Corvid Cognition In Terms Of Working Memory and Reasoning

Ansley Smoll

Abstract

Despite the drastic anatomical difference between primate and corvid brains, the animals share many similarities (and often rival each other in skill) when it comes to cognitive capabilities and behaviors. Corvids have repeatedly displayed signs of advanced cognitive ability once believed to only have existed in primates such as monkeys and apes, and are considered the problem solvers of the avian world. Corvids are renowned for their ability to perform delayed-response tasks (which indicates a high capacity for working memory, similar to that of primates). Corvids have also shown. In addition, when tested on trap-tube and trap-table paradigms corvids show causal and analogical reasoning, often beyond the ability of their primate counterparts. These primate-like abilities stem from the nidopallium caudolaterale, a part of the corvid brain that is functionally (if not structurally) similar to the prefrontal cortex found in primates. Here we review the similarities in cognitive capability between corvids and primates, using the indicators of working memory and causal/analogical reasoning. This information could help us better understand exactly how human-level cognition came to be, and how similar to us our non-primate relatives really are.

Introduction

Throughout history, people have watched corvids (a family of birds that contains crows, ravens, rooks, magpies, jackdaws, jays, treepies, choughs, and nutcrackers) with fascination, interest, and at times fear. Their problem solving skills, tool usage, and ability to remember faces and hold grudges have led to wide speculation about how these birds are so intelligent. Many different cultures sought to understand the behavior of the corvid, believing them to be supernatural beings connected to gods or witchcraft. They saw crows and ravens as (often trickster) gods and deities, much of the time taking pleasure in stealing from humans and bringing death where they went. For example, in Norse mythology, Odin relied on two ravens to fly through the nine worlds, spying and bringing him news. Ravens also were the inspiration/etymological root for the angelic figures known as Valkyries, who were able to predict deaths (Savage, 2015, pg. 18). During the witch craze in Western Europe, corvids were even widely regarded as signs of witchcraft or the physical manifestations of demons (Savage, 2015, pg. 19).

At the time, this was how different people understood corvid behavior. These behaviors included stealing trinkets, problem solving, and tool use beyond what was considered possible for a bird, forming strange bonds with humans, and others. Now, as we learn more about corvids with modern techniques, our understanding of these traits are not rooted in the supernatural, but of enhanced cognitive abilities beyond that of other birds. In fact, corvids are among the few non-primate organisms on Earth considered to have a high cognitive capability. Cognitive capability can in part be measured in terms of working memory and reasoning. Working memory and reasoning are connected due to the importance of a high working memory capacity for better reasoning skills. Without a large working memory capacity, the animal will not be able to retain enough information at any given time in order to have higher levels of reasoning. Because of the observed behavior of corvids in the wild, it can be hypothesized that these birds possess a working memory capacity and reasoning skills superior to other birds. In this paper, the cognitive capability of corvids will be investigated, as well as their cognitive capability, as defined by working memory and reasoning, with that of primates. I will discuss significant research advancements in uncovering mechanisms driving corvids' cognitive ability and draw attention to areas where gaps in knowledge still lie. Lastly, I will comment on what research on the remarkable intelligence of these birds means for the scientific community, and the understanding of cognition as a whole.

Cognitive Ability as Working Memory

One way to test a facet of cognitive ability is through tasks surrounding working memory. Working memory refers to the ability to process and maintain information that is no longer present in the environment for use in ongoing cognition, and can be measured by both accuracy and capacity. Working memory capacity is defined as the number of items or chunks of information the subject can hold in their working memory at one time (Cowan, 2014). This has been extensively studied in corvids such as the crow, revealing a WM (working memory) capacity comparable to that of some species of primates (Balakhonov & Rose, 2017). This level of working memory capacity allows corvids to succeed at tasks involving manipulation of information after the source of the information (in many cases, a sensory stimulus) has already disappeared, and lends itself to their impressive ability to reason (Cowan, 2014).

Working memory is a core component of cognition that is critical for planning, decision making, reasoning, and other related tasks. It is well established that working memory is not a passive storage, but that it requires active maintenance of information. Consequentially, working memory is not only vulnerable to distraction but also limited in duration and in capacity. It is actually estimated that healthy humans can maintain about three to five items in working memory. Capacity-limitation is a critical dampener on cognition, and has in fact been termed the "bandwidth of cognition" (Balakhonov & Rose, 2017;Wilhelm et al., 2013).

Working memory is maintained through the use of top-down control (the use of background knowledge and expectations to interpret new stimuli) (Fongaro & Rose, 2020). This control requires attention, and can occur in two different ways. Firstly, prior knowledge of what information is important can act as a gatekeeper, filtering out irrelevant stimuli so that only the important information is encoded into working memory. This process, however, relies on prior knowledge about the relevance of upcoming events, or 'pre-cues'. When that is not present, this type of filtering cannot work. The second way working memory is maintained is through the use 'retro-cues'. Retro-cues are information about what stimuli are important involved with the manipulation of working memory after the information has already been encoded (during the maintenance period). These two types of cues are together used to control working memory, keeping it accurate and working around its limited capacity (Awh, E., Vogel, E. K., & Oh, S. H., 2006).

Testing Working Memory in Corvids

There are multiple ways to test working memory capacity in humans, but in animals (which are incapable of speaking and completing many other tasks), options are limited. One such way to observe and test working memory in animals is by the use of change-detecting delayed-response tasks (Fongaro & Rose, 2020). During these tasks, the animals are required to acquire and maintain information about a stimulus or group of stimuli, before waiting momentarily until they are shown another stimulus/group of stimuli (often with a minor difference). They then must indicate if the new stimuli are the same, and which one has changed (if one has). This task has been studied in the context of both auditory and visual stimuli.

Working Memory Capacity

One way in which scientists can probe working memory capabilities on a change-detecting delayed-response paradigm is through adding pre and retro cues. This tests the animal's ability to control working memory (in relation to pre and retro-cues) before and after stimulus encoding, and is designed to explore the degree of control corvids have over their working memory (an important facet of working memory and cognitive capability). In such studies, the animals are tested on a change-detecting delayed-response paradigm, with and without cues (both pre and retro), and the results compared.

Even without pre and retro-cues, crows are capable of completing change-detecting delayed-response working memory tasks. Crows are able to perform the task at up to 6 items, but generally do best at 4 items, aligning with their estimated working memory capacity of 4 chunks (Balakhonov & Rose, 2017;Fongaro & Rose, 2020). However, when cues are added in, the crows' performances elevate substantially (Fongaro & Rose, 2020). The integration of both types of cues lead to an increase in working memory performance, much like in humans and some previously tested primates. This suggests that corvids are able to use cues to control working memory both before and after stimulus encoding.

The importance of this use of cues is that it shows that crows are truly using working memory in these tasks, not a different form of visual short-term memory which mimics working memory. The consistent results of such studies suggest that corvids are able to use a primate-like capacity and control over working memory to navigate the world and solve simple problems (Veit & Nieder, 2013). This is remarkable, given that many other animals have lower levels of working memory, and for a time, it was widely thought that animals did not posses the ability to manipulate working memory at all.

Similar working memory change-detecting delayed-response task studies have been performed several times on corvids, with extremely similar results (Veit & Nieder, 2013). Besides visual working memory, crows also display categorical auditory working memory, and are able to group novel audio cues into categories with sharp category boundaries (Wagener & Nieder, 2020). Perceptual categorization enables animals to group stimuli based on their sensory features, and contributes to the formation of concepts later for reasoning tasks (Pusch et al., 2022). This is similar to their ability to identify and categorize visual stimuli in relation to working memory. This proficiency with auditory working memory likely stems from their need to recognize, remember, and process auditory cues as a member of the songbird family.

Corvid vs Primate Working Memory

While corvids and primates have demonstrated similar working memory capacities, the influence of capacity on their working memory performance differs. As previously mentioned, primate working memory has been extensively studied and a growing body of literature is focusing on these same areas in corvids. When corvid and primate working memory is compared, scientists find that they overall share a working memory capacity of 4 items (Balakhonov & Rose, 2017). However, corvids and primates, despite having a similar working memory capacity, do have some differences when it comes to their cognitive ability. One way this is apparent is through their performance in relation to capacity. Crows generally have a slightly higher performance below capacity than rhesus monkeys, but after they exceed capacity, crow's performances drop faster than the rhesus monkeys'. In addition, crows' performances are more dependent on the number of items presented on the opposite side as (contralateral to) the target than monkeys' performances are (Balakhonov & Rose, 2017).

Neural Mechanisms of Corvid and Primate Working Memory

Overall, corvids and primates have similar cognitive abilities when seen through the lens of working memory tasks. They have a similar working memory capacity, with a few differences in their performance in relation to whether they are below or above their capacity. However (despite their similarity in relation to capacity) the area of primates and corvids' brains related to working memory are very different structurally (Colombo, 2019).

Corvids and primates have managed to gain similar working memory capabilities through convergent evolution. In primates, neurons in the prefrontal cortex (PFC) are responsible for working memory. Corvids, however, lack a prefrontal cortex. The PFC had, for a long time, been thought of as the most important part of the brain for higher level cognition. However, corvids (and some other animals) are able to display higher level cognition even without a PFC. Instead, studies have found that working memory in corvids occurs in a part of the corvid endbrain called the nidopallium caudolaterale, or "NCL" (Veit & Nieder, 2013;Rinnert et al., 2019). These are two very physically different structures, which makes their similar functioning (and even similar neural mechanisms related to working memory) even more remarkable of a feat.

In birds, rather than the neurons being arranged in layers (as they are in mammals and therefore primates), they are arranged in clusters. Despite a completely different neural architecture, the level of cognition supported by the avian brain is the same as in the primate brain (Colombo, 2019;Olkowicz et al., 2016). Neurons in the NCL are specialized to respond to certain stimuli/scenarios. These neurons can be divided into two general categories: cue-selective and delay-selective. Cue-selective neurons see an increase in firing rate when presented with a stimulus, then return to baseline activity when the stimulus disappears. Delay-selective neurons only see an increase in firing rate after the stimulus has disappeared, and do not return to baseline until the animal is done with the working memory task (Rinnert et al., 2019). In addition, different delay and cue-selective neurons respond to stimuli in different places in the visual hemifeild. These location-selective neurons are evenly distributed throughout the visual hemifeild, so that working memory performance remains the same wherever the stimulus is in the bird's field of vision (Rinnert et al., 2019).

Delay-selective neurons can further be categorized into storage units and response-preparation units. Storage units are responsible for maintaining information over periods of time, while response-preparation units see an increase in activity right before the animal uses the information to respond to the stimulus. Only a small amount of delay-selective neurons see a notable increase in activity right before a response, with nearly all of them categorized as storage units (Rinnert et al., 2019). This high percentage of neurons behaving as delay-selective storage units likely is what attributes to the corvid's primate-like working memory capacity. Their primate-like (and even human-like) level of working memory supports and explains the impressive cognitive ability of crows, given the connection between working memory and performance on tasks related to cognition, memory, and problem solving (Veit & Nieder, 2013;Awh, E., Vogel, E. K., & Oh, S. H., 2006).

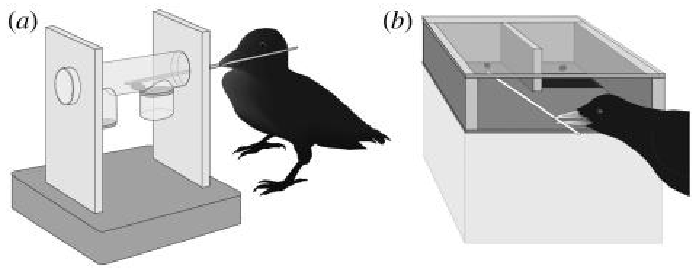
Cognitive Ability as Reasoning

Reasoning is defined as the process of using available information and known facts to create logical assumptions about the world. Because of this, the ability to reason is an important part of cognitive capability. The better an animal's reasoning skills, the greater ability they have to understand the world, and the better their cognitive ability. Corvids (and crows in particular) show evidence of strong reasoning skills. This is demonstrated whenever a corvid in the wild uses a tool, tricks another animal, or avoids a trap, all actions that require some form of reasoning. Interestingly, until recently, not much was known about corvid reasoning abilities outside of anecdotal evidence, with many more studies focused on the reasoning abilities of primates or mice and rats. However, this growing body of literature illustrates that corvids display remarkable reasoning skills in controlled lab environments.

Reasoning can be broken down into many different categories, two of which are causal reasoning and analogical reasoning. Crows manage to grasp both of these concepts. Causal reasoning is what many think of when they think of reasoning; It consists of identifying causality (for example: A causes B causes C, therefore A causes C), and applying that reasoning to a broad range of scenarios by using an observed feature (A is present) to make a generalization (C will be present) not relying on other arbitrary features to make generalizations (F was present last time, F is not present this time). Analogical reasoning builds on this concept, using analogies (understandings and comparisons between two things) to make sense of similar concepts. Analogical reasoning is widely thought of as an exclusively human way of thinking, but recent studies have shown that corvids have the ability to analogically reason. Their apparent ability to reason adds to their cognitive similarity to primates, and is another display of cognitive ability from these birds.

Testing Reasoning Skills in Corvids

In non-human animals, the standard way to test for causal and analogical reasoning skills is the use of the trap-tube task. In this task an animal must extract a piece of food from a horizontal tube by moving the food in a direction that avoids a trap. The trap-tube contains two causally relevant features: the hole and the trap base. The hole is relevant because objects only move horizontally along continuous surfaces, and would fall in the hole if moved in that direction. The trap base is relevant because objects cannot move through barriers (the trap base would block access to the food). The animal's ability to reason is inferred from their performance when different associative features are shifted. This is called "triangulation" (Taylor et al., 2009). Animals first learn an initial task and are then presented with transfer tasks. In the transfer tasks arbitrary (non-causally relevant) stimuli are changed, while the causal structure of the problem is kept constant. Successful performance across transfer tasks eliminates the use of associative cues and suggests the use of causal (instead of associative) reasoning. An alternative paradigm used to test causal understanding in animals is the trap-table task. In this task a subject must choose between raking in a reward behind a trap and raking in one on a flat surface without a trap.



(Figure 1) Drawing of two example experimental apparatuses. (a) A trap-tube. (b) A trap-table (Taylor et al., 2009).

Trap-tube and trap-table tasks

When tested using these trap-tube and trap-table paradigms, corvids show evidence for causal reasoning. In one such study three of the six tested crows succeeded on the trap-tube tasks, and showed evidence of either causal reasoning, or several associative rules (Taylor et al., 2009). The structure of this study was partially based off of a previous experiment concerning causal reasoning in rooks, another species of corvid. Rooks also showed signs of causal reasoning, although not as strongly as crows. In one trap-tube study, seven out of eight tested rooks were able to solve an trap-tube task, but had more varied results on the several following transfer tasks (Seed et al., 2006).

In the study by Taylor et al. 2009 to test whether the crows were using causal reasoning or associative rules to solve the trap-tubes, the birds were then presented with a trap-table task. The crows had to choose between using the tool to pull a meat block behind a rectangular trap (leading to failure) and to pull one resting on a continuous wooden surface (leading to success). The table was visually distinct from the tube in nearly every way, so it was unlikely the crows could use any associative rules learned from the previous trap-tube tasks. Successful transfer would instead indicate that analogical reasoning based on causal relations had been used to solve the task (Taylor et al., 2009).

Three out of the six crows originally tested succeeded on the trap-tube tasks. Of those successful crows, all three of them solved the trap-table task. The three crows also made the correct choice on their first trial. The performance in this task ruled out the use of two independent associative rules during the trap-tube tasks. In case success was due to a prior disposition to avoid holes, the crows that failed the initial trap-tube on the trap-table task were also tested. All three of these crows failed in the trap-table task, indicating that they did not have such a disposition, and that the three crows who succeeded really were using causal/analogical reasoning (Taylor et al., 2009).

Testing analogical reasoning in corvids

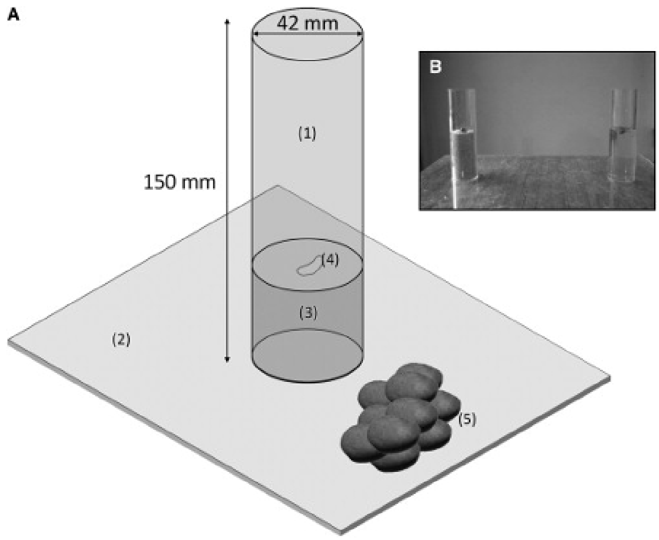
Analogical reasoning is often thought of as an uniquely human concept. However, there is evidence towards corvids using analogical reasoning to solve problems. One way to test analogical reasoning is by relational matching-to-sample tasks. In relational matching-to-sample (or RMTS) tasks, the choice of test pair BB would be correct if the sample pair were AA, whereas choice of test pair EF would be correct if the sample pair were CD. Critically, no items in the correct test pair physically match items in the sample pair, and only relational “sameness” or “differentness” is available to support accurate choice responding (Smirnova et al., 2014).

When tested on RMTS tasks, crows perform well, and exhibit highly accurate choices, even on novel categories that they were untrained for. The crows exhibited discriminative relational matching that was just as robust as their identity matching. Although physical identity could have guided the crows’ choice behavior on IMTS trials, this would not have been possible on RMTS trials, as no physical matches were possible between the sample pairs and the correct test pairs. These results suggest without relying on physical identity, crows are able to exhibit analogical reasoning (Smirnova et al., 2014).

Not only crows show this sort of analogical reasoning. Clark’s nutcracker’s (another species of corvid) displayed full concept learning at somewhere between set sizes of 64 to 128 items, similar to full concept learning by rhesus monkeys (Wright et al., 2016). When tested, black-billed magpies also performed well on same-different abstract matching tasks. Their performance was in fact equivalent to that of Clark’s nutcrackers, and better than that of pigeons, who required a somewhat larger training set (Wright et al., 2017).

Tool use

Tool use is a very unique and interesting corvid behavior, and is likely tied to their strong causal and analogical reasoning abilities. One of the most iconic examples of tool use in corvids is Aesop’s Fable (Jelbert et al., 2014). In this tale, a crow is said to drop stones in a pitcher of water, raising the water level until it is high enough to drink from. Though this is a fable, it is based in truth. When tested in a lab environment, crows and rooks would drop stones into a cylinder of water, raising the water level to reach a piece of food floating on the top (Bird & Emery, 2009). These birds would also choose to drop larger stones as opposed to smaller stones, heavy objects as opposed to light objects, and solid objects as opposed to hollow objects, tying into their causal reasoning skills. They were able to identify that it was not only stones/objects that caused the water level to raise, but the size and physical qualities of the objects (Jelbert et al., 2014) (Bird & Emery, 2009).



(A) Setup used in experiment 1 and 2. Sections (1) and (2) clear plastic, (3) water, (4) waxworm, (5) pile of stones. (B) Photograph of experiment 3 setup. The left tube contains sawdust, the right tube contains water. (Bird & Emery, 2009)

Corvids do not only display standard tool use, but metatool use as well. Metatool use is defined as the use of a tool to create/obtain another tool (which is then used to obtain food). This may seem easy, but it is actually a deceptively simple concept. In fact, many primates actually struggle to grasp the idea of metatool use. This is because metatool use has three distinct cognitive challenges. Firstly, an animal must recognize that tools can be used on nonfood objects (which may require analogical reasoning abilities). Second, an individual must initially inhibit a direct response toward the main goal of obtaining food. Third, an individual must be capable of hierarchically organized behavior. That means they must be able to flexibly integrate newly innovated behavior (tool→tool) with established behaviors as a subgoal in achieving a main goal (tool→tool→food) (Taylor et al., 2007).

Corvids, in a feat of convergent evolution, exhibit metatool use similar to some primates. In one study involving metatool use, food was placed in a deep horizontal hole, close to two identical “toolboxes”. A long stick was placed inside of one of the toolboxes, and a stone was place in the other. In front of the toolboxes, a short stick was placed. This tool was too short to extract the meat from the hole, but could be used to extract the long tool from the box. Successful completion of the task required a crow to use the short stick to extract the long stick from the box and then use that long stick to remove the food (Taylor et al., 2007).

Success on this task would require spontaneous metatool use. Of the seven crows that attempted this task, all seven managed to extract the food. Three of the crows showed spontaneous metatool use, and succeeded on their first try, while the others took more attempts (Taylor et al., 2007). These results are in line with another similar experiment concerning metatool use in crows, which used a similar paradigm (Gruber et al., 2019). This is evidence of clear spontaneous metatool use without prior training, and is another example of corvids' reasoning ability. This connection to tool use (and ability to obtain food) also suggest a reason for them to have evolved such cognitive abilities. The ability to retrieve otherwise unavailable food would be an evolutionary advantage for corvids, and would make metatool use a valuable skill to have.

Corvid vs Primate reasoning

Overall, corvids show more consistent evidence of both analogical and causal reasoning than most non-human primates. For example, when tested using the trap-tube/trap-table paradigm, success for many different primate species had been mixed. Gibbons and Vervet monkeys showed more success than capuchins and tamarins, but ultimately either still failed a large percent of the time, or had possible other explanations for their success (Taylor et al., 2009). Corvids also perform well on task requiring tool use (which often requires causal reasoning) (Bird & Emery, 2009). In relation to metatool use (which requires analogical reasoning), corvids have a success rate comparable (or greater than) to that of other primates. This is shown in the results of previous studies on metatool use in gorillas, orangutans, chimps, monkeys, capuchins, and macaques (Taylor et al., 2007).

For example, Capuchins and tamarins failed to solve the trap-table problem. Vervet monkeys performed above chance, but still failed in 35% of trials. Gibbons solved the trap-table problem, with one subject performing successfully even from the first trial. However, this gibbon's success may have been based either on learning to associate the continuous surface of the table with reinforcement during training, or through viewing the trap as an obstruction and avoiding it (Taylor et al., 2009). In all, evidence of true causal reasoning is extremely hard to find in non-human animals, and has even had inconclusive evidence in primates, with many seeming to rely on associative reasoning instead (Martin-Ordas et al., 2008). Corvids, however, display consistent evidence of reasoning skills (Taylor et al., 2009) (Taylor et al., 2007).

Conclusion

Throughout time, corvids have expressed behaviors that people have seen as strange, impossible, and even disturbing. For years, many people believed this was due to supernatural causes or some form of godlike ability, but now it is known that these behaviors are due to corvids' impressive cognitive capabilities. Corvids and primates show very similar cognitive capabilities, with corvids even surpassing primates in some tasks (such as causal/analogical reasoning tasks and tasks involving tool and metatool use) (Taylor et al., 2009) (Taylor et al., 2007). Despite their anatomical differences and evolutionary distance from each other, it seems as if corvids can be considered “feathered apes” in regard to their cognitive capabilities and neural functioning on the micro level (Emery, 2004).

Despite the interesting findings, there are still gaps of information waiting to be filled. With the abundance of studies relating to abstract analogical reasoning and metatool use in primates, it is natural that more research should be done towards these topics in corvids (given their comparable or even more impressive performance when compared with primates).

With more information relating to these topics, we could better understand what is needed for complex cognition to occur (for years it was thought that a primate PFC was required, but that is apparently not the case). The PFC is often thought of as the most efficient neural structure for complex cognition, but given the evidence of (often even more efficient and developed) complex cognition in corvids without a PFC, this idea is slowly becoming less likely. The Avian cluster-like neuronal structure of the NCL helps to pack more neurons into a small space, a similar function to the layers of neurons that form the ridges and folds of the PFC. Which of these structures are more efficient for complex cognition, and how did two brain structures evolve to be so structurally different if they serve the same purpose?

Overall, it is slowly becoming more clear that our primate relatives are perhaps not as much of the pinnacle of cognition as once thought. Other animals, especially avians such as corvids or some parrot species, display similar abilities and neural functioning (at times surpassing their primate counterparts). This idea, although counterintuitive, is fascinating, and could help us better understand exactly how human-level cognition came to be, and similar to us our non-primate relatives really are.

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