

Avian Models for Human Cognitive Neuroscience: A Proposal

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Research on avian cognitive neuroscience over the past two decades has revealed the avian brain to be a better model for understanding human cognition than previously thought, despite differences in the neuro-architecture of avian and mammalian brains. The brain, behavior, and cognition of songbirds have provided an excellent model of human cognition in one domain, namely learning human language and the production of speech. There are other important behavioral candidates of avian cognition, however, notably the capacity of corvids to remember the past and plan for the future, as well as their ability to think about another's perspective, and physical reasoning. We review this work and assess the evidence that the corvid brain can support such a cognitive architecture. We propose potential applications of these behavioral paradigms for cognitive neuroscience, including recent work on single-cell recordings and neuroimaging in corvids. Finally, we discuss their impact on understanding human developmental cognition.

Introduction

Our understanding of the neural basis of cognition in humans is limited to studying the human brain in action (cognitive neuroscience) and how it is affected by trauma or disease (neuropsychology). However, there remain significant practical limitations to studying the living human brain, especially in real-time social interactions or during the solution of cognitive problems that cannot be studied inside a scanner. Current techniques, although much improved, are still dogged by issues of poor spatial and temporal resolution, especially when compared to techniques that can be used on animals. The only invasive methods we have to study humans are disrupting neural function using transcranial magnetic stimulation (TMS); recording from neurons in clinical patients already suffering from a neural malady (and so running into problems in interpreting any findings), or evaluating the effects of different drugs treatments based on our understanding of brain chemistry. Therefore, we are still dependent on using animal models for which we can manipulate the brain directly.

Although many species are used as animal models to successfully uncover the neural basis of cognition, we are restricted in what questions can be asked about complex cognition, by which we mean reasoning, flexibility, problem solving, prospection, and declarative knowledge (Emery and Clayton, 2004). Common laboratory animals that are used in neuroscience—*Drosophila*, *Aplysia*, rats, mice, zebra finches, pigeons, and monkeys have all provided important information about the neurobiology of learning and cognition, but the extent to which any of these animals can model the more unique aspects of human cognition, such as mental time travel, theory of mind, and innovative problem solving is limited. It is not our intention here to go through detailed arguments for and against each of these species' merits or limitations in terms of their usefulness as models of human cognition. Rather, we would like to propose

an additional group of animals that has been relatively neglected in studies of cognitive neuroscience, but which have arguably demonstrated cognitive feats on a par with or even surpassing those of the great apes. We propose the corvids (members of the crow family) as (1) an animal model for human cognition that could be adapted for studying the neural basis of complex cognition, and (2) interesting subjects in their own right for understanding the evolution and neurobiology of cognition. Determining which features of the avian and mammalian brain play a critical role in specific cognitive functions, and which ones are unique, could dramatically increase our understanding of the neural basis of cognition, and how and why these functions have evolved.

Current primate models have revealed amazing insights into the structure and function of the primate brain and its role in perception, memory, attention, information processing, and decision making. However, monkeys are expensive, the facilities required to house them are difficult to set up, and there are ethical issues concerning using subjects in great numbers. It is not possible or indeed ethical to perform invasive experiments on our closest relatives, the great apes. An alternative may be to develop a model, not of the next closest species (which is a rather unsatisfying compromise), but in an animal much more distantly related to us, one which appears to demonstrate similar cognitive abilities. In 2004, we proposed that the complex cognition of corvids and apes has evolved independently to solve similar problems, such as coping with difficulties leading from life in a complex social group full of individuals with different personalities and relationships, finding food distributed in both space and time, and adapting to climatic and ecological challenges (Emery and Clayton, 2004). At the time, we suggested that corvids and apes did this with very different brains, but as we will discuss in the following section, this position has now been updated as our understanding of the organization of the

avian brain has changed, revealing it to share more features with the mammalian brain than previously thought (Jarvis et al., 2005, 2013).

As yet, almost nothing is known about the structure and function of the corvid brain, whereas we have started to amass convincing evidence for their sophisticated primate-like cognitive abilities. So far, this is unsurpassed by other non-primates and so makes corvids powerful candidates for making discoveries about the evolution and neural basis of complex cognition, which could be applied to humans. We will discuss some of this evidence later, as well as evaluating other avian and non-avian models of cognition and why they are unlikely to be sufficient for modeling the human mind. First, however, we shall assess the evidence that bird brains, and most likely, corvid brains, are capable of supporting a cognitive architecture similar to that of the great apes and potentially humans.

Avian Brains

Our understanding of the structure and function of the avian brain has changed dramatically since Edinger (1899) proposed that birds were incapable of complex, structured thoughts because he believed that their brains were composed primarily of regions evolved from the striatum, rather than the cortex. This erroneous view was rectified in 2004 when a consortium of avian neuroscientists using information from connectional, behavioral, neuropharmacological, evolutionary, and developmental studies, reported that the majority of the avian telencephalon was not striatal but cortical in origin (Reiner et al., 2004; Jarvis et al., 2005). A significant part of the avian telencephalon was derived from the pallium of a stem amniote ancestor shared among all mammals, reptiles, and birds. This evolved into the dorsal ventricular ridge (DVR) and dorsal cortex (reptiles/Wulst (birds) and the cortex (mammals). Consequently, contrary to Edinger's view, little of the telencephalon of reptiles, birds, or mammals is comprised of the striatum. In addition, studies on the role of the basal ganglia (striatum) in skilled motor learning, such as learning song (Doupe et al., 2005), have dispelled the idea that the striatum is primarily involved in instinctual or non-cognitive behavior. For example, during song learning, the basal ganglia is essential for modulating the response of motor circuits to changes in song variability, such as due to changes in social context (Jarvis et al., 1998; Hessler and Doupe, 1999). It remains to be seen what role the striatum may play in other forms of skill learning, such as learning to use a tool.

Reiner and the Avian Brain Nomenclature Consortium (Reiner et al., 2004) agreed important changes to the names of avian brain regions to reflect this updated knowledge, so that the names of structures with the suffix -striatum (e.g., neostriatum) were exchanged with terms ending in the suffix -pallium (e.g., nidopallium) to reflect their shared ancestry with the mammalian pallium (e.g., cortex) not the striatum (Figure 1A). Prefix terms suggesting age, such as paleo-, archi-, and neo- were also changed because birds are the more recently evolved group compared to mammals, so the suggestion that the avian brain regions were more ancestral was also in error. Comparable structures in the primate (monkey) brain are depicted in Figure 1C (similarities are highlighted with the use of the same colors).

A recent comprehensive study comparing the expression of behaviorally relevant genes across regions in the telencephalon of eight bird species has led to a call to refine the avian brain nomenclature further (Jarvis et al., 2013; see also Chen et al., 2013). Areas within the mesopallium and hyperpallium (below the lateral ventricle) were found to share a high percentage of functionally expressed genes, and are proposed as a cohesive structure (renamed the tertiary pallium). Jarvis and colleagues (2013) therefore split the mesopallium into dorsal and ventral sectors (Figure 1B). They also found that certain regions, such as the entopallium and the hyperpallium intercalatum displayed similar gene expression patterns and proposed that these structures should also be classified as a new structure (primary pallium; Figure 1B). Other regions with mirrored patterns of gene expression were the nidopallium and hyperpallium apicale, which was renamed the secondary pallium (Figure 1B). Whether these findings are sufficient enough for such changes to be adopted by the avian neuroscience community remains to be seen. The fact that a number of avian neuroanatomists, including Harvey Karten (Karten et al., 2013) agree with such changes is promising. However, it would seem premature to make such sweeping changes on the basis of one study, no matter how comprehensive. The original nomenclature changes were the result of a group-level discussion (Reiner et al., 2004) and something similar will probably need to be reconvened in the future to assess and confirm the validity of these proposed changes.

Although we now have a clearer picture of how the avian pallium evolved, there still remains the fact that it appears to differ significantly in structure and organization from the mammalian cortex. The subdivisions of the stem amniote pallium (the common ancestor of all reptiles, birds, and mammals, most closely resembling an amphibian) are divided into dorsal, medial, and lateral portions, surrounding the DVR. The three divisions of the dorsal pallium evolve into different structures in reptiles, birds, and mammals and there is good evidence that they retain similar functions. For example, the conventional view is that the dorsal pallium, responsible primarily for processing sensory information - especially visual and somatosensory - evolves into the dorsal cortex in reptiles, the Wulst (hyperpallium) in birds and the neocortex in mammals (Striedter, 2005; but see Chen et al., 2013; Jarvis et al., 2013 for an alternative view). The lateral pallium evolves into the lateral cortex in reptiles, piriform cortex in birds, and olfactory cortex in mammals and processes olfactory information in all three taxa. Finally, the medial pallium evolves into the medial cortex in reptiles, hippocampal formation in birds and hippocampus in mammals and plays an important role in navigation, including spatial memory (Salas et al., 2003). The striking difference between birds and mammals is that there is significant *dorsalization* of the pallium in mammals, with the expansion of the cortex and significant *ventralization* of the pallium in birds (and to a lesser extent reptiles), with the expansion of the DVR. Despite these differences in evolutionary pathways, the pallium of birds and mammals appear to be functionally similar, if not equivalent.

In mammals, the cortex is constructed of six layers of tightly packed cell bodies on the outer surface of the telencephalon (gray matter). Connections within or between layers tend to be short, with longer axons to other cortical regions and

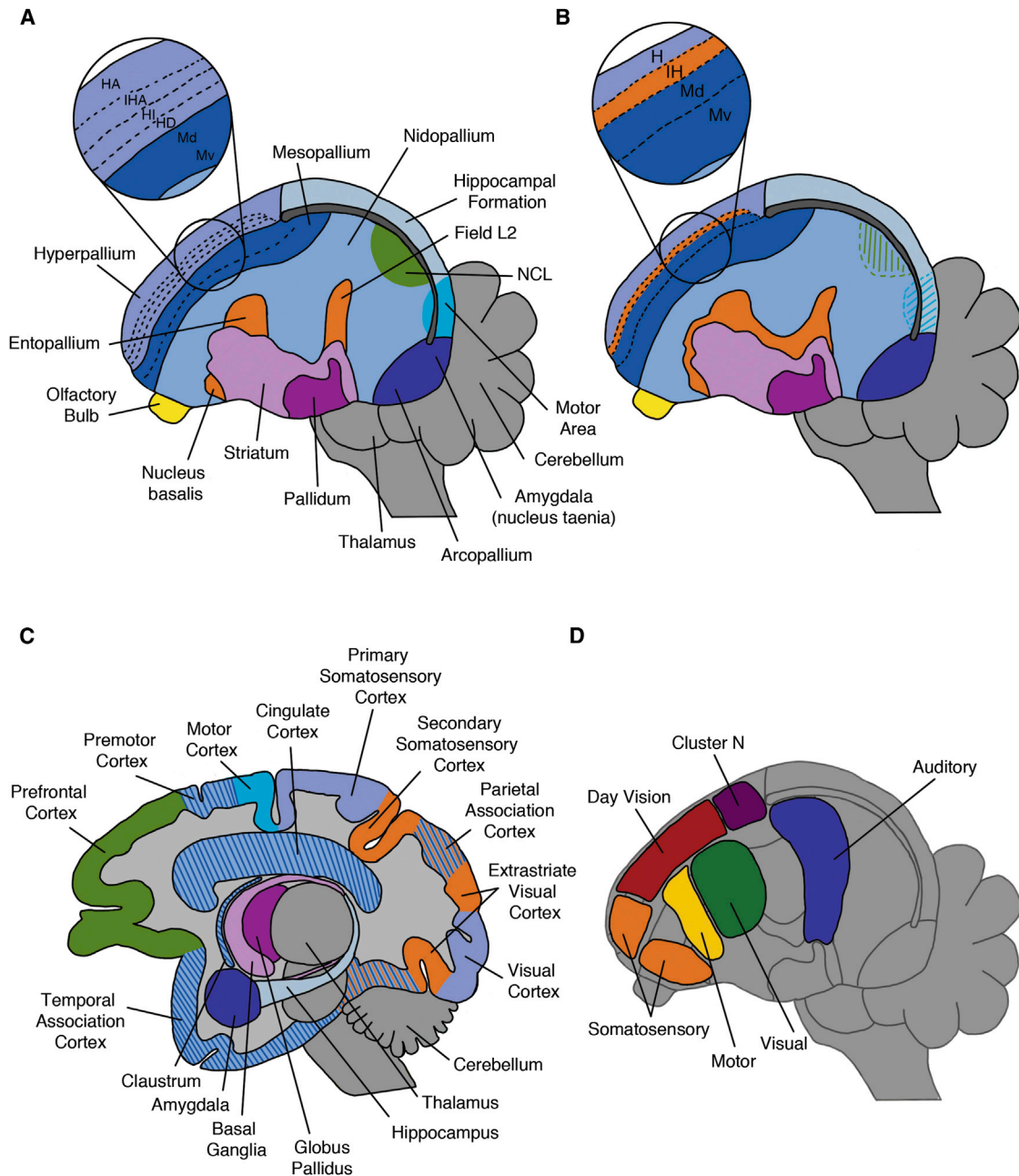


Figure 1. Schematic Representations of Avian and Mammalian Brains

All images are sagittal views, with rostral to the right. Areas that are either structurally homologous or functionally analogous have been given the same color (except D). In areas of the primate brain with hatching, it is not known which regions are functionally equivalent to the avian mesopallium, nidopallium, and entopallium. These images are not to scale and the position of different regions are approximate and for illustrative purposes only.

(A) Crow brain with terms and subdivisions based on the revised nomenclature of [Reiner et al., \(2004\)](#). The area in the circle displays the subdivisions of the hyperpallium in more detail.

(B) Crow brain displaying proposed boundary changes based on [Jarvis et al., \(2013\)](#). The area in the circle displays the boundary and nomenclature changes in the hyperpallium and mesopallium.

(C) Rhesus monkey brain with established nomenclature.

(D) Crow brain with overlaid functional columns (auditory [blue], day vision [red], motor [yellow], visual [green], somatosensory [orange], and cluster N [purple]), as proposed by [Jarvis et al., \(2013\)](#). HA, hyperpallium apicale; IHA, interstitial hyperpallium apicale; HI, hyperpallium intercalatum; HD, hyperpallium densocellulare; H, hyperpallium; IH, intercalated hyperpallium; NCL, nidopallium caudolaterale.

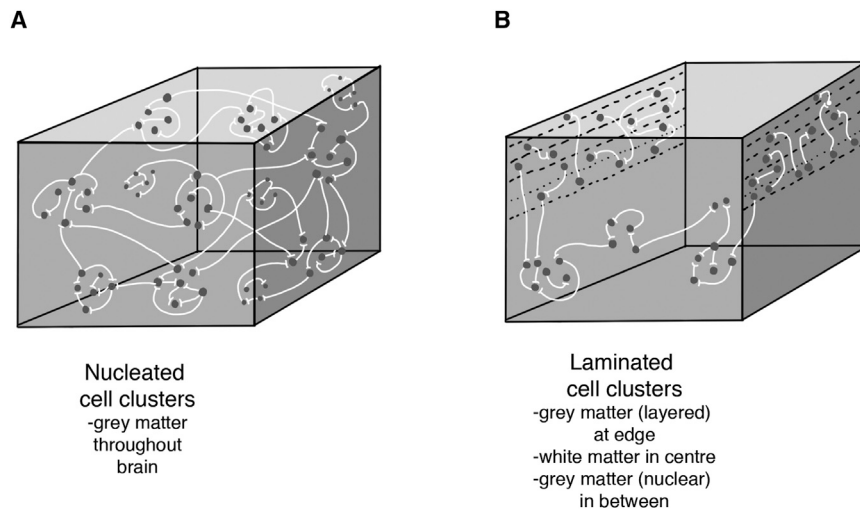


Figure 2. Nuclear versus Layered Organization

(A and B) The avian brain (A) and mammalian brain (B) represented as 3D cubes to display the differences between a nuclear (avian) and layered (mammalian) organization to the pallium and its relationship to sub-pallial areas.

sub-cortical structures via axonal tracts (white matter) under the cortex (Figure 2A). Deeper in the brain are subcortical structures, such as the striatum, thalamus, hypothalamus, midbrain, and brainstem influencing visceral functions and responses to external stimuli. These areas are not laminated, but consist of dense collections of nuclei with short connections within and between nuclei and back to the cortex. In birds, the majority of the pallium is organized into nuclei, with no significant tracts of underlying white matter and no significant lamination. The only possible exception is the Wulst that appears to be laminated in all birds (but is especially pronounced in owls), but this appearance is likely the result of stretching and squashing of the hyperpallial nuclei into something akin to layers (Figure 2B).

Although the overall organization of mammalian and avian brains is quite different, connections of sensory systems, such as visual, somatosensory, and auditory, as well as the motor system within each taxon possess many similarities (Medina and Reiner, 2000; but again see Jarvis et al., 2013 for an alternative view). For example, in birds and primates there are three main visual processing pathways. First, the lemnothalamic or thalamofugal pathway transfers visual information from the retina to the thalamus (principle optic nuclei in birds; dorsal portion of the lateral geniculate nucleus in primates), then projects to the primary visual processing areas (Wulst in birds; V1 or striate cortex in primates). Second, the collothamic or tectofugal pathway transfers visual information from the retina to the optic tectum (birds) or superior colliculus (primates), then projects to the thalamus (nucleus rotundus in birds; pulvinar and lateral posterior nucleus in primates) and finally the secondary visual processing areas (entopallium in birds; extrastriate cortex in primates). Third, the accessory optic system is involved in stabilizing retinal images during self-motion, which is particularly important for birds moving rapidly through a complex 3D world. An additional, relatively minor centrifugal pathway, projects back to the retina from regions in the brainstem and its role remains unclear. It may play a role in visual reflexes and modulating gaze sensitivity, especially during foraging on the ground, but it is not assumed to function in visual cognition (Miceli et al., 1999; Shimizu and Watanabe, 2012).

(especially in birds with lateral eyes), whereas lesions of the primate thalamofugal pathway cause severe visual deficits, which can result in blindness (Brown and Schafer, 1888). However, despite differences in connectivity, with no shared common heritage, the avian tectofugal pathway and primate thalamofugal pathway share functions in processing color and motion information and are subdivided along functional lines (e.g., Nguyen et al., 2004). As such, these functional similarities are likely to have evolved independently. Similar convergences in sensory pathways occur in the auditory, somatosensory, and motor systems of birds and mammals (Medina and Reiner, 2000), suggesting that other convergent pathways related to cognition may also exist in birds and mammals.

In the mammalian brain, regions with similar functions tend to be found clustered together, forming functional columns in the cortex. Their close proximity probably relates to an increased efficiency in neural wiring. Recent studies have found similar functional columns for a single modality or behavior in the avian brain (Wang et al., 2010; Kingsbury et al., 2011). By studying the expression of a suite of behaviorally relevant genes in response to different stimuli, Jarvis and colleagues (2013) demonstrated the equivalent of functional columns in the songbird brain that spanned pallial, striatal, and even pallidal structures (Figure 1D). They found clusters of neurons that expressed the same functionally relevant genes responsive to auditory, somatosensory, and visual (day and night vision) stimuli, as well as motor responses and a final cluster of the same gene expression, but with an unknown function. As with the proposed changes in nomenclature, we share the concerns of Montiel and Molnár (2013) that it would seem premature to suggest additional name changes based on similarities in gene expression profiles at this early stage, based on a single study.

What this study does tell us though, is that the nucleated avian brain may be more efficiently organized, along the lines of the mammalian cortex, than previously assumed. An analysis of the connectivity patterns of regions in the pigeon brain (Shanahan et al., 2013) concur with Jarvis and colleagues (2013) that the avian brain is organized using similar principles to the mammalian brain. Regions with a similar function share patterns

of connectivity and regions with the greatest density of connections are collected into hub nodes, through which the majority of neural information passes. A similar connectional organization was found for the primate brain (Young, 1993).

Of direct relevance to the issue of complex cognition is whether birds possess a region that is functionally equivalent to the primate prefrontal cortex (PFC). As we will describe in a later section, some corvids are capable of mental feats that have only so far been described in our closest relatives, the great apes. Although comparable neural studies have yet to be performed on apes or corvids, we know from human neuroimaging that retrospective and prospective memory, theory of mind, and insightful problem solving all depend on the medial PFC, whereas executive functions are dependent on the dorsolateral PFC, and reward learning and emotional engagement are dependent on the orbital PFC (Fuster, 2001). The nidopallium caudolaterale (NCL) has been proposed as the equivalent to the entire primate PFC based on its connectivity, development, electrophysiology, role in behavior, and neurochemistry (Güntürkün, 2005). We do not have the space to discuss these studies in the detail they deserve, but will briefly describe those that are the most pertinent.

First, NCL forms reciprocal connections with both primary and secondary/tertiary areas in the hyperpallium, mesopallium, and entopallium. It sends projections to the striatum influencing behavioral responses. It also receives and projects connections to and from motor and limbic areas. The NCL is therefore in a central position to receive information, process that information and then send it on to effect behavior (Güntürkün, 2005). This is parallel to what occurs in the primate PFC. Second, lesions of the NCL have dramatic effects on a series of executive function tasks, such as working memory, reversal learning, and inhibitory control (Mogensen and Divac, 1993). Third, the NCL receives dopamine efferent fibers from the ventral tegmental area and substantia nigra in the midbrain. The NCL is densely populated with dopamine (D1 and D2) receptors, it sends dopamine-rich projections to the striatum and blockade of D1 receptors affects working memory and discrimination reversal task performance (Durstewitz et al., 1999). Finally, NCL neurons in working memory tasks display their strongest responses in the delay period, coding an expectation of reward (Rose and Colombo, 2005).

Pigeons are the subject of many studies on avian brain structure and function (those not focused on song learning). Pigeons are proficient learners and exceptional at visual discrimination, but there is little evidence for complex cognition (e.g., theory of mind, mental time travel, self-awareness, and reasoning). The fact that pigeons have a brain region functionally equivalent to the primate PFC means either that pigeons are smarter than we previously thought (but yet to be demonstrated experimentally), or that executive functions are not as complex as previously thought, or that the pigeon NCL is equivalent to only part of the PFC complex; a region that maybe only plays a supporting role in more complex forms of cognition. We suggest that the pigeon NCL may be functionally equivalent to the primate dorsolateral PFC, playing a role in executive functions, and that the pigeon NCL may also share some functions with primate orbital PFC due to its multisensory connectivity, its role in reward

learning, and its extensive distribution of dopamine receptors (Güntürkün, 2005); however, because this role has yet to be investigated, we cannot comment on this further. We do not know whether pigeons have an equivalent region to the medial PFC, but feel it unlikely as this region in primates supports complex cognition that is absent in pigeons. However, we predict that corvids could have evolved a similar region due to their skills in these areas (see below).

Unlike most mammals other than humans, the songbirds (Oscines), of which corvids are included, are excellent vocal learners and we now know a lot about the behavioral processes that underlie avian song perception and production including when and how the songs are learned and from whom, as well as the neural circuitry controlling these processes. The avian vocal learning system has therefore been proposed as an excellent model for human speech and language (see Bolhuis et al., 2010; Brainard and Doupe, 2013; Petkov and Jarvis, 2012 for recent reviews). A recent proposal suggested that parrots may be a better model than songbirds because of their ability to imitate human speech, and the form of their complex social relationships (Colbert-White et al., 2014); however, this proposal fails to appreciate that corvids are songbirds that can imitate human speech and also have complex social relationships (Emery, 2006).

Complex cognition is not a universal trait across non-human animals. We have proposed that selective animal groups with a very specific socio-ecology, life history, and sophisticated neural systems are capable of general cognitive abilities as opposed to only those that have evolved to face specific challenges in their day-to-day lives (van Horik et al., 2012). Corvids and apes are two of those groups and their cognitive abilities are suggested to have arisen through convergent evolution not common descent. By this, we mean that not all related species from the common stem amniote ancestor of birds and mammals (including all reptiles) possess the same abilities as those in the corvid and ape families (Emery and Clayton, 2004). We are well aware that our argument for convergence as opposed to homology is based on a paucity of data from a select few avian and mammalian species and that more comparative studies need to be conducted. We suspect that similarities in cognition will also be found in parrots, dolphins, and elephants, for example, and that as with the corvids and apes, these are most likely to have evolved convergently because they all share a number of biological, ecological, and psychological traits related to complex cognition, including vocal learning (Petkov and Jarvis, 2012; van Horik et al., 2012). A case in point is object permanence, particularly the ability to track invisible displacements (Piagetian Stage 6), which only seems to be present in corvids, (Hoffmann et al., 2011; Zucca et al., 2007), parrots (Auersperg et al., 2014) and apes (e.g., Collier-Baker et al., 2006; however see Jaakkola, 2014 for an alternative account).

Corvids and apes differ from most other animal groups in that they share a suite of cognitive abilities that allow them to deal with their social and physical worlds (Emery and Clayton, 2004). We proposed four cognitive tools that would allow these two groups to solve problems outside their natural domains, namely causal reasoning, flexibility, prospection, and imagination. These tools are not mutually exclusive, for example,

prospection depends on imagination and flexibility may aid causal reasoning, and together they make possible the solution of novel problems. In the 10 years since we proposed this cognitive toolkit, evidence that corvids and apes possess these tools has proliferated. As such, our discussion of these abilities in corvids will largely be restricted, because of space, to our studies.

Avian Models of Learning and Cognition

Birds have been used as models for learning and memory and the neural basis of cognition for decades (Emery, 2006). Indeed, some species are considered the best models currently available. Three main species or groups of birds are currently used to address specific aspects of learning and cognition and their neurobiology: pigeons, domestic chicks, and songbirds.

Pigeons are the primary model system for understanding the processes of learning and spatial memory, in particular visual discrimination and navigation (homing). Studies on pigeons have substantially increased our knowledge of avian brain connectivity, including the suggestion of an avian equivalent to the mammalian prefrontal cortex (Güntürkün et al., 2014). Studies of the avian hippocampus have been instrumental in our understanding of the neural mechanisms of spatial navigation and homing behavior (Bingman et al., 2005).

Domestic chicks are the primary model for studying the development and neurobiology of learning and memory, especially using imprinting as a model behavior system (Nakamori et al., 2013). Chicks are also used as models for cerebral lateralization and behavioral function (Halpern et al., 2005). Studies on space, number, social, and physical cognition in chicks have revealed striking abilities in very young brains (Vallortigara, 2012).

Songbirds are the primary model for studying the processes underlying vocal learning and the avian song control system is one of the best-known systems for understanding the neural basis of learning and memory (Ziegler and Marler, 2012). Although all passerines (songbirds) sing, zebra finches have become the most popular model, and our knowledge of their neuroanatomy and behavior is unsurpassed (Mello, 2014). A second songbird, the black-capped chickadee is a model species for testing ideas concerning the neurobiology of spatial memory and its interaction with hormones, caching behavior, and environmental stress (Pravosudov, 2007).

Although all three models have advanced our understanding of the neurobiology and evolution of cognition in a taxon that has a very different brain architecture and shows vast differences in behavior, there are limitations in the application of these models to some aspects of human cognition, namely what we call complex cognition (Emery and Clayton, 2004). Recent work in corvids has revealed abilities in areas that have been proposed as uniquely human and not yet displayed in these other avian models and this is the main reason for our proposal for a corvid cognitive neuroscience and application of corvids as models of human cognition.

Potential Behavioral Candidates for Understanding Human Cognition

The vocal learning system of songbirds is not the only avian model for understanding human cognition. For almost 20 years,

evidence has accumulated suggesting that corvids have remarkable cognitive capacities, possessing feats that a number of researchers regard to be uniquely human. Corvids are therefore potential candidates for new animal models of human cognition. Three strands of evidence will be considered in this review: mental time travel (remembering the past and planning for the future), social cognition, and physical problem solving. We will review the research on these three aspects of cognition in corvids, and discuss how the same paradigms can be developed to study human cognition, particularly the application to neuroscience and developmental cognition (Figure 3). Comparative and developmental cognition both require the use of tasks that are, respectively, entirely or largely, non-verbal. It is important to note, however, that our purpose is not to ask questions about whether corvids show cognitive performances equivalent to humans, or of young humans of a particular age. Rather, the objective is to investigate two different kinds of mind, ones that have very different evolutionary histories and neural architectures yet similar patterns of large-scale network organization as discussed in the previous section, in order to compare and contrast the mechanisms they use to solve the tasks. This raises interesting questions about how information processing is achieved in these two kinds of mind given the striking differences in neural architecture and surprising similarities in connectivity and organization of avian and mammalian brains, particularly how the information is passed between nuclei in the avian brain as opposed to between layers in the mammalian cortex.

Mental Time Travel

Mental time travel refers to the ability to remember the past (episodic memory) and plan for the future (episodic future thinking). There has been considerable debate as to whether mental time travel is uniquely human (e.g., Suddendorf and Corballis, 1997), or whether we share this cognitive ability with other animals (e.g., Clayton et al., 2003). As we alluded to in the previous section, one difficulty is that mental time travel in humans has typically been characterized in terms of two features of phenomenological consciousness, neither of which is amenable to empirical evaluation in animals. The first feature is an awareness of the subjective sense of time, of re-experiencing now in the mind's eye an event that happened in the past and of pre-experiencing possible future scenarios; the second is an awareness of being the owner and author of these memories and forethoughts (e.g., Tulving, 2005).

In the absence of any agreed behavioral markers of consciousness in non-linguistic animals, it is not possible to evaluate empirically whether or not the phenomenological aspects of mental time travel are unique to humans. What we can do is focus on the behavioral criteria for episodic cognition, and this has been termed *episodic-like* cognition to explicitly acknowledge that such criteria ignore the involvement of phenomenological consciousness (Clayton and Dickinson, 1998). The retrospective component, episodic-like memory, needs to fulfill three criteria to meet the behavioral properties of episodic memory as defined for humans: namely content, structure, and flexibility (Clayton et al., 2003). In terms of the content of an episodic-like memory, the subject must remember what happened where and when based on a single past experience. Second, the what-where-and-when components form an

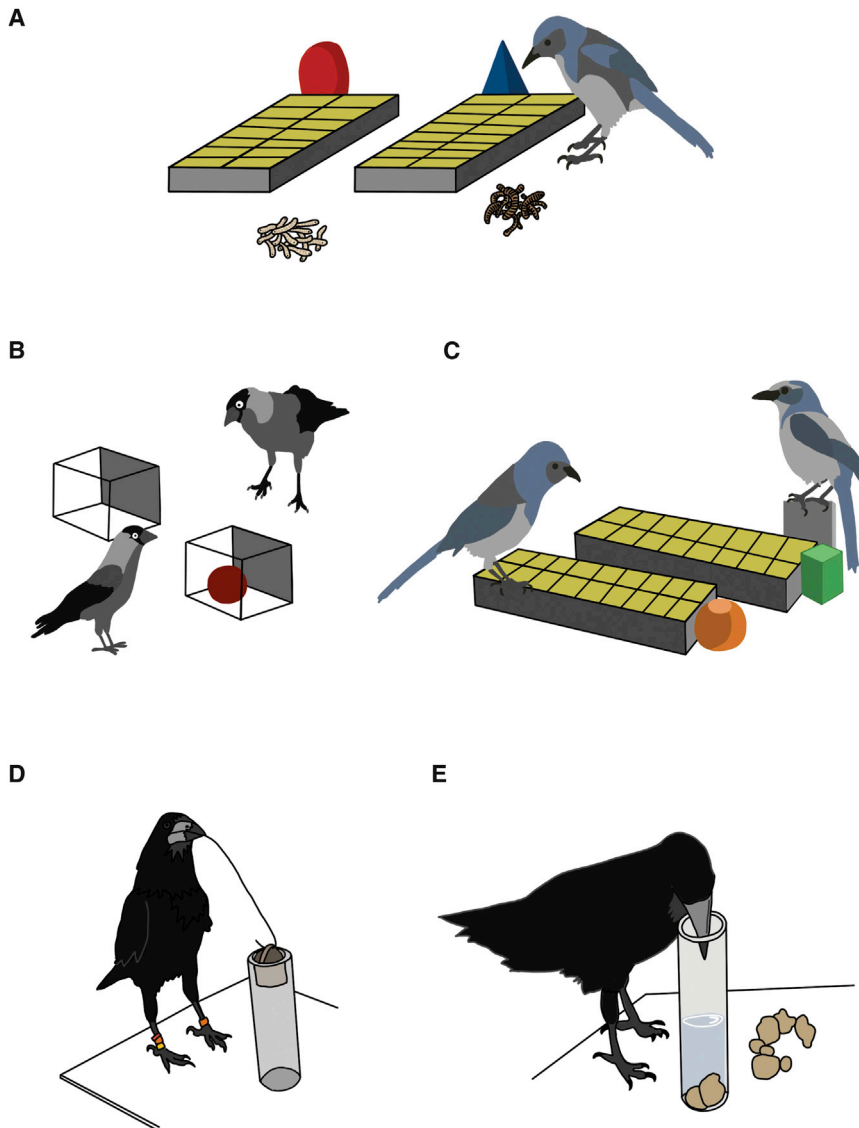


Figure 3. Different Corvid Cognition Tasks

(A) Caching paradigm used to test episodic-like memory (Clayton and Dickinson, 1998) and future planning (Raby et al., 2007) in western scrub jays. Two different foods (e.g., wax worms and mealworms) can be hidden in different locations (molds) in an ice cube tray and recovered after different delay periods. The trays are filled with sand or corn kibble, allowing the foods to be buried and each tray is made unique by the arrangement of various colored Lego Duplo bricks around each tray.

(B) Object choice paradigm used to test social cognition in jackdaws (von Bayern and Emery, 2009a, 2009b).

(C) Social caching paradigm used to test for visual perspective taking, knowledge attribution, and experience projection in western scrub jays (Emery and Clayton, 2001, Clayton et al., 2007).

(D) Tube-and-bucket paradigm used to test physical cognition and tool manufacture in rooks (Bird and Emery, 2009a).

(E) Aesop's Fable (water displacement) task used to test physical cognition and tool use in rooks (Bird and Emery, 2009b).

integrated structure: it is this binding that allows the subject to discriminate between similar episodes that occurred at different times and places. Finally, the information must be capable of flexible deployment, and as a result, it can be updated after the memory has been formed so that information can be generalized across situations.

Experiments on the caching behavior of western scrub-jays (Figure 3A) revealed that these birds episodically recall specific past caching episodes in terms of what happened where and when; i.e., they remember which foods they have hidden where and how long ago and search in places they had cached perishable worms after a short delay when they would still be fresh but switching to search in the peanut cache sites after a long delay when the worms would have rotted (Clayton and Dickinson, 1998). Subsequent tests have shown that the jays also remember which type of perishable foods they have hidden where and how long ago (e.g., worms versus crickets), irrespec-

tive of whether the foods had ripened or decayed. The jays also discriminated between similar episodes that occurred at different times and in different places, demonstrating that they formed integrated what-where-and-when memories. Furthermore, if the jays were given new information about how long a given food item takes to degrade in a particular place, but only after the caching event had taken place, then they could update their knowledge about the rate of perishability of the food and change their search behavior at recovery accordingly. As far as we are aware, this is the only published demonstration of the declarative flexibility with which animals can update their information after the time of memory encoding (Clayton et al., 2003).

Since the initial studies, a number of other laboratories have investigated whether animals have episodic-like memory using paradigms analogous to those used with the jays. There is now good evidence that a diverse range of animals can remember the what-where-and-when of past events including rats (Babb and Crystal, 2006), mice (Dere et al., 2005), magpies (Zinkivskay et al., 2009), and chickadees (Feeney et al., 2009), and more recently chimpanzees (Martin-Ordas et al., 2010) and cuttlefish (Jozet-Alves et al., 2013). Note that all of these studies have only focused on the content of episodic-like memory: they lack the cognitive sophistication to demonstrate that such memories have an integrated or bound structure, and can be deployed flexibly. For this reason, the scrub-jay paradigm remains the most appropriate model for application to models of human episodic cognition.

If what-where-and-when memories are an indicator of episodic cognition, then the animals that pass such tasks should

also be capable of planning ahead, and there is indeed evidence to support this claim in corvids. It has been shown, for example, that scrub-jays plan for tomorrow's breakfast without reference to their current motivational state, spontaneously caching in the evening in a room where they have learned they will never be served food in the morning (Raby et al., 2007). It is important to note that we can rule out an explanation in terms of mediated reinforcement of the anticipatory act because the birds were not given the opportunity to cache during training. Indeed, Shettleworth has argued that "two requirements for genuine future planning are that the behavior involved should be a novel action or combination of actions... and that it should be appropriate to a motivational state other than the one the animal is in at that moment... Raby et al. describe the first observations that unambiguously fulfill both requirements" (Shettleworth, 2007, p. 825). These results show that corvids are capable of both episodic-like memory and planning for breakfast.

Social Cognition

Corvids are highly visual animals and use social signals such as eye gaze and gestures, such as beak direction, to represent their attentional state (Pika and Bugnyar, 2011). The ability to read such signals presents individuals with an advantage in social interactions, possibly allowing them to predict another's future actions and so outwit them. In the next section, we will discuss this ability in relation to caching and specifically cache protection; however, corvids also interact outside of caching, especially with close companions and social partners. Jackdaws, for example, follow a conspecific's gaze toward the object of their attention concealing food, but only when the conspecific is their partner, not when unfamiliar to them (Figure 3B; von Bayern and Emery, 2009b). In a similar paradigm using human cues, jackdaws responded to social signals that were communicative (distal pointing and gaze alternation), not ambiguous or potentially threatening (von Bayern and Emery, 2009a). Finally, in a study of understanding other's attentional states—using a competitive paradigm where a human looked toward or away from food and the time taken for the bird to take the food was recorded—jackdaws took longer to take the food if the human was a stranger and their attention was focused on the food. If the human was familiar to them, they did not discriminate between attentional states (von Bayern and Emery, 2009a).

In these cases, jackdaws demonstrate a high level of flexibility in the way that they differentiate between similar social cues that differ in functional significance. They note the identity of the individual providing the cue and act accordingly; either using the honest or reliable cue of a partner in a cooperative paradigm or responding to the threat of a human stranger in a competitive paradigm. They also rely on communicative cues in a cooperative task, not attentional cues that could be misinterpreted in the same context. Finally, they also generalize their responses to social cues based on their function, not appearance, so act similarly to one eye open, two eyes open and profile directed away but with eyes toward the viewer, all representing the same attentional state.

Cache Protection Strategies

Much of the work on social cognition in corvids, however, revolves around the strategies these birds use to protect their caches from being stolen (pilfered) by other individuals. Most

food-caching animals only steal caches at the time they are being hidden, or when discovered opportunistically. Corvids, in contrast, can remember where they have seen other individuals cache based on observation alone, and can therefore steal the food at a later date once the cacher is no longer present to defend its caches (Figure 3C; reviewed by Clayton et al., 2007). This dramatically increases the risk of cache theft. An added complexity is that any one corvid may play the role of both cache protector and potential pilferer, and this role-playing may have driven the evolution of increasingly more complex cognitive strategies for pilfering and cache protection (e.g., de Kort and Clayton, 2006).

Corvids use a suite of cache-protection strategies that limit opportunities for potential pilferers to witness caching events: they preferentially cache behind barriers when others are looking, and use both distance and shade to degrade the visual information available to onlookers, preferences they do not show when others cannot see where they cache. If the potential pilferer can hear but cannot see, they conceal auditory information by caching in a substrate that makes little noise. In contrast, if they are alone or if others can see as well as hear the caching event, then the birds prefer to cache in noisy substrates. It has been suggested that this may serve as a cache protection strategy in its own right, allowing the cacher to detect a potential cache-raid should the bird be within earshot of a potential pilferer that it is unable to see. Jays also keep track of which particular individual bird watched them cache and when, and take protective action accordingly, such as moving the high-risk caches to new places once the potential pilferer has left. In deciding which cache protection tactics to use, the birds take into account the dominance status of the potential pilferer in relation to their own dominance status, using different strategies if they are dominant to the onlooker than if they are subordinate (reviewed by Clayton et al., 2007). Similar tactics have been found in several other species of corvids, in both the laboratory and the field, including ravens (e.g., Bugnyar, 2011), Clark's nutcrackers (Clary and Kelly, 2011), Florida scrub-jays (Kulahci and Bowman, 2011), and Eurasian jays (e.g., Legg and Clayton, 2014) and also in some parids, namely mountain chickadees (Pravosudov, 2008).

Experience Projection

The most striking finding is that only those birds who have been experienced thieves themselves in the past move food to new cache sites once the potential pilferer has left the scene (Emery and Clayton, 2001). Naive birds that have not stolen other birds' caches do not do so, ruling out the possibility that such cache protection strategies are hard wired. It is important to note that the jays were neither rewarded nor punished for re-caching, and in fact, they were not given the opportunity to recover their re-caches and thus discover whether re-caching was successful, and thus had no opportunity to learn about the benefits of re-caching. Instead, the inference is that the experienced pilferers engage in a form of social cognition called experience projection, anticipating what the onlooker might do in similar circumstances; i.e., to pilfer the caches they have seen another bird make, and thus move their caches to new places before the potential pilferer has the opportunity to do so. In terms of their applicability as an animal model of social cognition that can be developed for humans, there are two important things to note.

The first is that the responses of these experienced birds are highly flexible. The jays only re-cache food when a potential pilferer has observed them cache the food; they do not do so if the onlooker was their mate with whom they share their caches or if the potential thief did not witness the caching event (Emery and Clayton, 2001). The second is that this flexible deployment of information that we referred to in the previous section is seen in both studies of episodic cognition and social cognition, which is consistent with the human neuroimaging studies that suggest that mental time travel, theory of mind, and insightful problem solving are all dependent on the PFC (Emery and Clayton, 2004).

Physical Problem Solving

The final strand of evidence for corvid cognitive capacities comes from studies of physical problem solving, and in particular research on innovative tool use. The most famous example is that of Betty, a New Caledonian crow, who modified a piece of wire to make a hook-shaped tool, which was used to retrieve a small bucket containing a reward that was otherwise out of beak reach (Weir et al., 2002). Even more striking is the finding that rooks, which do not habitually use tools in the wild, will spontaneously craft these hooked shape tools in the laboratory and use them to obtain food (Figure 3D; Bird and Emery, 2009a).

A task that has the greater potential for application across species is the Water Displacement Task inspired by Aesop's fable "The Crow and The Pitcher." In this tale, a thirsty crow drops stones into a half-full pitcher of water to raise the level within beak reach so that it can drink. In the Water Displacement or Aesop's Fable task, rather than making the birds thirsty, the corvids were tempted with a worm floating on top of water half-filled in a vertical transparent tube (Figure 3E). A handful of stones were placed next to the tube, which the bird had to drop into the tube to raise the water level and reach the worm. Bird and Emery (2009b) found that rooks with experience of dropping stones into tubes, but not in the context of water, would spontaneously put the stones into the tube to raise the water level and obtain the worm. Furthermore, when the water level was varied, the birds matched the number of stones required to increase the water level and so reach the worm. The birds were also selective in their choice of stones, taking those that would most efficiently raise the water level. Subsequent experiments have shown that Eurasian jays can solve this task (Cheke et al., 2011), and that habitual tool-using New Caledonian crows showed a similar performance to that of rooks and Eurasian jays (Jelbert et al., 2014). In these latter studies, jays and crows flexibly responded to changes in the material of the "stones" (floatable or sinkable), as well as the substrate inside the tube (sand, sawdust, air or water), but did not manipulate the water when they could only see the result of their actions, not the actions themselves.

Costs and Benefits of the Different Animal Models

Why develop corvid models of human cognition when there already exist a number of rodent and non-corvid avian models that may be more amenable to neuroscientific investigation? We know significantly more about the rodent brain than the corvid brain, rodent genomes have been mapped in detail and gene knockouts have been used to model human neurocognitive disorders. Rodents are relatively simple and cheap to maintain in the lab, easy to obtain and we know a lot about their biology

and behavior. Similar cognitive tasks to those described for corvids have been developed for rats. For example, Babb and Crystal (2006) found that rats could remember *where* different types of food (*what*) were located in a radial arm maze and the relative time when they were available (*when*). It is important to note, however, that more stringent tests of flexibility and whether these individual components are bound together as an integrated representation remain an open question, having only been conducted on the corvids (see Clayton et al., 2003). Furthermore, the corvid models have the advantage of showing flexibility across all three domains, namely mental time travel, theory of mind, and causal reasoning.

With any animal model, there are pros and cons. A disadvantage of the rodent models is that rodents are primarily olfactory creatures, whereas corvids, like humans, are visual and auditory creatures. Indeed avian and primate brains have analogous visual and auditory pathways (Medina and Reiner, 2000). Many examples of non-verbal human social cognition are based on visual cues, such as pointing and eye gaze, and only non-human animals that can use those cues in their social interactions are relevant potential animal models of human social cognition (Emery and Clayton, 2009). Those few rodent species that either naturally use tools or have been trained to use tools (e.g., Okanoya et al., 2008) do not use tools in the same flexible manner as humans or corvids. Rodents are also inadequate models of human cognitive aging because they only live for approximately 1 year in captivity, whereas corvids can live up to 30 years.

However, corvid models of human cognition are not without their problems. Corvids are not traditional lab animals so they cannot be ordered from a lab breeder en masse but must be taken from the wild or hand-raised if they are to be studied in the lab, and this requires specialist technical assistance. To date, only one stereotaxic atlas of a corvid brain has been published (jungle crow; Izawa and Watanabe, 2007) and very little is known about neural connectivity or genome structure. In essence, the corvids make excellent behavioral models of cognition provided the space and expertise for their housing is available, but they remain to be developed as neurobiological models.

Potential Applications of the Corvid Models

The biological and cognitive similarities of corvids and humans reinforce our proposal that corvids represent strong models for some aspects of human cognition. Although avian brains are structured along very different principles from mammalian brains, we suggest that these differences are not a barrier to similarities in function. Although our earlier proposal suggested a significant degree of convergence in the cognitive systems of non-human apes and corvids (Emery and Clayton, 2004), we might now extend that proposal to include humans (albeit with clear warnings that many important differences still exist). Our proposal is not that corvids present perfect models of human behavior and cognition, rather that they are as good, if not better than current non-human mammalian models. We propose two applications of corvid models of human cognition: neuroscience and child development.

Neuroscience

Avian neuroscience has largely focused on two aspects of behavior: song learning and spatial memory. Research on

song learning has revealed selective neural circuits for perceiving song, circuits matching perceived song with remembered song, and circuits for producing song in specific contexts (Ziegler and Marler, 2012). Research on spatial memory has focused on the hippocampus; size differences in the hippocampus between caching and non-caching birds and changes in hippocampus size before and after caching, as well as neurogenesis in the hippocampus (Pravosudov, 2007). This research on the interplay between brain and behavior has been largely restricted to traditional avian models, such as the zebra finch (song) and the chickadee (caching). In contrast, there has been little research on the corvid brain. We shall focus on two studies that have direct relevance to our cognitive models and which have the greatest potential for further development.

The first concerns the role of the NCL in corvids. Although there is good evidence that the NCL of birds is functionally equivalent to the primate PFC, much of this research is the result of studies performed on pigeons. Corvids have a much larger cerebrum than most other birds (Emery and Clayton, 2004) and this dramatic increase in brain size in corvids is reflected in a larger nidopallium and thus larger NCL (Rehkämper et al., 1991). Furthermore, studies comparing the performance of corvids and pigeons on learning sets showed that pigeons were rote learners, solving each set of visual discriminations afresh, whereas the corvids were rule learners and therefore capable of adopting an abstract rule, namely win-stay lose-shift, that could thereby be generalized across sets of new discriminations (Wilson et al., 1985). If the pigeon NCL is functionally equivalent to the primate PFC, or at least the dorsolateral PFC, then what do we expect the corvid NCL neurons to do? As mentioned in the first section, the work on pigeons suggests that in working memory tasks the NCL neurons display their strongest responses in the delay period, coding an expectation of reward (Rose and Colombo, 2005). Similar studies to those on pigeons have recently been performed on carrion crows. Neurons in the crow NCL respond during the delay period of Delayed Matching and Non-Matching to Sample Tasks (Veit and Nieder, 2013). Interestingly in these tasks, the crows use an abstract rule (match or non-match) using an arbitrary tone or shape presented in the delay period. Veit and Nieder (2013) found that a population of neurons in NCL fired in the delay period before the crows were presented with their choice stimuli and so encoded the properties of these abstract rules. Some neurons also fired if the crow was going to make a behavioral error, with a weaker or inverse discharge rate. Other neurons in the crow NCL continued to respond to a previously presented visual stimulus during the delay period of a working memory task even though the stimulus was no longer present, suggesting that the image was being retained in working memory before the crow had to make a behavioral choice (Veit et al., 2014).

The second concerns the use of neuroimaging methods in corvids. Marzluff and colleagues (2012) examined the brain responses of anaesthetized crows in a PET scanner to the presentation of threatening faces versus benign faces (predicting food). Neural networks typically responsive to fear (to the threatening faces) and motivation (to faces predicting the presentation of food) in mammalian brains were also found responsive

in crow brains. It remains to be seen how sophisticated such avian neuroimaging studies will become as scanner resolution increases and techniques can be applied to awake rather than anaesthetized birds (De Groof et al., 2013). We envisage a renaissance of avian neuroscience with the application of optogenetics, which can be used to disrupt activity in selective neural circuits with the application of focused light. This technique has started to be used in zebra finches to study vocal learning (Roberts et al., 2012); however, it could be adapted to our corvid models. For example, it would be fascinating to investigate the role of the hippocampus in both episodic-like memory for past caching events and the jay's ability to plan for tomorrow's breakfast. Would disruption of the corvid hippocampus and NCL inhibit both of these abilities, as one would predict from human neurocognitive imaging studies and a recent comparative analysis in animals (Allen and Fortin, 2013)? This is an important question because although it has been well established that the hippocampus plays a crucial role in spatial memory in both birds and mammals, and that lesions to the hippocampus disrupt memory for caches in food-storing birds including corvids (e.g., Krushinskya, 1966), recent work on the neuroanatomy of the pigeon hippocampus suggests that it only receives visual and olfactory input. Rattenborg and Martinez-Gonzalez (2011) have therefore argued that in contrast to the mammalian hippocampus the avian hippocampus does not have connections with most higher-order association areas (but see Allen and Fortin, 2013 for a counterargument in favor of evolutionary continuity). Studies of corvid connectivity would be crucial in this regard.

Child Development

The second application of corvid models is for studying the development of cognition in young humans. For example, we can investigate whether, and to what extent, young children show the same pattern of development in their performance on what-where-and-when tasks inspired by the scrub-jay caching to that found in other tests of mental time travel (reviewed by Clayton, 2015). Performance on what-where-and-when memory tests does indeed show a similar developmental trajectory (e.g., Hayne and Imuta, 2011; Scarf et al., 2013), namely that young children generally fail the tasks at 3 years of age, show a transitional state of performance at 4 years of age, and pass at 5 years of age. Similarly, when children were tested on a task analogous to the planning for breakfast experiment for scrub-jays, in which the children were given the opportunity to plan for tomorrow's playtime as opposed to breakfast, they did not pass the task until they were 4 years of age (Atance et al., 2015). In essence, the children's performance on the scrub-jay based paradigms shows a similar developmental trajectory to that found in other tests of episodic cognition in young children, thereby establishing them as appropriate models for studying human and avian cognition.

Corvid models of insightful problem solving have also been adapted to study cognitive development, and such studies show that these abilities develop surprisingly late in childhood. Indeed, studies investigating the hook-making abilities of young children suggest that it is not until children reach about 8 years of age that they can solve such tasks, and even then, only about half of the children were successful on the task (e.g., Cutting

et al., 2011). Furthermore, in line with the developmental trajectory for hook-making abilities, young children did not pass the critical aspects of the water task, such as spontaneously dropping objects that sink into the tube as opposed to those that float until they were 8 years of age (Cheke et al., 2012).

What Do the Corvid Analogs Tell Us about Human Cognition?

Intuitively, one might have thought that social and episodic cognition tasks required more complex forms of cognitive process given that they both require forms of perspective taking (other minds and other times respectively). Perhaps the fact that children pass these tasks earlier than the physical problem-solving tasks is a reflection of the effects of extensive technological enculturation on physical problem solving. For example, in Western mechanistic societies, children gain considerable experience of devices with hidden mechanisms, from smart phones and computers to light switches. It would be fascinating to conduct cross-cultural studies to investigate these issues further. Such comparisons would allow us to investigate whether, and to what extent, a child's understanding of the physical world is in general developmentally delayed compared to that of perspective taking and whether this applies specifically to children who have been raised in mechanized cultures. In doing so, we should gain a better understanding of the mechanisms controlling the various behavioral decisions that children make in problem-solving tasks, including how they bring to mind and coordinate the various actions required of the more complex physical tasks involved in the hook manufacture tests (Cutting et al., 2014). The hope is that these models will stimulate future research to identify these cognitive milestones and explore the mechanisms underlying these abilities in both children and corvids (Clayton, 2015).

Conclusions

Our understanding of corvid cognition, especially with respect to abilities thought to be uniquely human, has not been reflected in our understanding of corvid neurobiology. In the 10 years since our general understanding of the avian brain was reassessed, we still know little about those birds that would make plausible models for human cognition, namely corvids and parrots. We propose that neuroscientists interested in the neurobiology of complex cognition start to incorporate avian models into their paradigms, most effectively by collaborating with comparative psychologists, ethologists, and behavioral ecologists with expertise in working with these unusual species. Computational neuroscientists will be able to think clearly about the issues surrounding differences in neural and cognitive systems between birds and mammals that will make the best use of data resulting from these interdisciplinary relationships.

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