuronal populations.

Modules: segregated network communities that promote specialized and local information processing.

Pallium: the upper part of the cerebrum that incorporates the cortex or cortex-homolog structures as well as the hippocampus, pallial amygdala, olfactory bulb, and claustrum.

Small-world network: a network that combines the ability of random networks to have short connections to some distant nodes with the high local clustering of nearby elements that is typical of regular networks. Thus, a small-world network is both globally and locally efficient.

Topological integration: a network that enables short pathways between distant network components by a densely connected core of hub nodes.



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Figure 1. Smart birds. (A) African gray parrot Alex working on a task in which he had to name objects according to their color or tell the color of a certain object [10]. Picture credit by Jenny Pegg and The Alex Foundation. (B) A New Caledonian crow holding a leaf stalk, a tool used to forage beetle grubs. Picture credit by Gavin Hunt. (C) A sulfur-crested cockatoo opening the lid of a household bin to scavenge food [13]. Picture credit by Barbara Klump. (D) A pigeon working on an orthography task in which it had to peck the word or the star for correctly or incorrectly written words, respectively [25].

motor self-regulation in corvids follows the mammalian sequence [21]. Domestic chicks [22] prefer a left-to-right orientation of ascending numerosities – the mental number line – like adult human subjects [23] and newborn babies [24]. Pigeons learn the orthography of a limited number of four-letter English words (Figure 1D) and thereby utilize the same cognitive strategies as primary-school children [25]. Keas exhibit complex statistical inference by integrating relative quantities as well as physical and social information, thereby utilizing domain-general thinking similar to that of humans and great apes [26].

These studies show that birds and mammals operate with highly similar mental processes when facing a cognitive task, but this does not imply that all mammal species or all bird species are identical with respect to the same levels of cognitive performance. Although both pigeons [27]

and chickens [28,29] can master unexpectedly complex tasks, comparisons of pigeons, corvids, and parrots tested with similar procedures reveal important differences [30]. Pigeons acquire these tasks much more slowly [17], require more exemplars to learn an abstract rule [31,32], discount more steeply in delay studies [33], and have problems in transferring their knowledge to other kinds of stimuli [34]. A detailed analysis shows that pigeons simply need more trials to learn an association and generalize less successfully to similar features [30].

Taking these findings together, birds and mammals utilize similar mental algorithms when working on cognitive tasks. Within the avian clade, corvids and parrots reach levels of cognitive performance throughout all domains that match those of great apes. These involve abilities like prospection of future encounters, reasoning about the causality of observations, imagining the perspectives of others, flexibility to transfer learned rules to other tasks, and several more. This collection can be seen as a toolkit for 'complex cognition' [14–16,35]. Since corvids, parrots, and great apes show equal abilities for complex cognition, the idea that large and isocortical brains are a prerequisite for complex cognition is challenged. In the following sections, we present scientific results that show how this riddle could be solved. More importantly, these insights could pave the way to understanding which neural features really matter for complex cognition.

Not size but content matters

The size of mammalian brains varies enormously, from 0.074 g in the lesser bamboo bat (*Tylonycteris pachypus*) to about 9 kg in sperm whales (*Physeter macrocephalus*). Bird brains overlap with those of mammals in the lower range of this distribution. The brain:body ratios of mammals and birds are also comparable [1]. The main difference is that mammalian brains can become very large when their body size increases, while bird brains remain small, even when their body size enlarges. In mammals, complex cognitive abilities were reported in animals with large brains of 400–1600 g, like dolphins, pinnipeds, and Hominidae (humans and great apes) [36,37]. This is in stark contrast to birds. Ostriches are the largest living birds and surpass human body weights but have brains of about 40 g [38]. Around 50 000 years ago, 600-kg dromornithids were the largest birds that ever roamed the Earth but had brains of only 123 g, about one-third of a chimpanzee brain [39]. Corvids and parrots have brains of just 1–25 g [4]. How could these birds become so smart with walnut-sized brains?

A landmark study showed that bird brains contain twice as many neurons per unit brain volume as primates and up to four times more than rodents [40]. Since neurons are the computational processing unit of brains, more neurons per gram brain should produce more processing capacity. Pallial neurons are especially relevant for flexible cognition since they can orchestrate brain processes along a common goal. While the percentage of cortical neurons is 19% in primates, the corresponding numbers are 62% and 78% in parrots and songbirds, respectively [38,40]. Consequently, rooks and marmosets have identical brain weights but rooks have three times more pallial neurons. Within 111 bird species, pallial neuron numbers were determined to be the best predictors of complex cognition [5]. So, do large pallial neuron numbers explain the similar cognitive capacities of corvids, parrots, and great apes? Not quite. While parrots and corvids are cognitively on par with apes [14–16], their pallial neuron numbers still differ widely (kea: 1.28 billion neurons; raven: 1.2 billion neurons; chimpanzee: 7.4 billion neurons) [40,41]. Thus, high neuron densities and a higher proportion of pallial neurons reduce the quantitative gap between birds and primates without closing it.

However, birds have one more card up their sleeves. Experience-dependent flexible cognition may be especially related to the number of associative neurons that are situated between sensory and motor systems [42]. It was demonstrated that crow species have a selectively greater

number of neurons in their associative pallial areas than chickens, pigeons, and ostriches [43]. This was especially visible when corvids were compared with ostriches. Here, crows had twice the number of associative neurons although their brains were 2.5 times and their bodies more than 200 times smaller than those of ostriches. In addition, the number of corvid associative neurons was roughly on par with prefrontal neuron numbers in chimpanzees [41,43]. This comparison is not entirely fair since mammalian associative neurons also reside beyond the PFC, but it highlights the unexpected quantity of associative neurons in crow brains of just 8–10 g. How do birds cope with the huge energy demands of so many neurons? Recently, it was discovered that the energy budget of pigeon neurons is three times lower than that of mammals [44]. So, birds can afford so many pallial neurons because they are fuel efficient. However, as we see later, avian cognition depends not only on the quantities of neurons, but also on their organization.

A new view on the avian forebrain

The last common ancestor of today's birds and mammals lived about 324 million years ago [45] and over time the two taxa developed vastly different forebrains. In the mammalian lineage, the dorsal **pallium** developed into the cerebral cortex, the majority of which is isocortical. By contrast, the homologous avian dorsal pallium became the hyperpallium, which has a nuclear appearance. Most of the remaining avian pallial nuclei are located under the lateral ventricle and are jointly called the dorsal ventricular ridge (DVR). This area has no direct counterpart in mammals and its putative homologies to various components of the mammalian pallium are debated (Box 2).

These major differences between mammals and birds are reflected by the overall pallial pattern. While the topographic arrangement of functional cortical areas in mammals can essentially be projected on an 'unfolded' 2D cortical surface, this is not possible with the 3D architecture of the avian pallium. In addition, the locations of the avian functional pallial areas differ both topographically and topologically from those of mammals [46,47]. Despite such major differences, the pigeon pallial **connectome** with its **small-world network**, its hierarchical arrangement of specialized **modules**, and its densely interconnected core of central **hub nodes** strongly resembles its mammalian counterparts [48,49]. Thus, the dynamics of information flow within

Box 2. Tracing the genetic makeup of the avian pallium

Across vertebrates, the early embryonic pallium is patterned by the conserved expression of a small number of master developmental regulatory genes [110]. According to the field **homology** model [111], this patterning subdivides the amniote pallium into four pallial domains: medial (hippocampal formation), dorsal (isocortex), lateral (claustrum, insula), and ventral (olfactory cortex, pallial amygdala) (see Figure 2B in the main text). These partitions are seen as highly conserved such that homologies between structures in, say, mammals and birds can be determined by their location in the same embryonic pallial field [112]. The alternative model is the cell type/circuit homology model, which assumes that homology can be traced back to specific neurons and neuronal circuits of an amniote ancestor and can be identified in extant species by their cellular identities [113]. As a result, structures as diverse as laminated isocortex and nuclear DVR can harbor homologous neuronal systems by virtue of cellular homologies [47,114]. It is easy to see that these models are quite often at odds with each other: While the field homology model sees, for example, the NCL as part of the avian amygdala since it is part of the ventral pallium, the cell type/circuit homology model could easily see it as cortical [47,115]. Colquitt *et al.* [116] offered a solution by studying neurons in two nuclei of the song system that are both located in the DVR. According to the field homology model, they should be part of the ventral pallium and therefore cannot be cortical. When studying the expression of genes that encode transcription factors of these songbird glutamatergic neurons, the authors discovered strong similarities to the mammalian ventral pallium. If, however, activity-related effector genes that are more closely related to cellular functions were studied, strong parallels to cortical neurons became visible. This finding shows that pallial domains do not severely restrict the developmental trajectory of cells. Thus, cortex-equivalent systems can emerge from outside the dorsal pallium [117]. An extreme example is the finding of Stacho *et al.* [56], who discovered a fully laminated avian sensory isocortex with iteratively repeated canonical circuits in the avian lateral and ventral pallium. This finding implies that the embryonic location of neurons in a certain pallial domain must neither predict the morphology nor the function of a neuronal system and thus cannot be used to determine the adult form.

macroscale circuitries are remarkably similar, although the pallial architectures differ importantly. However, many species, regardless of cognitive aptitude, have a universal set of features like specialized modules, high **topological integration**, and short pathways that are driven by the evolutionary pressure for efficient systems communication [50,51]. Thus, similarities between avian and mammalian pallial macroscale connectomes may be insufficient to explain cognitive parallels. What is needed are analyses in which the pallial connectomes of species from the same vertebrate class with high and low cognitive prowess are contrasted.

The absence of cortical architecture was always seen as a major primitive hallmark of the avian pallium. However, local tracing studies in the past years showed layer- and column-like patterns in several sensory pallial areas and started to cast doubt on the idea that the bird pallium is completely devoid of isocortex-like areas [52–55]. A combination of 3D polarized light imaging and various tracing techniques showed that the entire avian sensory pallium is characterized by layers and columns, which are embedded into an orthogonal pattern of horizontal and vertical fibers [56]. This sensory ‘isocortex’ of birds constitutes more than half of the pallial volume and encompasses all sensory areas of the hyperpallium and DVR. Detailed reconstructions of connectivity patterns within these areas revealed iteratively repeated columnar canonical circuits that are highly similar across all sensory domains and nearly identical in barn owls and pigeons, two phylogenetically distant species [57]. In addition, this avian ‘isocortex’ harbors long-range axonal systems that horizontally link columns and connect them to hippocampal, ‘prefrontal’, and (pre)motor areas (Figure 2A). Thus, mesoscale circuitries in the avian ‘isocortex’ also resemble the mammalian isocortex. It is, however, important to note that these avian ‘isocortical’ mesoscale circuitries are visible only in the sensory pallial areas and do not comprise associative and motor pallial structures, which all display a nuclear arrangement.

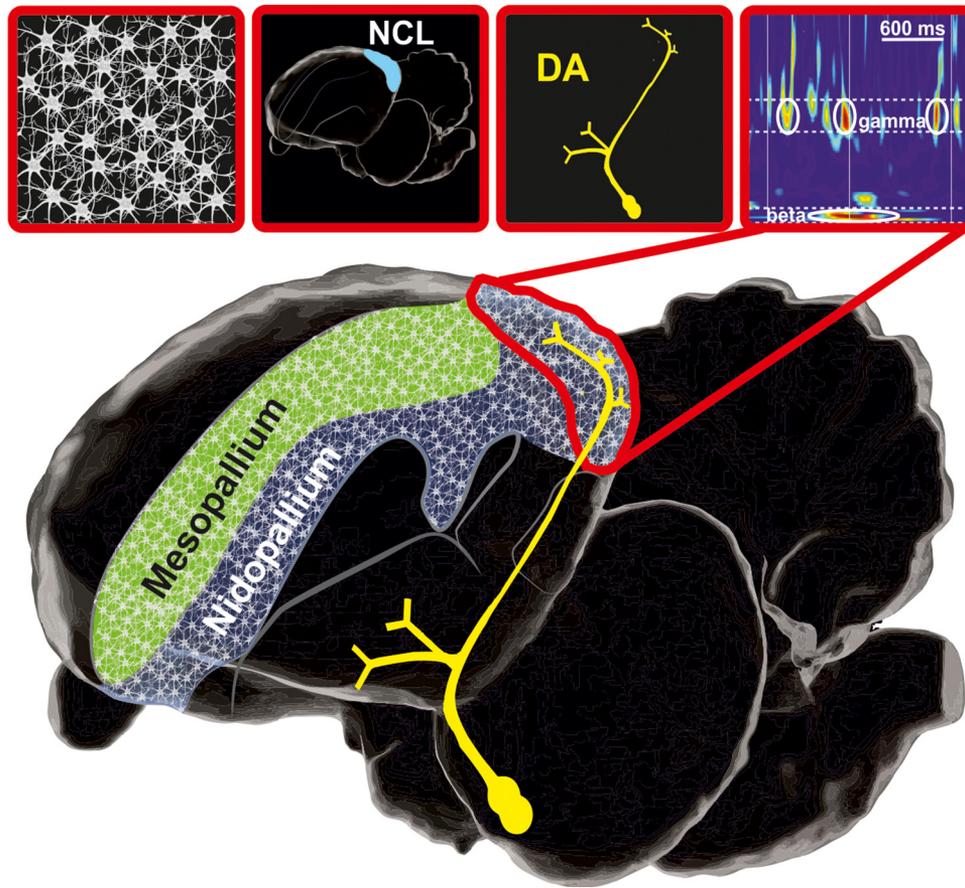
Our knowledge of microscale circuitries is far less detailed. The connections within avian ‘isocortical’ canonical circuits resemble those of mammals but display two important differences (Figure 2, C1–C3). First, while the main thalamocortical input layer IV in mammals receives only limited feedback from other cortical layers [9], the avian thalamopallial input lamina receives massive feedback [56]. This could potentially change the computational dynamics in the avian canonical circuit. Second, the avian ‘isocortex’ in the DVR has no layer that provides descending output systems like cortical layers V/VI, but funnels its descending output to the arcopallium, a nuclear structure, from where subpallial projections emerge [56]. Finally, we know little about the microcircuitries of the nuclear pallial areas of the DVR. As we see later, they play the most important role in cognition.

An avian ‘prefrontal area’

What kind of role do these nucleus-shaped pallial areas play in cognition? Surprisingly, the most posterior part of these non-isocortical pallial areas harbors the nidopallium caudolaterale (NCL), which constitutes the functional equivalent of the mammalian PFC. Both the NCL and the PFC are involved in virtually all aspects of cognition (Figure 3, Key figure), show the highest density of dopaminergic innervation in the pallium, and connect with all associative and premotor structures of the pallium [14,58]. The representation of information in the PFC can best be understood as a flexible code for relevant information [59,60]. The same holds for the NCL, where sensory information is represented in a categorical manner [61]; for instance ‘long’ versus ‘short’ [62] or numerical categories [63,64], even including the numerosity zero [65]. Another typical prefrontal function is the representation of abstract rules [66] regardless of whether they are presented as stimuli [67,68] or implicit and derived from feedback on errors [69]. Unsurprisingly for a structure at the apex between perception and sensation, prefrontal and NCL neurons can present stimuli in a retrospective (see later) or a prospective [70,71] manner depending on task demands and

Key figure

Neural features for complex cognition



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Figure 3. The top row depicts, from left to right, the proposed hard-to-replace features for complex cognition: (i) large numbers of associative pallial neurons; (ii) a prefrontal cortex-like area like the avian nidopallium caudolaterale (NCL); (iii) dense dopaminergic innervation of association areas; and (iv) dynamic neurophysiological fundamentals for working memory (figure based on [89]). A schematic representation of these features is exemplified in a pigeon brain (figure based on [58]). The meso- and non-primary sensory components of the nidopallium represent associative pallial areas of the avian brain. Abbreviation: DA, dopamine.

temporal patterns within a trial – only when averaging multiple trials does it appear continuously sustained. This pattern is found not only in single neurons but also in **local field potentials (LFPs)**; working memory-related increases in LFP power occur in short bursts and are not continuous across the memory delay [88]. A more detailed analysis of these bursts further revealed that gamma bursts are associated with bottom-up processes such as the encoding of novel stimuli into working memory; beta bursts, by contrast, are more involved in top-down processes and inhibit gamma [87]. We recently found strong evidence for these dynamic processes also in the NCL of crows, supporting the notion that, even in the absence of cortical layering, the microcircuits of avian cognition produce comparable dynamics of neural activity along with similar neurophysiological fingerprints, not just in single neurons but also in the local sum of electrical

activity – the LFP [89]. How do these dynamics unfold over the whole brain? Pigeon dreams permit us to see that.

When pigeons dream

Cognition in mammals emerges from a cortical network that is activated during tasks and connects nodes with various subfunctions that continuously share information [90,91]. Thus, cognition is not supported by highly specialized neurons in one specific brain region but by functional networks that are transiently and context-dependently activated [92]. To understand the neural fundamentals of avian cognition, we therefore must switch from studying singular areas to studying pallial networks.

To this end, an functional magnetic resonance imaging (fMRI)-based operant Go/NoGo paradigm for pigeons was run under ultrahigh magnetic field conditions with close to zero motion artifacts over hundreds of trials [93]. During a color discrimination task, they could disambiguate neural networks that were active during the different trial components, such as when seeing the Go stimulus or when inhibiting their own response during NoGo trials. This novel method can uncover avian neural networks during all critical task components. Recently, the same approach was used to identify brain activations in naturally sleeping pigeons during rapid eye movement (REM) and non-REM sleep [94]. In humans, REM sleep is associated with widespread neural activity patterns of internally generated sensory activity that is often associated with vivid, bizarre, and emotional dreams [95]. As in humans, blood-oxygen level-dependent (BOLD) activity during REM sleep in pigeons was found in limbic and premotor areas as well as in visual and multimodal pallial regions. A detailed analysis of both brainstem and telencephalic BOLD signals evinced activations in areas that process optic flow during self-motion with additional local motion signals of moving objects [96]. Furthermore, cerebellar areas that process tactile input from the wings and the overall body as well as pallial areas for frontal and lateral vision were active [97–99]. Obviously, the interpretation of these and further BOLD signals remains currently speculative. However, it is tempting to venture the idea that the pigeons might have dreamed about flying while avoiding accidents with other objects.

These studies also show that, in birds, cognitive processes go along with transient activations of widespread neural networks. Although these activated networks resemble those in mammals, some differences become visible. Most importantly and different from mammals, both during REM and non-REM sleep pigeons evinced no hippocampal activation [94]. In mammals, the interplay of the hippocampus and cortex during sleep consolidates memories that are at least partly stored at the cortical level, with the different sleep cycles having diverse contributions [100]. Key elements of this process like hippocampal sharp-wave ripples during non-REM sleep, thalamocortical spindles, and a hippocampal theta rhythm during REM sleep are absent in birds [101–103]. In addition, the hippocampus–prefrontal connection that enables memory consolidation and context-dependent memory retrieval does not exist in birds [48]. Thus, in sharp contrast to the discovered similarities between birds and mammals, it is conceivable that birds found a different way to consolidate and retrieve memories. This alternative pathway seems to perform exceptionally well. Ravens plan for the future, and food-caching birds hold memory records among non-human animals, are naturally selected for their memory performance, and depend on their hippocampus to remember their caches [11, 104, 105].

Concluding remarks

We began with a simple question: what constitutes a smart brain? The first answer was size, and it proved to be wrong [38,40]. A more likely answer is large numbers of associative pallial neurons that constitute computational units akin to hidden layers in deep neural networks (Figure 3).

Outstanding questions

What are the neural networks of avian cognition? To reveal these, we need techniques like imaging with which transient activity patterns of the brain can be tracked while birds are actively pursuing a task.

How do birds make memories? Crucial components of the neural systems with which mammals store, consolidate, and retrieve information seem to differ in birds, while their memory capacity is comparable with that of mammals.

What are the cellular and computational dynamics within the avian ‘isocortical’ canonical circuits? Research on this point is currently in its infancy but will be crucial to understand the neural fundamentals of sensory processing and beyond.

How are the neuronal networks in the nuclear ‘prefrontal’ NCL and motor arcopallium organized? Although a wealth of studies has revealed single-unit properties of NCL neurons during various tasks, the network structure of these nuclear areas is unknown in both birds and reptiles.

How do cortical/pallial connectomes of comparable species with high and low cognitive prowess differ? Such a research avenue could provide important insights into the network structure of cognition.

We hypothesize that large numbers of associative pallial neurons, a prefrontal-like pallial structure, dense dopaminergic innervation of associative pallial areas, and a highly dynamic neuronal fundament of working memory are essential neural components of complex cognition, while an isocortex is not. Can this conclusion be generalized, possibly even outside the realm of vertebrates?

The second answer was the isocortex and this was also wrong, at least partly. The mammalian isocortex derives from the dorsal pallium and contains all sensory, associative, and motor areas (Box 1). Birds also have an 'isocortex', but it contains only the sensory and not the associative and motor areas [56]. In addition, the DVR, which derives from the lateral and ventral pallia, also constitutes parts of the avian 'isocortex'. These DVR components of the avian 'isocortex' (lateral and ventral pallium) can therefore not be homologous to the mammalian isocortex (dorsal pallium) but must have evolved convergently to process sensory input, thereby possibly representing a hard-to-replace mechanism for this kind of neural computation (Figure 2A,B). Possibly, an isocortex is an optimal neural architecture for the representation of the sensory maps from the retina, cochlea, and body surface. However, since critical parts of avian cognitive functions are processed in the nucleus-shaped NCL, an isocortex seems to be dispensable for complex cognition.

Both mammals and birds have an associative prefrontal area that is densely innervated by dopaminergic fibers to provide feedback signals for successful actions and for flexible selection of relevant information. Since the NCL is part of the DVR, the NCL and PFC cannot be homologous but result from **convergent evolution**. Since crocodiles also have a tiny NCL with dense dopaminergic innervation [106,107], the NCL and PFC seem to have evolved in parallel in mammals and archosaurs. It might also exist with similar key properties in other kinds of species that underwent evolutionary selection for complex cognition.

Finally, working memory as a representation of flexible cognitive capacity shows overlapping neuronal temporal patterns. This makes it likely that similar meso- and microcircuits with the same dynamic neurophysiological fingerprints have convergently evolved in birds and mammals. All of these components possibly also represent hard-to-replace mechanisms.

Obviously, this is a speculative list of neural features that characterize convergently evolved neural systems for complex cognition in birds and mammals. This collection and the concepts from which they originate need thorough empirical testing in a large variety of species. We are confident that our collection of critical features (Figure 3) is not exhaustive and further components will be added over time (Box 3). To study these and other endeavors is not easy, but its reward could be the discovery of universal neural mechanisms for cognitive prowess. If indeed nature faces limited degrees of freedom to evolve smart brains, we should be able to identify such common neural patterns across a wide variety of species (see [Outstanding questions](#)).

Box 3. Putative further candidates for complex cognition

A potential future candidate for complex cognition is the cerebellum, which is tightly connected to cognitive processes in humans [118]. Parrots not only have excellent cognition but also a drastically enlarged avian-specific midbrain structure that serves as a link between the arcopallium, a premotor structure, and the cerebellum [119]. This corresponds to the enlargement of the mammalian pontine nuclei, which are especially large in great apes. That said, parrots and corvids do not have a larger cerebellum than other birds [120], making it possible that the avian cerebellar contribution to cognition is differently organized than in primates.

A further candidate is the high body temperature of 40–42°C of birds [121,122]. This is considerably warmer than the 36–37°C of eutherian mammals like rats and humans [123]. This temperature difference could potentially be another factor that makes birds smart. Temperature has multiple effects on neural function. It acts on biophysical properties of neurons such as membrane potentials, synaptic transmission, and channel kinetics and has a positive impact on conduction velocity, energy consumption, and refraction [124,125]. These effects are large enough to produce significant benefits to neural processing. For example, warming the eyes of swordfish results in higher temporal resolution of vision [126] and brain temperature is a controlling factor in the speed of birdsong [127]. Furthermore, higher temperatures reduce the energetic costs of action potentials [128] and, along with the small size of neurons, this might explain the overall low energy consumption of the avian brain. This low energy consumption in turn might explain why birds can afford high neuron numbers and generate the fast action potentials and the high firing rates that are especially beneficial to small neurons [44,129].

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No interests are declared.

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