Focus Article

Corvid cognition

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Numerous myths and legends across the world have suggested that corvids are intelligent. However, it is only in the last two decades that their cognition has become the subject of serious scientific investigation. Here I review what we currently know about the temporal, social, and physical cognition of this group. I argue that, while the work to date establishes corvids as one of the most intelligent groups of animals on the planet, the real scientific potential of the *Corvidae* has yet to be realized. However, a novel 'signature-testing' experimental approach is required if we want to unlock this group's promise and gain insights into the evolution of human and animal minds.

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INTRODUCTION

Many old stories contain a kernel of truth. Some do not. One of the most interesting developments in animal cognition over the last 20 years is the claim that the intelligence attributed to corvids in myth and folklore has at least some basis in reality. Aesop suggested in his fable 'The Crow and the Pitcher' that these birds are highly inventive.[1] In Native American mythology the raven is seen as the creator of light and as a trickster[2–4] while in Western Bering folklore the raven is seen as 'the transformer of the world', who teaches humans the skills they need to survive in the world.[5] Thus the raven caws to make people speak and invents the fire-drill by twisting his forefinger (the drill) into the base of his other foot[5] (the drill base). Nordic mythology tells the story of two ravens Huginn (thought) and Muninn (memory), who are sent out each dawn by the God Odin to fly all over the world.[6] They return at dusk to whisper to Odin what they have seen, so ensuring Odin is wise.[7] Similarly, Celtic art depicts crows speaking into the ears of men,[8] as in Celtic mythology crows were considered to have oracular powers.[8,9] These myths and stories, then, suggest that corvids are not only intelligent but, through their intelligence, have something to teach us. Here I review recent advances in our scientific knowledge of corvid cognition to examine whether this is really the case.

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WHAT IS A CORVID?

The family *Corvidae* consists of the crows, magpies, jays, and their allies. In total this family contains 117 species, with the crows (genus *Corvus*) comprising around 40 species. This family is part of the 'core Corvoidea', a group of some 750 oscine passerine species that originated in Papua New Guinea around 50 million years ago (mya) and then radiated from there across the globe.[10] The crows themselves (genus *Corvus*) arose around 11 mya (range 9–15 mya) in the Palaearctic.[11]

WHAT MAKES THE CORVIDAE INTERESTING?

The *Corvidae* have two particularly intriguing characteristics. The first is the frequency with which this group produces complex behaviors. Overall, the species within the *Corvidae* are responsible for a higher number of foraging innovations and instances of tool use than any other bird group,[12–14] though psittcaids (parrots) come to a close second. Individually, certain species exhibit various complex behaviors (Figure 1). For example, tool-making New Caledonian crows are the only species, beside humans, chimpanzees and orang-utans, to craft their tools into a particular three-dimensional form using a sequence of behaviors,[15,16] and the only species except humans

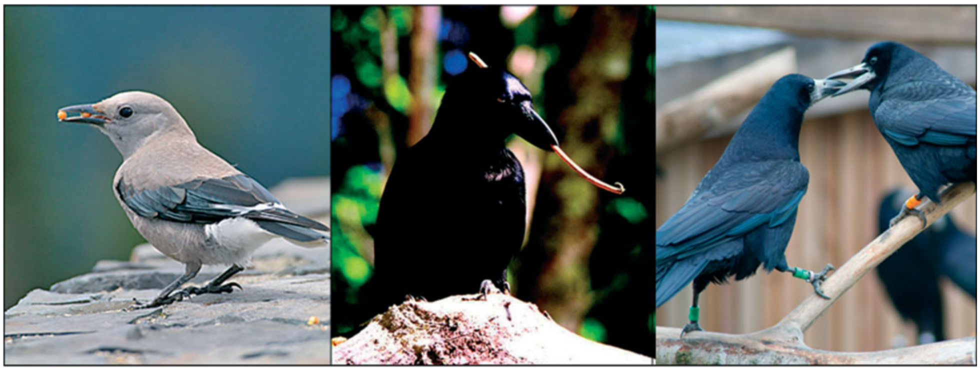

FIGURE 1 | Examples of complex behaviors in the Corvidae. From left to right: a Clark's nutcracker caching (Photo credit Dave McShaffrey), a New Caledonian crow with a hook tool (Photo credit Gavin Hunt), and rooks bill-twining after a fight (Photo credit Julia Leijola).

that manufacture hook tools in the wild.[17] Clark's nutcrackers bury up to 33,000 pine seeds in the ground before winter and recover them months later.[18] Both rooks and ravens exhibit similar conflict management behaviors to those seen in primates: ravens make up with each other after fights[19] (reconciliation), while rooks will bill-twine with their partners after fighting another rook[20] (third-party affiliation).

The second key feature of the corvids is their degree of brain encephalization (ratio of brain size to body size). Remarkably, corvids have an encephalization ratio similar to that of chimpanzees,[21,22] and larger than any other bird group, save the psittcaids[23] (parrots). The most enlarged areas of the corvid brain are the nidopallium and mesopallium,[24–26] which are thought to be analogous to the areas of mammalian brain used in complex cognitive processes (the prefrontal cortex). While there is ongoing debate on how closely encephalization correlates with intelligence,[27–29] the degree of encephalization in this group is particularly striking, given the energetic demands imposed by flight and by brain tissue. Flight exerts a strong selective pressure to maintain low body weight and keep energetic costs down.[30,31] Despite this selective pressure, and the incredibly high energetic costs of maintaining brain tissue,[32] corvids have evolved relatively large brains. For this to have occurred these brains have to be (literally) pulling their weight and providing large adaptive advantages in the environment.

SO WHAT DO WE KNOW ABOUT CORVID COGNITION?

The *Corvidae* have bigger relative brain sizes and produce more complex behaviors than any other bird group. The increased brain size suggests this group has the potential to think in more sophisticated ways than other birds. The high rate of behavioral innovation suggests the same: if all birds thought as the corvids do, then one would expect them to produce the same amount of complex behaviors. Yet they do not.[12,14] However, only carefully controlled behavioral experiments can show us what cognitive mechanisms members of this group actually possess. Here I highlight the key findings in corvid cognition to date.

Imagining the Past and Future

Corvids use sophisticated cognition when remembering the past and planning for the future. Clayton and Dickinson[33] found that when allowed to cache both peanuts and worms, scrub jays preferred to recover their favorite food, the worms, if only a short time has passed (4 h). However, when a longer time had passed (124 h) the jays preferentially recovered the nuts they had stored, as worms degrade after 124 h and so are not worth eating. In contrast, jays given experience of non-degrading 'magic' worms, through the replacement of degraded worms with living ones by the experimenter, still preferred to recover worms after 124 h. Thus the jays used their experience of how food degrades to guide their cache-recovery behaviors. This work suggests that jays encode 'what', 'where', and 'when' (WWW) during caching. That is, they remember whether they have cached peanuts or worms, where they cached the object, and whether 4 or 124 h has passed, though there is continued debate as to how the 'when' aspect of their memory is encoded.[34,35] The presence of WWW memory in jays suggests that their behavior can approximate episodic memory in humans, thus this corvid species has been described as having episodic-like memory.[33] The critical difference is that in humans episodic memory is based on a conscious re-experiencing of the past[36,37] (autonoetic consciousness). Given limitations in our

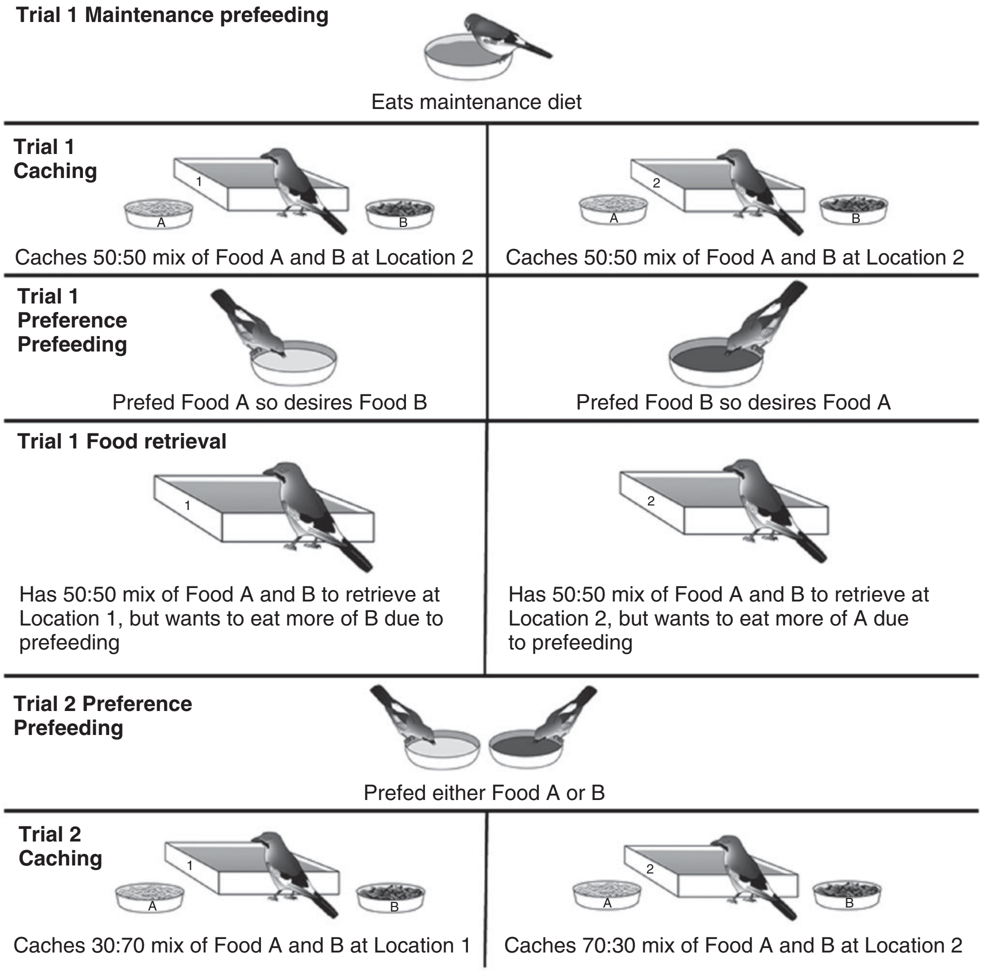

FIGURE 2 | Experimental outline of planning for two future desire states study in Eurasian jays. Note on any one trial a jay would receive either the conditions on the left or the right column of the diagram.

understanding of consciousness, we have little idea whether jays are also capable of self-projection into the past.[38]

While several studies have found intriguing evidence for future planning in corvids,[39,40] there are alternative explanations for these results.[41] Perhaps the most convincing evidence comes from a recent study on Eurasian jays by Cheke and Clayton.[42] In humans, the more you eat of one food, the less you want of it compared to other foods. Similarly, jays show such specific satiety: after eating a particular food they then want less of it, but are happy to eat new food types. After being fed their normal food, these jays were allowed to cache two food types (A and B) at two different locations (locations 1 and 2). Initially the jays stored an equal amount of each food type at each location. After 3 h they were then allowed to eat as much as they wanted of one of the two food types (specific satiation), and then were allowed to recover their caches from one of the locations they had cached in. Thus at this point the jays only wanted to recover caches of the food they had not been just fed, though they had previously filled the cache site with both types of food. A day later the jays were fed the other food type to satiation and then were allowed to retrieve food from the second food location (where they had cached food 27 h before). Again the jays only wanted to eat the food type they had not just been fed, though they had already cached both food types. On the second trial of the experiment the jays changed their caching behavior to reflect the future feeding events they had experienced on trial 1 (Figure 2). Even though they were fed to satiety on one of the food types before caching began, when caching they hid more of the food type in each tray that they knew they would not be fed on later. Thus they remembered that in 3 h they would be fed one food type before being allowed to retrieve their caches and in 27 h they would be fed the other before being allowed to retrieve their cache. This work indicates that these jays can actually plan for two different desires at two different time points in the future while ignoring their own current desires. As with work on episodic memory it is unclear whether jays consciously project themselves into the future in order to plan for different desires at different times.[38,42]

Social Cognition

Several ancient Greek writers suggested that jackdaws could be trapped using only a dish of oil.[43] The trap was effective because these birds were highly social and so became sufficiently absorbed by the reflected image that they would fall into the dish. What is not clear from this anecdote is what aspect of the jackdaws' social lives led them to fall in. Did each jackdaw recognize itself as a distinct individual separate from the other jackdaws in its life and thus fall into the oil in effort to get a closer look at itself? Or did they simply see another jackdaw in the oil they wanted to interact with? Work by Prior et al. on mirror recognition in magpies suggests that either of these explanations could have driven the jackdaws' fall.[44] When initially confronted by a mirror, magpies performed social behaviors such as aggressive displays and jumping toward the mirror. However, over time several of the magpies changed their behavior and began to perform behaviors such as looking behind the mirror. The magpies were then given the mark test. Here, either a black dot or a colored dot was placed underneath their throat. While neither dot could be seen by the animal without a mirror, only the colored dot could be seen in the mirror, due to the black dot blending into the magpies' black feathers. When the colored dot was placed on the magpies, throats and a mirror was present, two of the six individuals tested performed a high number of self-directed behaviors toward it. For example they attempted to scratch the dot off with their leg, rather than toward the reflection of the spot in the mirror. When a black dot was placed on the magpies' throats, or the mirror was not present, these behaviors were performed significantly less often. Thus, just like great apes,[45] elephants,[46] and dolphins,[47] a proportion of the magpies tested by using mirror reflections to notice changes to their own bodies. Recent work suggests that passing the mirror test indicates an animal can differentiate between itself and others and has a restricted sense of self-awareness, based on an ability to generate and compare multiple mental models of its own physical appearance.[48] This raises the possibility that the jackdaws in Greek legend fell into the oil because they became so absorbed by looking at the reflection of their own *body*, though it does seem more plausible they jumped in as part of an aggressive social display. What is still a complete mystery is whether corvids have a concept of *self* as humans do.

Corvids go beyond discriminating between their bodies and other conspecifics. Recent work by Boeckle and Buygnar has shown that ravens remember for over 3 years not only whether particular individuals are familiar or unfamiliar, but also the valence of their relationship with these individuals[49] (whether they get on with them or not). After housing a group of juvenile ravens together as a non-breeding group and monitoring their social behavior, the group was spilt into breeding pairs. After 3 years, calls of various past group members and of unknown birds were played back to the ravens in each pair. Birds changed the calls they made to these recordings based not only on whether individuals were familiar or not, but also based on their past relationships with familiar individuals (whether they affiliated with these individuals or not as juveniles in the non-breeding group). This work demonstrates that ravens have long-term memory for social interactions, though it is unclear whether the ravens remembered experiences with specific individuals, or remembered categories of individual such as affiliates and non-affiliates. Other work by Marzluff et al. has shown that corvids' memory for social interactions extend beyond within-species interactions. American crows caught and released by humans wearing a unique mask scolded any human wearing the mask for up to at least 2.7 years after the initial catching event.[50] Thus, this corvid species is capable of discriminating between humans using facial characteristics and so can remember masks, and likely faces, over long periods of time.

Corvids seem to be able to use their own experiences in the world in order to predict the future behavior of their conspecifics. One of the key problems faced by caching scrub jays is theft. If a competitor can observe where a jay has hidden his food, he can get an easy meal simply by digging up the cache. It therefore pays to recache: to dig up hidden food and hide it again, particularly if the first hiding event was observed. Emery and Clayton manipulated the experience of two groups of hand-raised scrub jays.[51] One group had previous experience of stealing other birds' caches. The second group had no experience of being a thief. Both groups were then given the opportunity to cache when alone and when observed by a conspecific. Only the jays that had experience of being a thief recached their food when the initial hiding event was observed. Thus, not only can scrub jays remember whether they were being watched during caching, but they may also engage in experience projection, where they use their experience of being a thief to create cache protection strategies, possibly by using their experience to mentally simulate the viewpoint of a potential thief. This work raises the possibility that corvids may have some type of theory of mind: the ability to attribute mental states, such as beliefs, knowledge, perspectives, and desires, to conspecifics.

Several studies have focused more explicitly on whether corvid species have theory of mind. Scrub jays remember who watched them during caching and use this information to decide, when being subsequently watched by either knowledgeable or uninformed competitors, whether to rehide their food or leave it alone.[52] As this behavior does not depend on the behavior of the competitor, it raises the possibility that these jays can attribute knowledge and ignorance to conspecifics. However, alternate explanations exist.[53] While a recent model based on stress driving recaching[54] has been disproven,[55] another possibility is that, on seeing a particular individual watch a caching event, a jay could form a negative association between this individual and the location it is caching in, rather than attributing 'knowledge' of the item's location to the individual. The jay would then recache often in this location when watched by individual it has ascribed this 'negative' tag to. Thus the content associated with a particular individual is unclear: jays need not think as humans do and so decide that a particular individual *knows* where the food is.[52,53,56,57] A similar critique applies to work on ravens. This corvid will rush to steal hidden food only when it is possible for a visible competitor to also see the food being hidden.[58] While this work suggests that ravens not only remember who was watching, but also whether this individual's viewpoint was blocked or not, it does not require the ravens to have attributed *knowledge* to a particular competitor. Instead, simply observing that a competitor has a line of sight with food currently being hidden could have been associated in the past with losing food, leading to the raven learning to rush to steal the food before the competitor.

Recent work by Ostojić et al. suggests that Eurasian jays might attribute desire to conspecifics.[59] Male Eurasian jays choose food to give to their mates during courtship. It would therefore be advantageous if the males could predict what the females actually wanted to eat, given that it would reduce the cost of foraging for unwanted food items and potentially make them a more attractive mate. Just as in Cheke and Clayton,[42] this experiment was based on specific satiety: once jays have eaten a large quantity of one food type, such as meal worm larvae, they want less of it, but will still eat a new food type, such a wax worms. Males in one set of trials were allowed to see their mates eating a large portion of one food type and then were given the choice of what to feed their mate next (seen condition). In a second set of trials the males did not see that the female had eaten a large portion of one food type, but could still potentially use her body language after the eating event to judge what she wanted (unseen condition). In the seen condition, males did not give females the food they had just been eating, while in the unseen condition the males gave both food types. This indicates it was the males' observation of the females eating a food type that drove his decision about what to share with his mate, rather than the females' subsequent behavior. Importantly, the males were able to dissociate their desires from those of the females. After watching the females eat a large portion of one food type, the males did not then choose to eat the other food type themselves. Thus, observing a female eat lots of wax worms led to the male giving mealworm larvae to the female, but continuing to have a healthy appetite for wax worms himself (Figure 3).

These results suggest that male Eurasian jays can attribute a desire for a particular food type to a female jay, given that the female's behavior alone did not guide giving and that males differentiate between the food they want and food their mates want. Their behavior may also be further evidence of experience projection, as males may have used their own experiences with eating lots of one particular food type to predict that females would not want to eat more of a food they had already gorged themselves on. However, further work is required to substantiate these conclusions. One key behavioral criteria put forward for the explicit attribution of mental states to others is that animals should be able to judge the similarity between perceptually disparate behavior patterns linked to an unobservable mental state.[60] This criterion has been championed by leading skeptics in the field.[53] In Ostojić et al.'s experiment the sight of females eating lots of one food type drove the males' provisioning behavior. If these jays really do attribute desires to each other one would expect that a perceptually disparate behavior pattern would also drive provisioning behavior. Thus a male should react the same if he sees his mate enter a room with lots of worms and then later leave an empty room. Such flexibility in the inputs used for desire attribution would be highly adaptive, as it would be highly costly for provisioning males to be constantly monitoring what their mate is eating. If a male can remember what food he has given his mate, and what is left when he returns from a foraging trip, he can make inferences about what the female has eaten, and thus

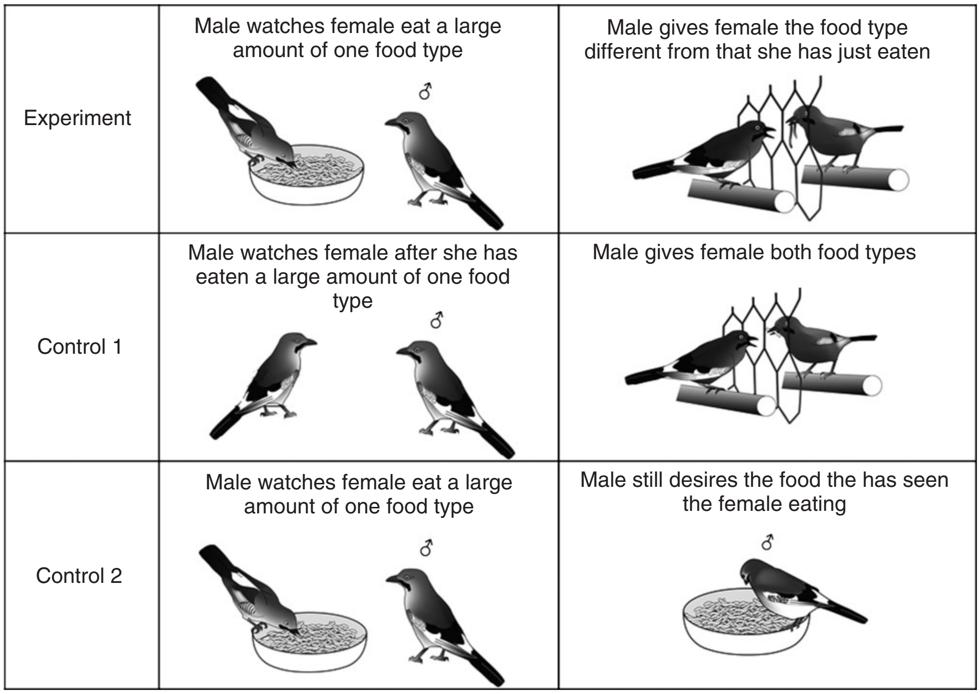

FIGURE 3 | Experimental outline of desire attribution study in Eurasian jays.

her desire state, without keeping her within his line of sight.

Tool Use and Causal Understanding

A third line of work on corvid cognition has examined what this group of birds think about tools and the causality underpinning events in the world. Much of this work has focused on New Caledonian crows, because of their tool-making abilities in the wild[15,17,61] and rooks, which produce impressive tool behaviors in captivity.[62] New Caledonian crows can choose tools of the right length for the task in hand,[63] can make tools of the right diameter for a problem,[64] and will risk their tools, rather than their beaks when faced with hazardous objects such as a model snake[65,66] (context-dependent tool use). Rooks have been shown to choose between functional and non-functional tools, to spontaneously use sticks as tools and to spontaneously modify sticks so they can be used as tools.[62] Both species have also produced meta-tool behaviors[62,67–69] where they use tools to gain access to other tools which can be used to get food. One of the most impressive behaviors produced by both these corvid species is the bending of man-made material into hooks.[62,70] After using a wooden hook to pull a bucket by its handle from a tube, Betty, a New Caledonian crow, subsequently bent a straight piece of wire into a hook shape in order to do the same.[70] Rooks, given similar experience using a wooden hook to pull a bucket from a tube, also then bent wire to make a functional hook.[62]

More recent work has shown that New Caledonian crows will use stones as tools after limited experience pushing a platform with their beaks[71] and that rooks, crows, and Eurasian jays[72–74] can, like children over the age of 7,[75] learn the functional properties of stones and stone-like tools when dropping these objects into a water-filled tube. Finally, both rooks and New Caledonian crows have been able to solve the trap-tube problem, where an animal has to pull food from within a horizontal tube while avoiding a trap. One rook, Guillem, was able to solve various transfer tasks that required him to switch between treating the same cues as negative or positive.[76] Three New Caledonian crows solved several transfer tasks, including the trap-table problem, a problem with an identical causal structure to the trap-tube task, in that an animal must avoid pulling food into a hole, but with very different perceptual elements.[77,78] In contrast, chimpanzees fail to transfer from the trap-tube to the trap-table problem when required to use tools to do so.[79]

However, the cognitive mechanisms behind the impressive performance outlined above have not been pinpointed. While these studies show that the crows' behavior is not guided by simple learning mechanisms alone, there are also instances where their impressive performances include odd (but informative) mistakes that humans would not make. The ability to generalize tool use from out-of-reach food objects to out-of-reach tools when solving metatool problems[62,67], and to generalize from the trap-tube to trap-table[77], shows that these birds are not bound by the law of stimulus generalization[80], but can instead form abstract categories not tied to specific perceptual features.[67,77] Similarly, the ability to invent novel wire tools,[62,70] novel stone dropping behaviors,[71] and novel metatool sequences[62,67,68] shows that these crows are not bound by learning phenomenon such as resurgence, chaining, and conditional reinforcement when creating novel behaviors.[67] Finally, both the trap-tube and stone-dropping studies[73,74,76,77] show that several corvid species have the ability to quickly learn the functional properties of objects, but not to learn arbitrary properties rewarded with the same consistency. This demonstrates that the crows' learning is based on more than co-variation levels between objects in the environment and outcomes.[81]

However, these corvids clearly make errors in their problem-solving performances that it seems unlikely humans would make. After inventing stone-tool use, one New Caledonian crow dropped a feather onto a platform in an attempt to collapse it, despite the feather's weight being insufficient for the platform to be collapsed in this way.[71] When wire bending, New Caledonian crows and rooks often make use of the non-functional end of a tool first, despite this course of action being highly unlikely to succeed.[62,70,82] New Caledonian crows make a variety of errors when solving metatool problems,[66,68,69] which brings into question whether they create hierarchically structured plans to solve these tasks. Finally, while New Caledonian crows can transfer from the trap-tube to the trap-table, they failed to solve a trap-tube which contained two holes, only one of which has a base and so worked as a functional trap. Thus these crows cannot transfer from using the holes in a trap-tube to using the base of a trap as the critical feature that predicts success.[77]

This paradox in corvids' understanding of causality is neatly exemplified by two recent studies on New Caledonian crows. These corvids can, in a matter of seconds, spontaneously solve the string-pulling paradigm, where a string must be pulled and then stepped on repeatedly in order to bring hanging food within reach.[83,84] However, studies by Taylor et al. have found that when New Caledonian crows are not given feedback on the effect of their actions on the hanging food[85] or feedback is interrupted,[84] they stop producing coherent performances, even if they have done so in the past.[84] Thus, when faced with novel string-pulling problems involving man-made objects, corvids seem to use the perceptual-motor feedback created from observing the effects of their actions on the world to drive their performance, rather than mentally imagining a plan of action toward the string and then executing it.[85,86] In contrast, there is evidence of mental simulation by this species when it thinks of hidden causal agents. The ability to mentally simulate the potential causal interactions of a hidden animate object is highly adaptive. For example, understanding that the rustling of the leaves in a forest canopy indicates the presence of a predator would allow an animal to make evasion decisions before the predator is seen. This ability is also a precursor to a number of highly complex human cognitive abilities, including theory of mind, scientific reasoning, and religious reasoning.[87–90] Taylor et al. recently examined whether New Caledonian crows could infer that the backward and forward movement of a stick from a hide was caused by a human they had seen enter the hide.[91] The crows seemed able to 'join the dots' and infer that the hidden human was the cause of the stick's movement. Thus when the human left the hide, the crows reasoned that the stick could not move again and so it was safe to forage in close proximity to the hide. Though associative accounts for the crows' behavior have been suggested[92,93] they do not seem able to explain the results in their entirety.[94,95] These results are therefore in stark contrast to those found with string pulling paradigms (Figure 4).

SO HOW DO CORVIDS REALLY THINK?

The studies outlined above suggest that corvid species use sophisticated cognition when thinking about temporal events, conspecifics, tools, and the causality of the world. The field of corvid cognition has, therefore, made substantial progress in demonstrating that the two hallmarks of intelligence seen in this group, (large relative brain size and behavioral complexity), are because of this group actually thinking in sophisticated ways. In fact, in several of the cognitive spheres discussed here, the evidence for intelligence rivals that found for primates,[23,42,56,59,77,96] which is highly impressive, particularly given that primate cognition has been studied for far longer. Because of this, the corvids are now established as one of the most intelligent groups of animals on the planet.

However, a number of key questions remain unanswered. Certain corvid species seem to remember the past and plan for the future in a flexible way that goes beyond the Bischof-Kohler hypothesis, which states that an animal cannot plan for a future desire

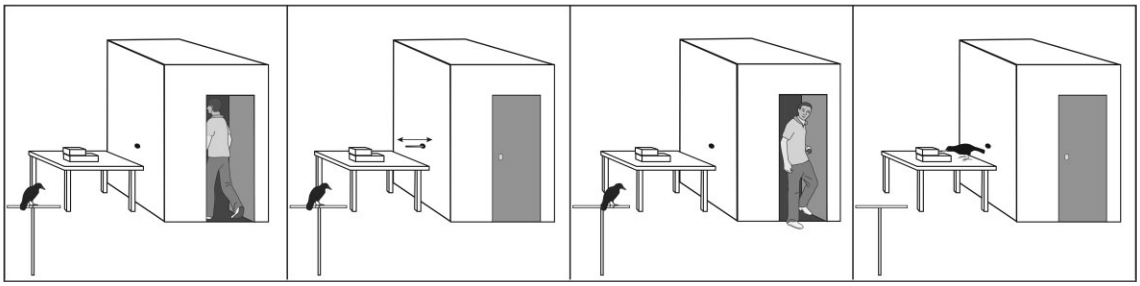

FIGURE 4 | Experimental outline of reasoning about hidden causal agents study in New Caledonian crows. Crows infer that the movement of this stick is caused by the hidden human and so that the stick will not move again when the human leaves.

state.[35,97] However beyond this, it is unclear whether any corvid can mentally imagine itself in the past or future, as humans do.[37] When thinking about themselves there is evidence that at least one corvid species has a limited form of self-awareness,[44,48] but we has little idea how similar the corvid concept of self is to that of humans.[48] When thinking of others a similar situation exists: work on experience projection[51] and desire-state attribution[59] raises the possibility that both Eurasian and scrub jays have some kind of theory of mind, but further work is required, particularly given how controversial this area of science is.[53,56,57] The mix of results surrounding tool use and causality show several corvid species are not limited by simple psychological mechanisms but do make mistakes that humans would not. This suggests that, when problem solving, corvids use forms of cognition intermediate between humans thought and simple learning. However, few, if any, theoretical cognitive mechanisms have been proposed which could predict the mix of success and failures seen to date. Similarly, while recent work raises the possibility that one corvid species, the New Caledonian crow, is able to mentally simulate the actions of hidden humans,[91] other work shows that such simulation is not used with novel man-made objects.[85] This suggests that mental simulation in this corvid species is highly dependent on context and experience, and so may be different from that used in humans. What form it therefore takes, in this species and others, is something of a mystery. Finally, it is not yet known the degree to which the species with the *Corvidae* share the same patterns of thinking. We have little idea which cognitive traits are ancestral, though it does appear the common ancestor of the *Corvidae* was a moderate cacher.[98] The species in this group may think in very different ways, depending on the evolutionary pressures they have been subjected to, or they may all share a corvid mode of thinking, using many of the cognitive mechanisms discussed above.

CONCLUSIONS: WHAT NEXT?

Despite the many questions still surrounding corvid cognition, this group has already taught us that sophisticated types of intelligence are not just found in ourselves and our closest relatives. However, there is far more that we can learn from them. In particular, pinpointing the cognitive mechanisms used by this group has the potential to provide insights into the evolution of not only the human mind, but intelligence in general. By comparing the life histories of various corvid species to the cognitive mechanisms they possess, it should be possible to discover whether particular selective pressures, such as group living or tool manufacture, are sufficient for the evolution of specific cognitive mechanisms that are highly important to humans. Corvids, therefore, offer us a way to peer into our own past and discover why we think the way we do. Furthermore, examination of these cognitive mechanisms in detail will show us the extent to which the structure and form of cognitive mechanisms evolve convergently. Thus work in this area has the potential to allow us to build a deep understanding of how intelligence evolves.

However, these exciting research possibilities are predicated on one crucial point that behavioral convergence does not equal cognitive convergence. While it has been claimed that corvids are ‘feathered apes’,[23,96] it is currently difficult to know whether corvids produce similar behaviors to apes because they think in the same way, or because different cognitive mechanisms have evolved to produce the same behavioral output. Evidence of *behavioral* convergent evolution in corvids and apes is not evidence of *cognitive* convergent evolution: that these two groups have actually evolved the same ways of thinking.

When Alan Turing proposed the Turing test as a way of assessing machine intelligence he made a crucial point about the machine’s cognitive limitations.[99] He noted that the machine would need to mirror both the strengths and the *flaws* in human cognition if it was to be attributed with human intelligence. If given an arithmetical problem, the machine would need to not give an accurate answer immediately, but instead take around 30 seconds to reply, and occasionally make errors.[99] Clearly, it is more probable that a machine and a human have the same cognitive mechanisms if they not only solve the same problems, but also process problems at similar speeds and exhibit similar error rates. These additional points of similarity increase the chance that the cognition being used is the same. Similarly, it is more likely primates and corvids use the same cognition in decision making if corvids mirror humans[100,101] and capuchins[102] in exhibiting the bias of loss aversion and it is more likely scrubs jays use the same memory system as humans if they make the same retrieval errors.[34,103] Thus, if different minds produce the same errors, have the same biases in information processing, and have the same limitations, it is far more likely they share the same cognitive mechanisms than if they only produce the same solutions to a problem. Each additional similarity found along these dimensions increases our confidence that the underlying cognition is the same.

Therefore, if we wish to use the Corvidae to understand the evolution of intelligence, and so realize this group's full scientific potential, we need to change our experimental practice. We should adopt a 'signature-testing' approach, where experimenters explicitly set out to search for the signatures of various cognitive mechanisms in terms of their errors, biases and limits, rather than a 'success-testing' approach where experimenters simply examine whether a problem can be solved or not. The use of brain imaging techniques on corvids[104] should greatly help with this search. Only this signature-testing approach can allow us to gain true insight into how our own intelligence evolved and how intelligence may evolve more generally on our planet and others. This could lead to the intelligence of the Corvidae teaching us far more than even ancient myths and legends suggest.

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