What is Behind the Intelligence in Corvids?

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Introduction

The study of animal intelligence has almost always been focused on primates, since they are quite similar to humans in many ways. However there is no reason to think that primates represent the epitome of animal cognition. *Corvidae*, a family of oscine passerine (oscine is Latin for "songbird", passerine is any bird of the order Passeriformes) birds that contains the crows, ravens, rooks, jackdaws, jays, magpies, treepies, choughs and nutcrackers have also been credited with intelligence.[1] In particular, the corvids, a casual term for the crow family is known for their enhanced cognitive abilities that rival and sometimes exceed those of primates. The crow has a significantly larger brain compared to other avian species (with the exception of some parrots); in fact, their brain is relatively the same size as the chimpanzee brain.[2] Research has shown that the neurological basis of a corvid's intelligence lies in their nidopallium caudolaterale (discussed below), in addition social, environmental, ancestral and behavioural factors all contribute towards their intelligence. By studying avian cognition in these intelligent species researchers hope to find alternative solutions to the realization of complex cognition. The study of avian cognition not only will progress our understanding of intelligence but will also benefit towards the creation and advancement of artificial intelligence.[3]

The main objectives of this report are to reveal the neurological basis of a corvid's intelligence by a comparison of the corvid's brain and that of a primate's; further reinforced by scientists' experiment and research articles. In addition this report will look at how their social behaviour, ancestry and youth development contribute towards their intelligence. The purpose of this report is to express that there is more to avian cognition than we may think, and to explain that nature has other ways of achieving complex cognition in an entirely different species with different evolutionary origin from the primates.

Mammals and birds shared a common ancestor some 300 million years ago,[4] from that point on they started down their own evolutionary path, and highly intelligent species evolved from both vertebrate classes through convergent evolution.[5] Convergent evolution is when two organisms with different evolutionary origins evolve the same structure or characteristic due to having to adapt to equally challenging environments.[6] The prefrontal cortex (PFC) in mammals is the seat of the so-called executive functions.[7] Executive functions manage cognitive processes such as planning, cognitive flexibility, decision-making, and inhibiting inappropriate actions.[7] Analogous to the prefrontal cortex (PFC) in avian species would be the nidopallium caudolaterale (NCL).[7] These two structures are amazingly similar in that the PFC is densely innervated with dopaminergic fibres (i.e., fibres that facilitate dopamine related activity),[7,8] whereas the NCL is "densely innervated by catecholaminergic fibres of probably dopaminergic nature".[7] Furthermore, dopaminergic innervation is usually taken as a characteristic of the PFC.[7] This provides evidence of the similarity in the two brain structures. Moreover, similarity in their connectivity[7] and lesion studies[9,10] further provide evidence supporting that the PFC and the NCL are functional analogues. Shown in Figure 1 is an illustration of the PFC and the NCL. Note the position of the NCL and PFC; the PFC covers the front part of the frontal lobe, whereas the NCL is at the rear end of the cerebellum. Many studies have pointed out that the non-laminated NCL is able to generate the same executive functions as the PFC; therefore lamination must not be a requirement for higher cognitive functions.[7,12] We can indeed see this in Figure 2, which shows the different arrangements of the nerve cells in the PFC and the NCL.

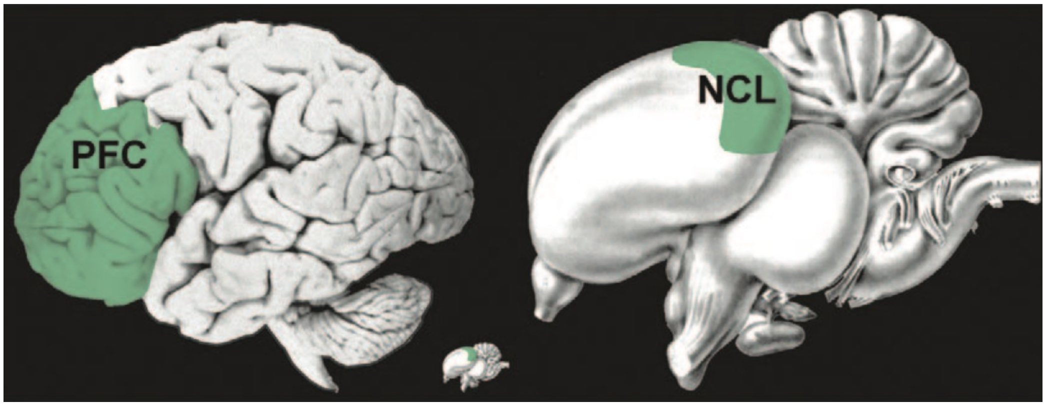

Figure 1. Side view of a human (left) and of a pigeon (right) brain. The prefrontal cortex (PFC) and the nidopallium caudolaterale (NCL) are depicted in green. The smaller brain at the bottom of the figure is the pigeon brain in proper scale to the human brain.[7]

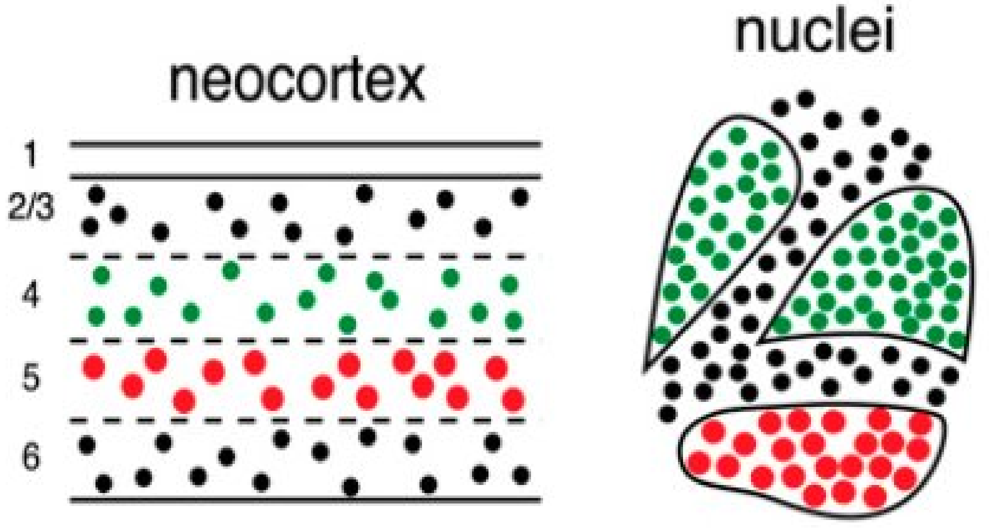

Figure 2. Nerve cells in the mammalian neocortex are highly organized in laminated structures (left), whereas the bird cerebral cortex is organized in a nuclear fashion, clumped together (right).[11] The cerebral cortex is sometimes called the neocortex, because it consists of six layers or six laminae.

The development and behaviour of corvids also need to be considered. Corvids as young birds require bi-parental care and are altricial (meaning they need to be taken care of for a long duration after being hatched). Adult birds have stable social relationships and form monogamous couples over breeding season, both parents take care of the chicks, although the female invests more effort.[13] These birds also show high levels of social tolerance and exchange affinitive behaviours such as preening and regurgitation.[13]

It is known that corvids have innovative foraging techniques, such as making tools, eating novel food, caching (hiding) food for later consumption, etc. Food-caching birds (in the Corvidae family) can also prevent pilferage of their food cache by re-caching to new places when the conspecific is not looking. They are able to cache in over 200 locations and accurately recover their cache.[14] Furthermore, they also know which food items are perishable and thus would attempt to consume these before they decay.[14]

Evidence has shown that corvids are able to take the presence of other birds into account,[2,15] exhibit episodic-like memory (able to recall or remember past events),[2,15,16] flexibly provide for future needs,[2,15] master "elaborate tests of object permanence" (object permanence is the understanding that objects continue to exist even when they are out of sight)[17], and like other songbirds exhibit vocal learning.[18] It is worth pointing out however, that the European magpie (*pica pica*) is the only avian species that can recognize itself in a mirror, demonstrating self-recognition, a trait thought to be associated with humans.[19] Figure 3 (a) shows a magpie with a yellow mark on its neck, if it recognizes itself in the mirror, it would be able to identify the yellow mark as not being part of itself, and attempt to get rid of it. Figure 3 (b) (c) shows the magpie pecking and scratching at the mark in front of a mirror, thus displaying mental recognition of a "self". A few primates (e.g., chimpanzees and orangutans) have also passed the mirror test.[20] These behaviors demonstrate the intelligence of corvids and are closely related to how they have adapted to their ecological niches and successfully colonized almost every environment.

This report will analyze the neurological basis of a corvid's intelligence, where most of the evidence is obtained from an experiment performed by related researchers, then followed by a comparison of the PFC and the NCL and an interpretation of the results. Other factors that contribute towards their intelligence will also be examined.

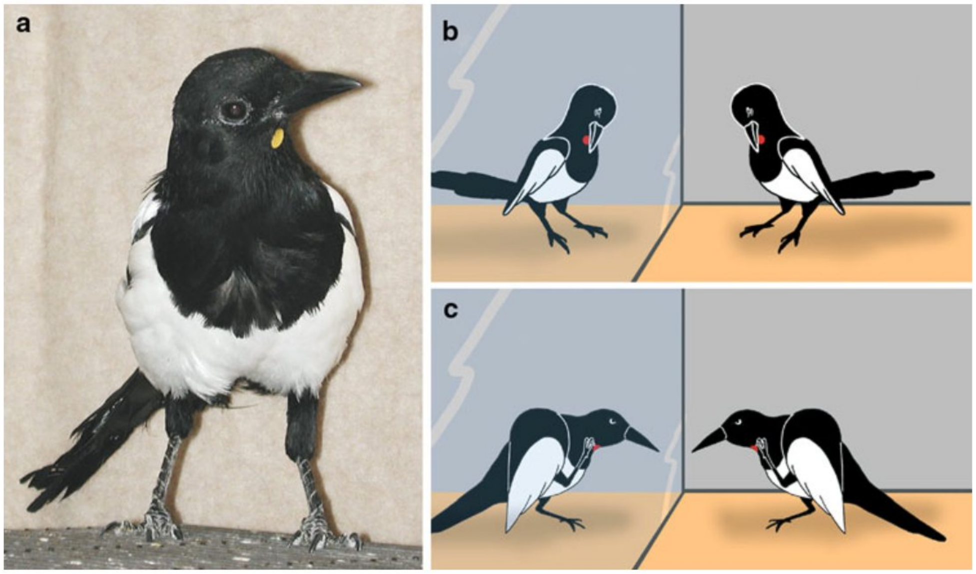

Figure 3. (a) Magpie *pica pica* with yellow mark on throat. (b),(c) Schematic depictions of magpies' attempt to remove marking after seeing its reflection in the mirror.[7]

Neurological basis of a Corvid's intelligence

The Carrion Crow Experiment

Neurobiologists from the University of Tübingen have found the neuronal foundation of corvid cognition to be based on the functions of the nidopallium caudolaterale (NCL).[5] Their findings were published in *Nature Communications* 2013, which demonstrates how corvids' make decisions based on abstracted principles they obtained from the rules of the experiment.

In their experiment two carrion crows (*Corvus corone corone*) were to carry out memory tests on a computer screen, electrodes were implanted in their NCL region and through observation of their neural activity the researchers were able to deduce the functioning's of the NCL and to further testify that the NCL is indeed where the executive functions lay in the avian brain. Figure 4 shows a simple illustration of the structure and steps of the experiment. The memory task consists of two tasks (one rule for each task) that would be completed interchangeably, signified by different cues. The first task was the 'nonmatch task' also called the delayed nonmatch-to-sample task (DNMTS), upon hearing a burst of white noise or seeing a red circle, the crows were to peck at a different image then the sample image they were shown a few moments before. There was always a delay period right before they were required to make a decision or after an image was shown. This allowed the neurons to process the image and forced them to retain the image for later judgement; also allowing the neurons to fire leading to a decision in the crow.

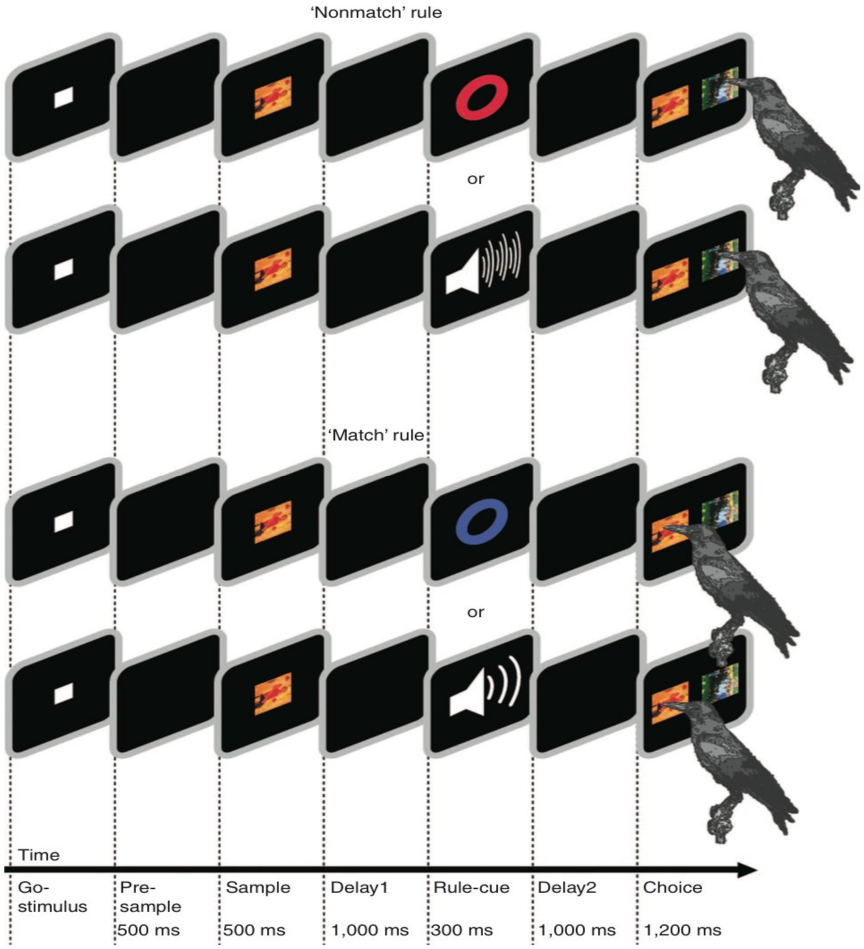

Figure 4. Schematic depiction of crows performing memory task on computer touch screen. The task consists of two rules ('nonmatch rule' and the 'match rule') signified by different cues.[5]

The 'match rule' also called the delayed match-to-sample task (DMTS) required the crows to peck at the image that was identical to the one that was previously shown. The cue would be a blue circle or an auditory upward sweep. The reason for the different sensory modality cues (either visual or auditory) was not to mix up the neural activity stimulated by the rule (i.e., the images) with those stimulated by the cue. Only one cue was presented in each trial and all four cues were used randomly within a session. After completing each trial the crows would receive a reward. Both crows performed correctly above 90% of the time. Figure 5 (a) shows the location at which the electrodes were implanted. In Figure 5 (c) we see the NCL region clearly; the NC is the nidopallium caudale.

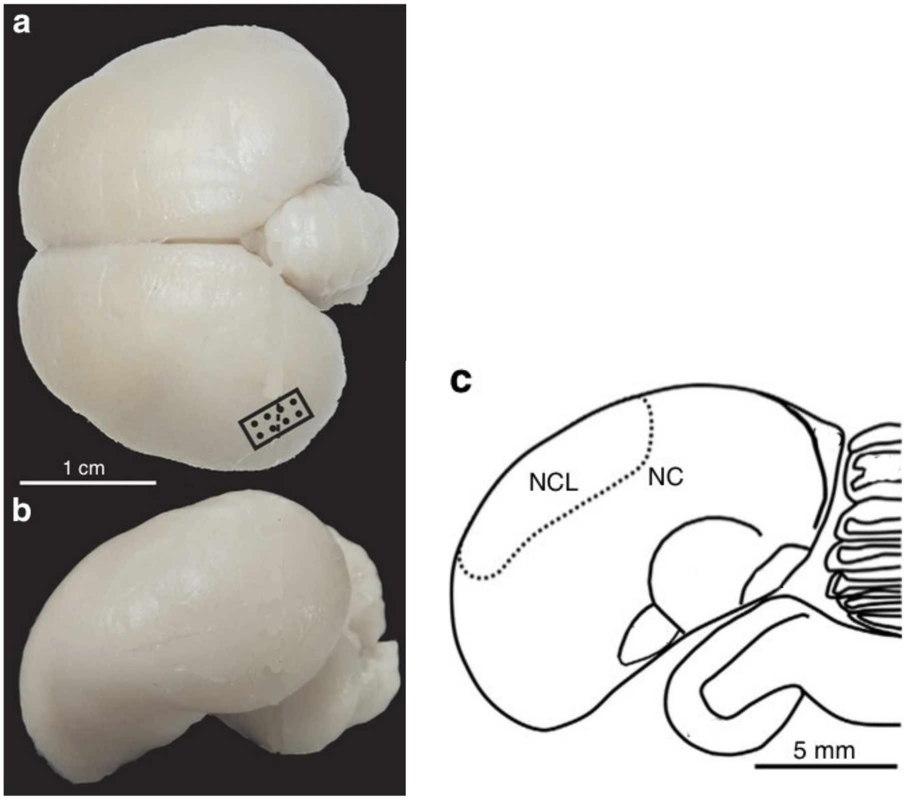

Figure 5. (a) Dorsal and (b) lateral view of the crow's brain. The dots in **a** represent penetration sites of the eight electrodes (2×4 grid) (c) Coronal section through the brain of a carrion crow illustrating the borders of the NCL in the caudal telencephalon.[5]

The neural responses of the corvids can be seen in Figure 6, at the beginning of the Delay2 period, there was a strong sensory influence by the cue modality, shown by the grey line shooting upwards. By the end of the Delay2 period, the abstract behavioural rule (green line) was the strongest variable responsible for the variance in firing rates. This demonstrates that the neurons in the NCL were successful at sustaining the rule information until a behavioural choice was required. Figure 7 shows that 15% of all neurons recorded from the NCL encoded only the abstract rule. An additional 5% of all neurons exhibited other main factors in addition to the behavioural rule. These 20% of the neurons are responsible for abstracting over the different sample images and different cues. The rest of the neurons were either ‘match’ cells or ‘non-match’ cells, cells that preferred one of the two rules. The crows were able to switch between the match and non-match rules and abstract the different sample images and different sensory rule cues. This demonstrates the cognitive flexibility of crows to go beyond “fixed stimulus-response associations” and to choose between strategies according to rules, which are characteristic of executive functions.[5] In fact, this function of the NCL is very similar to the functions of the prefrontal cortex (PFC) in mammals.[7,18]

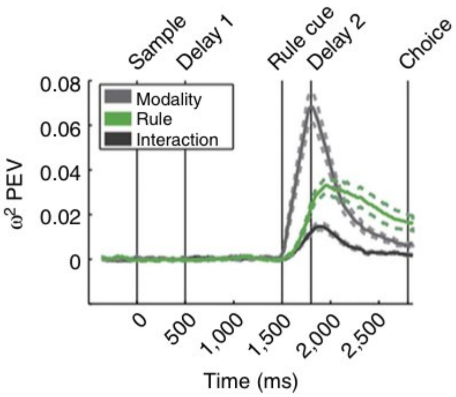

Figure 6. The different firing rates of the neurons in different time periods. Vertical lines mark transitions between task periods.[5]

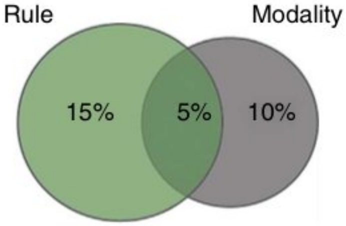

Figure 7. The results of a three-way analysis of variance (ANOVA) with the factors ‘sample picture’, ‘cue modality’ and ‘behavioural rule’.[5]

A similar experiment (there was also a ‘match’ and ‘nonmatch’ rule) was carried out on monkeys, but instead of testing the neural basis of the NCL, it was the PFC in monkeys.[18] The same conclusion was reached in the experiment with monkeys, stating that the PFC was crucial in abstracting general principles, and allows for the cognitive flexibility and adaptability of the individual, which is central to intelligent behaviour.[18] The activity of NCL neurons can be compared directly with neurons in the PFC of primates, which was proposed as the functional analogue of the avian NCL.[18] In addition, a similar proportion of neurons in both monkeys and crows (~20%) encoded the abstract rule.[5,18]

Comparison of the Prefrontal Cortex (PFC) and the Nidopallium Caudolaterale (NCL)

This section will compare and analyze the two brain structures (the PFC and the NCL) and conclude on what information can be obtained by this comparative brain analysis about the intelligence of corvids. Research done by neurobiologist Lena Veit *et al* have shown that NCL neurons are responsible for a corvids' visual working memory, where it serves to bridge delay periods (gaps in between being stimulated and making a decision), thereby offering a workspace for processing the stimulatory visual information.[8] Another notable similarity between the two structures is the dopaminergic innervation, the PFC and the NCL both are densely supplied with fibres containing the neurotransmitter dopamine.[7,8] The neuroarchitecture and connectivity of the PFC is also shown to be similar to the NCL.[7] There is a slight difference in the brain connectivity of the two ("the dopaminergic input onto GABAergic interneurons")[7] and the arrangement of the nerve cells (the PFC being laminated and the NCL being nuclear).[7] Aside from these differences, the PFC of mammals and the NCL in birds are surprisingly similar in function and neuroarchitecture.

It has been proposed many times and confirmed by many researchers that this similarity is due to convergent evolution (homoplasy).[2,5,7,8,12] Where natural selective pressures have forced the two species to evolve this common structure. The non-laminated avian NCL is able to generate the same executive functions as the mammalian PFC; therefore lamination must not be a requirement for higher cognitive functions.[7,12] Furthermore, it can be hypothesized that since the anatomical and neurochemical conditions of the NCL and the PFC are virtually identical, there must be a limited solution for the realization of higher cognitive functions.[7] The freedom to create different neural structures that generate the same executive/cognitive functions seem to be very restricted.[7] As a result, the selective pressure for complex cognitive functions probably caused the convergent evolution of the highly similar forebrain structures in the primates and corvids.[7] This is why corvids have such outstanding cognitive abilities that rival and sometimes exceed those of primates.

To be comprehensive, lesion studies done by researchers on the NCL of pigeons yielded the same result as those done on primates.[21] Lesions in the pigeon NCL caused deficits in delayed alternation, visual working memory and reversal learning in pigeons, which is comparable with the dysfunctions after damage to the PFC.[21] Delayed alternation allows the assessment of spatial working memory, usually in a T or Y maze.[23] Figure 8 shows a Y-maze; in the first trial an animal is placed at one end of the start arm and has to choose between the two other arms that are baited.[23] Once the animal makes its choice, it is removed and after a delay period is placed back into the start arm.[23] In the second trial the baited arm is now the opposite arm of the animals first choosing, and the animal has to make a different choice in order to obtain the reward.[23] It is worthy to note however that after NCL ablation there were no visual discrimination deficits (i.e., they had no trouble distinguishing between two objects).[21,22] Evidence provided from the lesion studies yet again confirms the significance of the NCL, as well as its relationship with the PFC—functional analogous via convergent evolution.

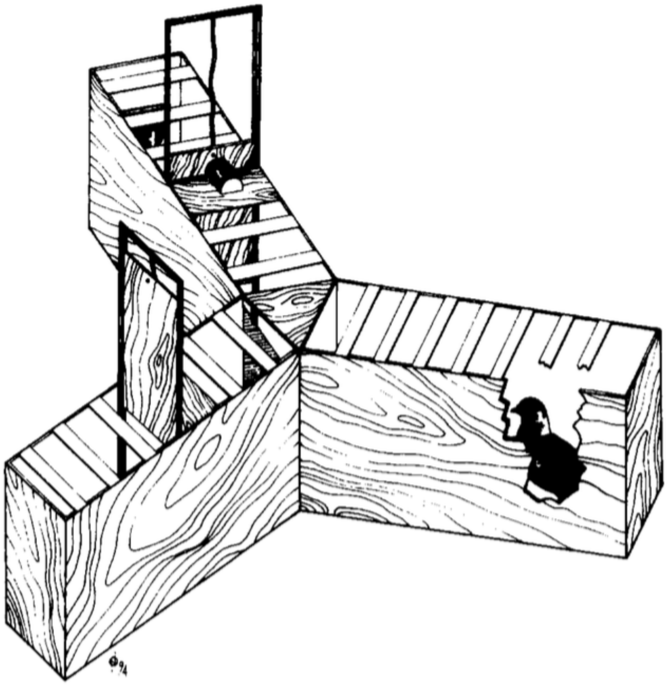

Figure 8. An artist's depiction of the Y-maze for the delayed alternation task.[22]

Other contributors to a Corvid's intelligence

The natural selective forces that have been suggested to shape brain size evolution mostly emphasize the need for enhanced cognition in three main contexts: foraging, parental care and social relationships.[24]

Foraging techniques

It is important to note that larger neural centers allow some animals to be more flexible than others in their foraging techniques, along with an increase in innovation.

Ravens, scrub jays, nutcrackers and many others have been shown to hide food or cache food for later consumption.[2,14~16] Recent experiments with caching corvids have provided evidence for episodic-like memory, future planning and possibly mental attribution, and demonstrating theory of mind, all cognitive abilities that were thought to be unique to humans.[16] Theory of mind (ToM) refers to the ability to attribute other individuals with mental states (e.g., beliefs and desires) in order to understand and predict their behaviour.[15] These remarkable cognitively demanding behaviours support Overington and his colleague's hypotheses: larger-brained species perform a wider variety of innovative behaviour.

The adaptive specialization hypothesis, predicts that food-cachers should have larger hippocampal volumes, relative to overall brain size, than non-cachers.[25] The hippocampus is involved in functions other than spatial memory and it has been suggested that the hippocampal formation might serve both spatial and episodic memory.[25] Comparative analyses done by Selvino and Nicola confirm that food-caching species have relative larger hippocampal volumes than non-cachers. The reason might be that they have to remember the location of their cache and the nature of the cached food (i.e., whether it is perishable or not). In addition, they may cache in hundreds of locations, and would have to remember roughly in which region to retrieve their cache. Furthermore, by phylogenetic reconstruction, the two researchers discovered that the common ancestor of the corvids was a moderate cacher. Therefore, it seems likely that all extant corvid species evolved from an ancestor that showed the basic adaptations to caching. These evidence show that large brain size might enhance survival in nature. Moreover Lefebvre and Sol suggested that environmental change might be a key factor in the evolution of enlarged brains.[24] More importantly, studies lead by Knud and others have demonstrated that large brains had already evolved in the ancestor of crows, leading to a generally high cognitive ability to deal with new challenges for crows and other corvid lineages.[26] These evidence can now explain the success of the corvid ancestors in colonizing and adapting to new environments as well as their success in overcoming challenges such as unpredictable food sources and unknown predators.

Parental Care

Corvids require long periods of parental care The social brain hypothesis suggests that individuals living in social groups with complex interactions have bigger brains in order to manage social relationships.[27] Shultz and Dunbar found that relative brain size in birds is strongly related to bi-parental care, pair bonding, stable social relationships and altricial development. Many corvids form stable monogamous couples over breeding seasons and both parents take care of the chicks, although females invest more effort.[13]

Social Relationships

Corvids form complex relationships with other conspecifics, they also exchange affinitive behaviours such as preening and regurgitation.[13] Corvids (especially the Western Scrub Jay) are known to mourn over their dead.[28] Once discovering a dead conspecific, the scrub jay will vocalize and alert others. Many more scrub jays will gather around and result in a “cacophonous aggregation”.[28] Their behaviour is speculated to be potentially communicating risks with conspecifics. Their social communications with each other are quite effective from this example and demonstrate their cooperative spirit. They work together to reduce the risks to conspecifics. These behaviours strongly suggest that corvids have the cognitive abilities to manage a complex social relationship.

Figure 9 shows a good summary of the traits of intelligence animals. Note that all five species have a relatively complex social system, with interactions and cooperation with each other. Furthermore, the figure also shows innovative tool use among these species, such as stick use by New Caledonian crows, wood-tool aid to opening palm nuts in hyacinth macaws, termite fishing in chimpanzees, sponge-tool use by dolphins and fly switching by elephants. Underlying all of these similarities is behavioural flexibility as applied to solution of problems faced by living in an unpredictable environment. As Van Horik and colleagues pointed out, those species with a varied and unpredictable diet, that lived in a complex (not necessarily large) society, that had a relatively large brain, went through a long developmental period, lived a long life, and lived in a fluctuating habitat, could all be candidates for convergent evolution.[6]

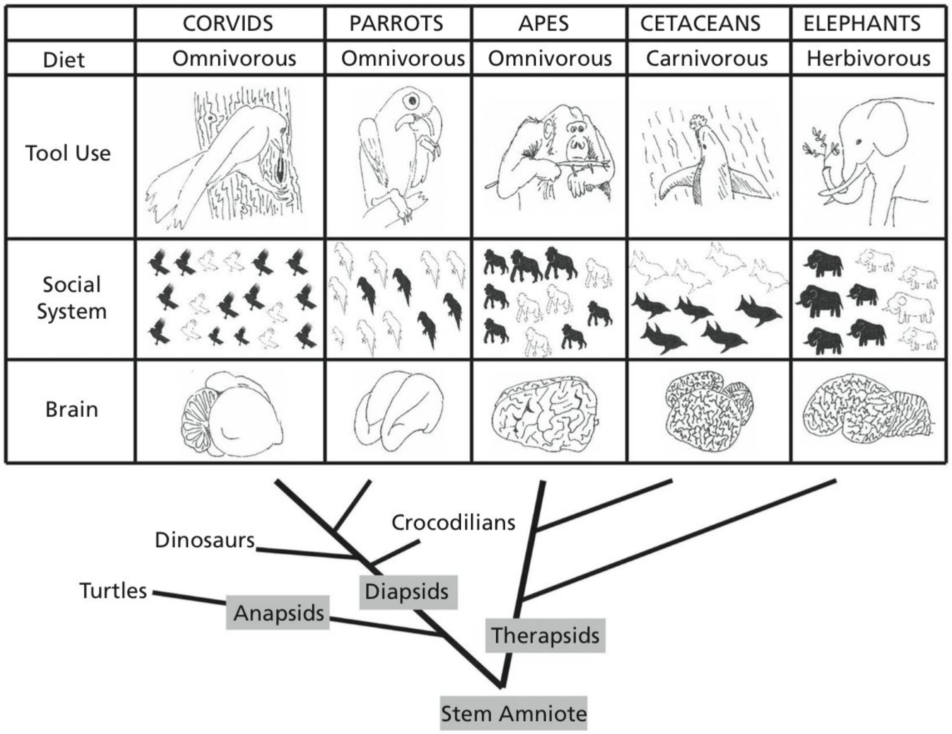

Figure 9. The common characteristics of big-brained animals and their evolutionary relationships.[6]

Conclusion

The intelligence of corvids cannot be questioned, as it has been demonstrated their remarkable behaviours such as caching over 200 food items and accurately recovering their cache, preventing pilferage by using theory of mind, manufacturing innovative tools, recognizing one-self in the mirror, etc. Researchers have found the neurological basis of their intelligence, namely the nidopallium caudolaterale (NCL), which plays a key role in the abstraction of general principles, mirroring the functions of the PFC in mammals. The amazing similarity in neuroarchitecture and anatomy in these two brain structures of two distantly related species of different evolutionary origin strongly suggests that corvids and primates have convergently evolved this common structure, as there is only a limited solution for the realization of higher cognitive functions. In addition, lamination was not required for achieving higher cognition, as the nuclear avian NCL had almost the same functions as a primate PFC.

The natural selection forces that have been suggested to shape brain size evolution mostly emphasize the need for enhanced cognition in three main contexts: foraging, parental care and social relationships. Corvids have innovative behaviours such as eating novel foods and using tools. They are altricial and require long periods of parental care; they are also capable of managing complex social relationships. Most importantly, research has shown that the ancestors of corvids had already evolved large brains and were moderate cachers. The novel environments further stimulated them and caused their independent evolutionary path to converge with the cognitive structures of the primates.

Ultimately, what drove the corvids to ecological domination and success was their intelligence. Convergent evolution has allowed them to overcome the challenges in their environments and converge intellectually towards primates, resulting in similar brain structures (the PFC and the NCL) that would permit complex cognition. The ability to adapt to a changing environment is perhaps the best explanation as to why corvids have the complex cognitive abilities they do and have convergently evolved their remarkable avian brains that are so similar to primates.

References

1. Dos Anjos L: Family Corvidae (Crows). Handbook of the Birds of the World Bush-shrikes to Old World Sparrows 14:494–641.
2. Emery J. Nathan, Clayton S. Nicola. 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. Science New Series 306(5703):1903-1907.
3. Jessica Lindblom. Sept 2001. Social situatedness of natural and artificial intelligence. (Master's thesis). Retrieved from: http://www.diva-portal.org/smash/get/diva2:3017/FULLTEXT02
4. Evans, S. E. in Evolutionary Developmental Biology of the Cerebral Cortex. (eds Bock, G. & Cardew, G.) 109–113 (John Wiley & Sons, ltd., 2000).
5. Veit Lena and Nieder Andreas. 2013. Abstract rule neurons in the endbrain support intelligent behaviour in corvid songbirds. Nature communications
6. Van Horik O. Jayden, Clayton S. Nicola and Emery J. Nathan. 2011. Convergent evolution of cognition in corvids, apes and other animals.
7. Güntürkün Onur. 2005. The avian 'prefrontal cortex' and cognition. Current Opinion in Neurobiology 15:686-693.
8. Veit Lena, Hartmann Konstantin and Nieder Andreas. 2014. Neuronal correlates of visual working memory in the corvid endbrain. The journal of neuroscience 34(23):7778-7786.
9. Gagliardo Anna, Bonadonna Francesco and Divac Ivan. 1995. Behavioural effects of ablations of the presumed 'prefrontal cortex' or the corticoid in pigeons. Behavioural Brain Research 78:155-162.
10. Mogensen J, Divac I (1993) Behavioural effects of ablation of the pigeon-equivalent of the mammalian prefrontal cortex. Behavioural Brain Research 55:101– 107.
11. Dugas-Ford Jennifer, Rowell J. Joanna and Ragsdale W. Clifton. Cell type homologies and the origins of the neocortex. PNAS 109(42):16974-16979.
12. Güntürkün Onur. 2011. The convergent evolution of neural substrates for cognition. Psychological Research 76:212-219.
13. Emery J. Nathan *et al* 2007. Cognitive adaptations of social bonding in birds. Phil Trans. R. Soc. B 362:489-505.
14. Clayton Nicky, Emery Nathan and Dickinson Anthony. 2006.The rationality of animal memory: Complex-caching strategies of western scrub jays. Rational Animals? (Book):197-216.
15. Dally M. Joanna, Emery J. Nathan and Clayton S. Nicola 2010. Avian Theory of Mind and counter espionage by food-caching western scrub-jays (*Aphelocoma californica)* European journal of developmental psychology 7(1):17-37.
16. Grodzinski Uri and Clayton S. Nicola 2010. Problems faced by food-caching corvids and the evolution of cognitive solutions. Philosophical Transactions of the Royal Society 365:977-987.
17. Zucca, P., Milos, N. & Vallortigara, G. Piagetian object permanence and its development in Eurasian jays (Garrulus glandarius). Anim. Cogn. 10, 243–258 (2007).

18. Wallis D. Jonathan, Anderson C. Kathleen and Miller K. Earl. 2001. Single neurons in prefrontal cortex encode abstract rules. Nature letters 411:953-956.
19. Prior Helmut, Schwarz Ariane and Güntürkün Onur. 2008. Mirror-induced behaviour in the magpie (pica pica): evidence of self-recognition. PLoS Biology 6(8):1642-1650.
20. Povinelli J. Daniel, Rulf B. Alyssa, Landau R. Keli and Bierschwale T. Donna. 1993.Self-Recognition in Chimpanzees (*Pan troglodytes*): Distribution, ontogeny, and patterns of emergence. Journal of comparative psychology. 107(4):347-372.
21. Hartmann Beate and Güntürkün Onur. 1997. Selective deficits in reversal learning after neostriatum caudolaterale lesions in pigeons: possible behavioural equivalencies to the mammalian prefrontal system. Behavioural Brain Research 96:125-133.
22. Gagliardo Anna, Bonadonna Francesco and Divac Ivan. 1995. Behavioural effects of ablations of the presumed ‘prefrontal cortex’ or the corticoid in pigeons. Behavioural Brain Research 78:155-162.
23. Delayed alternation task [Internet]. 2013. Panlab, Harvard Apparatus. Available from: http://www.panlab.com/en/tests-solutions/delayed-alternation-task
24. Lefebvre Louis and Sol Daniel 2008. Brains, lifestyles and cognition: are there general trends? Brain, Behaviour and evolution 72:135-144.
25. De Kort R. Selvino and Clayton S. Nicola. 2005. Evolutionary perspective on caching by corvids. Proc. R. Soc. B 273:417-423.
26. Jønsson A. Knud *et al* 2010. Major global radiation of corvoid birds originated in the proto-Papuan archipelago. PNAS 108(6)2328-2333.
27. Péron F., Rat-Fischer L., Lalot M., Bovet D. Cooperative problem solving in African grey parrots. 2011 Anim Cogn 14:545-553.
28. Iglesias T.L., McElreath R. and Patricelli G.L. 2012. Western scrub-jay funerals: cacophonous aggregations in response to dead conspecifics. Animal behaviour 84:1103-1111.