

Corvids infer the mental states of conspecifics

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Received: 24 April 2015 / Accepted: 26 October 2015 / Published online: 12 November 2015
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Abstract It is well known that humans represent the mental states of others and use these representations to successfully predict, understand, and manipulate their behaviour. This is an impressive ability. Many comparative psychologists believe that some non-human apes and monkeys attribute mental states to others. But is this ability unique to mammals? In this paper, I review findings from a range of behavioural studies on corvids, including food caching, food recaching and food sharing studies. In order to protect their caches from being pilfered, corvids successfully keep track of observing conspecifics, employ a number of caching and recaching strategies, and exploit environmental factors to reduce the amount of visual and auditory information available to observing conspecifics. When giving food items as gifts, corvids give items for which conspecifics have developed a preference. I argue that the available evidence supports the hypothesis that corvids attribute mental states to conspecifics. I further hypothesize that corvids do so through process-driven simulation and the running of non-verbal multimodal rules accomplished by a class of mental representations called semantic pointers.

Keywords Mental state attribution · Social cognition · Theory of mind · Simulation · Semantic pointer · Corvid · Comparative psychology · Philosophy

Introduction

Traditionally, humans have been the center of discussion when it comes to matters of the mind, and for good reason. Humans employ a number of sophisticated cognitive skills that enable us to interact successfully in highly complex social

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environments. We represent the mental states of others and use these representations to successfully predict, understand, and manipulate their behaviour. This is an impressive ability, but is this ability unique to humans?

In the late 1970s, David Premack and Guy Woodruff (1978) raised this question by asking whether chimpanzees represented the mental states of conspecifics. This seems like a natural place to start looking for mental state attributions in non-human animals—if any non-human animal were to share in our ability to attribute mental states to a conspecific, then presumably it would be one of our closest living relatives. Despite some disagreement (Davidson 1982; Lurz 2011), many comparative psychologists now believe that Premack and Woodruff's question has been answered. Over the past 15 years, evidence has accumulated that some nonhuman apes and monkeys, especially chimpanzees and rhesus macaques, attribute mental states to others (Call and Tomasello 2008; Kaminski et al. 2008; Marticorena et al. 2011). Thus, the most interesting question in this area of comparative psychology is no longer whether humans are unique in this respect. Instead, we might ask whether the ability to attribute mental states is unique to primates or even mammals. For example, do birds attribute mental states to others?

In this paper, I review findings from a range of behavioural studies on corvids, the family of birds that includes crows, ravens, and jays. I argue that the available evidence supports the hypothesis that corvids attribute mental states to conspecifics.

The social, cognitive, and neurological profile of corvids makes them intriguing candidates for the ability to attribute mental states. Corvids are highly social animals. Not only do they interact with their conspecifics, they do so within complex hierarchical social systems (Clayton and Emery 2007). And in line with the “social brain hypothesis,” which posits a positive relationship between cognitive sophistication and the complexity of social relations (Dunbar 1998), corvids are extremely intelligent. They are excellent problem solvers, they make tools, and they reason about hidden causes (Taylor et al. 2012). Like great apes, corvids have large brain-to-body-size ratios (Emery 2006). And while corvids do not have a neocortex as it is found in the mammalian brain, homologs of relevant neocortical structures (the layer 4 input and layer 5 output neurons) have been discovered in a part of the avian brain known as the dorsal ventricular ridge (DVR) (Dugas-Ford et al. 2012). The presence of the homologous DVR in the avian brain makes mental state attribution without a neocortex more plausible.

A recent trend in comparative psychology recognizes that species differ in which mental states they attribute and how they might represent such states. For example, whereas normally developing humans can attribute knowledge and goals, beliefs and desires, many primatologists have concluded that chimpanzees and rhesus macaques can attribute knowledge and goals but not beliefs or desires (Tomasello et al. 2003; Kaminski et al. 2008; Marticorena et al. 2011; Martin and Santos 2014). Thus, to ask, “Can corvids attribute mental states?” is not to ask whether corvids can do what we humans do. If corvids have such abilities, they are likely to be much more limited than our abilities.

Not only would any such corvid ability be more limited than ours, it would also be non-linguistic. Donald Davidson has argued that in order to have any form of thought or reason and consequently in order to be able to represent the mental states of

conspecifics, an animal must have language (1982). Without good reason to believe that non-human animals have language, Davidson concludes that no non-human animals are able to represent the mental states of conspecifics. Despite the lack of evidence for language in non-human animals, the examples of chimpanzees and monkeys suggest that language is not required to represent others as having mental states. If corvids do represent the mental states of conspecifics, they do not represent them linguistically. Humans have language and often explicitly attribute and discuss other people's mental states, but it is not necessary that corvids do this in order to represent the mental states of conspecifics. Elisabeth Camp (2009) has argued that some animal beliefs may be based on imagistic representational systems. Camp says that these imagistic systems can account for the social knowledge that baboons have and eliminate the need for a language of thought. Though it is convenient for us to talk about a corvid's representations in a linguistic way, for example "the cacher has the representation that 'the conspecific will steal my food,'" this does not mean that a corvid's representations must be linguistic in nature. I will argue that a corvid's representations are multimodal, meaning they are composed of different kinds of perceptual information.

The term "theory of mind," first introduced by David Premack and Guy Woodruff (1978), is typically associated across disciplines with the ability to attribute mental states. Despite its wide use, there is much ambiguity associated with the term. While psychologists tend to associate the term with the mere ability to represent the mental states of others, some philosophers associate the term with particular approaches to explaining this ability. As a result of the ambiguity surrounding "theory of mind," the terms "mindreading" and "mentalizing," endorsed by Shaun Nichols and Stephen Stich (2003) and Alvin Goldman (2006), have been used to replace the term "theory of mind" to refer to the ability to represent the mental states of others. Though these terms have been widely used in philosophy, they may not be so widely used across disciplines. For simplicity and clarity, I will call the ability what it is, the ability to attribute mental states to others, and avoid the use of these terms.

Corvids may not be the close relatives to us that chimpanzees are, but they may share with us an impressive ability. In the next section, I will review studies on the food caching, food recaching, and food sharing behaviours of a number of corvid species. I argue that the available evidence supports the hypothesis that corvids have the ability to attribute mental states to conspecifics. In the section "[Mechanisms for mental state attribution in corvids](#)," I discuss the nature of the mechanisms that make mental state attribution in corvids possible. I hypothesize that corvids are able to infer the mental states of conspecifics through process-driven simulation and the running of non-verbal multimodal rules accomplished by a class of mental representations called semantic pointers.

Evidence for mental state attribution in corvids

Caching, recaching and pilfering behaviours

Many animals cache food so that it may be retrieved at a later time (Vander Wall 1990). To survive, some corvids must successfully store food during times of

abundance for future consumption when there is a shortage of food. Caching food for future consumption requires the caching animal to have a well-functioning spatial memory so that they may be able to recover their caches successfully and efficiently (Clayton et al. 2001). In addition to having good spatial memory, which makes for good caching abilities, corvids also have good observational spatial memory, which makes for good pilfering abilities. An individual can use its observational spatial memory to watch a conspecific cache its food items and then return at a later time, when the conspecific is not present, and steal its caches. Thus, in order to increase chances for successful caching and survival, corvids employ strategies to protect their caches. Dominant individuals may not need to employ non-aggressive cache protection strategies if they are able to defend their caches aggressively (Dally et al. 2005b; Heinrich 1999). Western scrub-jays, ravens, and Eurasian jays have been the subjects of a number of experiments focused on non-aggressive cache protection strategies, which I will discuss here.

Observation and context

In addition to caching food items, corvids also recache (move to a new location and rebury) food items. In one study, jays cached food items in a sand-filled tray (Emery and Clayton 2001). Researchers manipulated whether the caching jay was observed by a conspecific (observed condition) or cached in private (private condition). Afterward, all the jays were allowed to recover their caches in private. Observed jays recached significantly more food items than unobserved jays. In addition, observed jays preferentially recached in new sites, whereas unobserved jays showed no preference between new and old sites. One follow-up study ruled out the hypothesis that the results were due simply to the presence of a conspecific, as opposed to a conspecific actually observing the caching behaviour (Emery and Clayton 2001). Another follow-up study (Thom and Clayton 2013) ruled out the hypothesis that the results were due to stress (Van der Vaart et al. 2012). Overall, the results suggest that jays remember the social context of specific past events and adjust their behaviour to prevent their food from being stolen. Researchers have observed similar results with Clark's nutcrackers (Clary and Kelly 2011). Clary and Kelly's results also suggest that the nutcrackers can be alerted of potential pilfering conspecifics, and thus prompted to engage in cache protection strategies, through auditory information alone. That is, caching nutcrackers may not have to see that a conspecific is observing them caching, they may only have to hear that a conspecific is near enough to potentially observe the caches being made.

Emery and Clayton argue that a good explanation for this caching behaviour is that the cacher attributes a mental state to the observing conspecific and uses this representation to guide subsequent behaviour. More specifically, on this hypothesis, the cacher represents the observer as knowing where the food was placed. Then, based on this representation, the cacher decides to recache the food. Importantly, the attributed mental state is not the same as the cacher's own mental state. If the cacher were attributing its own knowledge to the observer, then the cacher would have no reason to preferentially recache in new sites in the observed condition but not the private condition—after all, the only way for a cacher to keep track of which sites

are new versus old is to know which sites the observer saw food items cached at. The fact that cachers preferentially recache in new sites in the observed condition suggests that they distinguish between their own knowledge and an observer's knowledge.

Further supporting this interpretation, additional studies showed that cachers keep track of which conspecific observed them cache which food item [Western scrub-jays: (Dally et al. 2006); ravens: (Bugnyar 2010); Clark's nutcrackers: (Clary and Kelly 2011)]. In one study, a cacher hid food in tray A in the presence of an observer A while a second tray, B, was present but covered so that the cacher was unable to hide food in tray B. After the food was hidden in observer A's presence, observer A was then removed and observer B was introduced. At the same time, tray A was covered and tray B was uncovered. The cacher was then allowed to hide new food items in the presence of observer B. Three hours later, the cacher was allowed to return to trays A and B and was given the opportunity to recache their initial food caches in one of four conditions: in the presence of observer A, in the presence of observer B, in the presence of a naïve conspecific (observer C) who was not present during any of the original caching, or in private. The jays preferentially recovered the caches that the present observer had seen them make during the time of the initial caching. That is, in condition one where observer A was present during the recovery phase, the cacher selectively recached the food items from tray A. In condition two where observer B was present, the cacher selectively recached the food items from tray B. By contrast, when a naïve conspecific (Observer C) was present, the cacher recached no food items. And when allowed to recache privately, the cacher recached food items from both trays A and B.

One possibility is that cachers are simply reading the behavioural cues of observers. Perhaps observer A gives subtle cues that it is disposed to approach tray A, observer B gives subtle cues that it is disposed to approach tray B, while the naïve observer gives no such cues. This could explain the observed results. A follow-up study addressed this interpretation (Dally et al. 2006). In this study, a primary cacher was allowed to cache in tray A in the presence of observer A, and in tray B in the presence of observer B. After the primary cacher had cached in both tray A and B, a secondary cacher (C) was allowed to cache in both trays while being observed by a new observer (D). Later, the primary cacher was allowed to return to trays A and B and had the opportunity to recache their initial food caches in the presence of observer D. In the presence of observer D, primary cachers did not recache items from either tray, similar to the recovery phase where a naïve conspecific was present in the previous experiment. Dally, Emery, and Clayton concluded that it is unlikely that patterns in recaching behaviour can be attributed simply to the reading of behavioural cues produced by observing conspecifics.

Researchers working with ravens have found that as pilferers (not just as cachers), ravens keep track of the different perceptual states of observing conspecifics and avoid divulging cache location information to naïve observers (Bugnyar and Kotrschal 2002; Bugnyar and Heinrich 2005; Bugnyar 2007).

Overall, these results support the conclusion that corvids keep track of who was watching and when. In other words, corvids are sensitive to the different knowledge states of the observers. They can generate a unique representation for the mental

states of multiple observers. Moreover, they use these representations to guide their own decision-making.

Exploiting environmental factors: lighting, distance, barriers, sound

In addition to recaching, Western scrub-jays employ other strategies to protect their caches. To reduce visual and auditory information available to observers, the jays exploit environmental factors such as variations in lighting, distance from the observer, barriers, and the amount of noise that caching in a particular location will produce.

Researchers found that Western scrub-jays selectively cached in shaded locations when caching in the presence of an observing conspecific (Dally et al. 2004). Jays were divided into two conditions, a private condition in which they were not observed, or an observed condition in which a conspecific observed them. Then they were allowed to cache non-degradable food items in two separate trays. One tray was well lit while the other tray was shaded. Jays from the observed condition cached preferentially in the shaded tray, while jays in the private condition showed no preference for either tray. During the recovery phase, jays from the observed condition preferentially recached items from the well-lit tray, while jays from the private condition reached items indiscriminately. These results suggest that the jays try to limit relevant information available to the observer and, thus, take into account the observer's knowledge state.

The jays' preference for caching in the shaded tray cannot simply be explained by an aversion to the light source, as the jays cached equally in the shaded and well-lit trays during the private condition. Also, the jays could not have been representing their own knowledge states in the observers. If the cacher were simply representing its own knowledge states in the observer, then we would not expect to see a preference for caching in one tray over another, since the cacher's knowledge of cache location is unaffected by the visibility of the tray. As in the experiments discussed in the section "[Observation and context](#)," the jays cached more food items in the observed condition and preferentially recached food items that were at high risk of being pilfered.

Corvids also selectively cache in locations that are farther away from the observing conspecific [Western scrub-jays: (Dally et al. 2005a); ravens: (Bugnyar and Kotrschal 2002; Heinrich 1999); Eurasian jays: (Shaw and Clayton 2012)]. Researchers divided Western scrub-jays into two conditions, private and observed, and allowed them to cache food items in two different trays: one near to the observer and one far away from the observer (Dally et al. 2005a). All jays were later allowed to recover their caches in private. The jays from the observed condition preferentially cached in the far tray during the initial caching phase, and during the recovery phase they recached a significantly higher proportion of food items from the near tray than from the far tray and they preferentially recached in new locations. The jays from the private condition exhibited no preference for either tray when caching or recaching. The results suggest that jays use relative distance from conspecifics as a way to degrade the information about cache locations that the observer has, thus decreasing the chance that their caches will be pilfered.

In order to completely conceal visual information about their caches' locations, corvids selectively cache in locations hidden from observing conspecifics [Western scrub-jays: (Dally et al. 2005a); ravens: (Bugnyar and Kotrschal 2002); Eurasian jays: (Legg and Clayton 2014)]. In one study, Western scrub-jays were divided into two conditions and allowed to cache food items in two separate trays. In the first condition (the free condition), an observing conspecific was able to freely move about an enclosure and view either of the trays, but could not simultaneously view both trays due to an obstructing barrier. This meant that one tray was "near and seen" and one tray was "far and unseen" but which tray was which was determined by the location of the freely moving observing conspecific. In the second condition (the constrained condition), the observing conspecific was constrained to one side of the enclosure and could only ever view one of the two trays. This meant that one tray was always "near and seen" and the other tray was always "far and unseen." Again the jays were later allowed to recover their caches, always in private. Jays from both the free and constrained conditions preferred to cache in the far and unseen sites. During the initial caching phase, jays would move items that were cached in view of a conspecific around multiple times before finally depositing them in one location. Both jays from the free condition and the constrained condition exhibited this behaviour, but it was much more frequent in the jays from the free condition. In a control condition, jays were given un-cacheable food items (powder). These jays spent an equal amount of time in all areas of the cage, ruling out the possibility that jays experience an aversion to open areas or areas near the observing conspecific.

In many of the studies reviewed here, jays moved items around multiple times before finally depositing them in a location (Dally et al. 2005a; Emery and Clayton 2001). One possibility is that jays do this to confuse observers about the actual location of the food item. This is similar to the technique used by magicians to confuse audience members of the location of a ball hidden under a cup. The magician quickly moves the ball between cups while at the same time rapidly changing the order of the cups. Just as the magician's strategy makes it more difficult for an audience to accurately keep track of the location of the ball, the jay's strategy makes it more difficult for the observer to keep track of the cached food item's true location. Ravens have exhibited similar behaviours with the apparent goal of confusing observers about the actual location of a food item (Heinrich 1999; Bugnyar and Heinrich 2006; Bugnyar and Kotrschal 2004).

In addition to visual information, corvids may also use auditory information to locate and pilfer caches (Shaw and Clayton 2014). In order to reduce the auditory information available to conspecifics, corvids selectively cache in quiet substrates thus reducing the amount of noise they make while caching [Western scrub-jays: (Stulp et al. 2009); Eurasian jays: (Shaw and Clayton 2013)]. Researchers allowed jays to cache in one of three conditions: while being observed by a conspecific who could see and hear the caching (seen-and-heard condition), while being observed by a conspecific who could hear but not see the caching due to a barrier (heard-but-not-seen-condition), or while in private (private condition) (Stulp et al. 2009). There were two available trays for the jays to cache in. One tray was filled with pebbles that made noise when caching (the noisy tray) and another tray was filled with soil

that did not make noise when caching (the quiet tray). There was no recovery phase in this experiment. The jays preferentially recached in the silent tray when the observer had to rely on auditory information only (the heard-but-not-seen condition). Researchers have observed similar results with Eurasian jays (Shaw and Clayton 2013).

This preference for the silent tray in the heard-but-not-seen condition cannot be attributed to a preference for the silent tray because in the other two conditions, they jays did not exhibit this preference. The jays' preference also cannot be attributed to a behavioural rule like "cache in the silent tray in the presence of a conspecific" because in the seen-and-heard condition, a conspecific was present and the jays did not exhibit this preference. Finally, the preference cannot be attributed to a learned associative rule because the jays had no previous experience with either substrate (pebbles and soil) used for caching in this experiment. Stulp, Emery, Verhulst, and Clayton note that one explanation for these results, which has not been ruled out, is that the jays act to reduce noise so that they can listen to what the observing conspecific is doing behind the barrier. Though this explanation is consistent with the results, Stulp, Emery, Verhulst, and Clayton conclude that it is more likely that they jays are concerned with protecting their caches than with listening to the conspecific behind a barrier. Stulp, Emery, Verhulst, and Clayton conclude that the jays are sensitive to both visual and auditory information available to a conspecific and that they reduce the amount of auditory information available only when a conspecific must rely on auditory information alone.

Though many of the food caching studies that I reviewed in detail in this paper have featured Western scrub-jays as the subjects of interest, it is important to note that the studies done with ravens suggest that ravens, like Western scrub-jays, are sensitive to the different knowledge states of observers (Bugnyar 2013; Heinrich 1999). These behaviours in ravens are easily explained by attributing mental states to conspecifics and are unlikely to be the result of the reading of behavioural cues or learned associative rules, just as they are in Western scrub-jays and Eurasian jays. The studies done with ravens should be considered as further candidates for mental state attribution in corvids.

When considered in their entirety, this set of results suggests that corvids not only attribute mental states to conspecifics, but that these attributions are appropriately, and often cleverly, sensitive to environmental factors affecting perception. The results are easily explained by postulating that corvids attempt to reduce the amount of perceptual information available to observers by preferentially caching in locations that are shaded, hidden, or farther from the observer.

Food sharing behaviours

In order to attract mates, male Eurasian jays give females gifts. One common gift is food. All jays, male and female, develop specific satiety when feeding (Dickinson and Balleine 1995; Balleine and Dickinson 1998; Correia et al. 2007). That is, after being fed, say, a lot of moth larvae, jays would prefer to eat a mealworm larvae instead of another moth larvae. Researchers exploited this behavioural tendency to investigate whether Eurasian jays could represent a conspecific's *desires* or

preferences (Ostojić et al. 2013). If a male jay can represent the desire states of a female partner, he could give preferred gifts and therefore increase his attractiveness.

Male jays were divided into two groups. Males in the seen condition were allowed to watch their female partners being pre-fed on one of two kinds of food items, moth larvae or mealworm larvae. The females were pre-fed in order to achieve specific satiety. Males in the unseen condition were not allowed to watch their female partners being pre-fed. The males were then given the opportunity to choose a food item to give to their female mate. Researchers found that males in the seen condition were less likely to share the type of food that the females had been pre-fed. By contrast, males who had not observed the females being pre-fed did not share less of the food that females had been pre-fed, ruling out the possibility that male sharing behaviour is driven by a female's behavioural cues. A follow-up study ruled out the possibility that males in the seen condition developed specific satiety vicariously—that is, by watching their female partners being pre-fed—and then offered the females gifts that expressed their own food preference. Another study found that male jays were still less likely to share the type of food that the female had been pre-fed even when their own desire states were in direct contrast to the female's (Ostojić et al. 2014). Thus, overall, the results suggest that jays can attribute desires or preferences to conspecifics and use these attributions to guide important social interactions.

Mechanisms for mental state attribution in corvids

I have already said that to ask, “Can corvids attribute mental states?” is not to ask whether corvids can do what we humans do. Any such corvid abilities are likely to be much more limited than our abilities. In the section “[Evidence for mental state attribution in corvids](#),” I reviewed evidence for mental state attribution in corvids. In this section, I will discuss the mechanisms that are responsible for this ability.

Emery, Clayton, and Dally have suggested that what enables the jays in their studies to employ affective cache protection strategies is experience projection, a form of simulation (Emery and Clayton 2004; Dally et al. 2005a; Clayton et al. 2007). Alvin Goldman (2006) distinguished between two types of simulation: theory-driven simulation and process-driven simulation. In theory-driven simulation, the source (the individual running the simulation) and the target (the individual being simulated) have different mental mechanisms and the source must rely on a theory of the target's mechanisms in order to run the simulation. By contrast, in process-driven simulation, the source and the target share similar mental mechanisms, and the simulation is run by engaging in shared processes and operations. That is, the source is able to simulate the target by considering the perceptual input available to the target and then running their own mental mechanisms just as the target would, but with the notable exception that during simulation, the mechanisms are run offline (i.e. without acting). Process-driven simulation is more economical than theory-driven simulation since it requires fewer conceptual resources. If corvids are using simulation to infer the mental states of conspecifics, they are using

process-driven simulation. What is missing is a good account of how process-driven simulation is possible in corvids. I propose that process-driven simulation in corvids is accomplished by a class of multimodal mental representations called semantic pointers.

Chris Eliasmith's theory of biological cognition introduces semantic pointers as a class of mental representation. As described by Blouw et al. (2015, p. 2), semantic pointers, roughly speaking, are "neutrally instantiated, symbol-like representations that can be transformed in numerous ways to yield further representations that function to support cognitive processes like categorization, inference, and language use." These representations are multimodal, meaning they can combine different kinds of perceptual information, and can include motor, sensory, and emotional representations. Semantic pointers have been used successfully in the world's current largest functioning model of the human brain to account for a range of perceptual, cognitive, and motor behaviours (Eliasmith et al. 2012; Eliasmith 2013). Although semantic pointers can support language use, they do not require linguistic information in order to support complex cognition; therefore, semantic pointers provide an explanation as to how complex cognition in non-linguistic animals, including corvids, may be possible.

Paul Thagard (2015) describes how semantic pointer theories of communication and inference can explain interactions between people in romantic relationships. Important for relationships are inter-agent inferences, where one person thinks and makes inferences about the other person's mind and behaviour. Inter-agent inferences generate either attributions of mental states or predictions about likely behaviour through the application of rules. These rules are an important kind of belief with an if-then structure. They can be conscious and verbal, but they can also be unconscious and multimodal. The rules applied in inter-agent inferences express regularities in the transitions that obtain between cognitive states. Because these rules may be non-linguistic and multimodal, they are best expressed with the following notation: $\langle condition \rangle \rightarrow \langle action \rangle$, where $\langle condition \rangle$ is a semantic pointer to be matched to the current situation, and $\langle action \rangle$ is another semantic pointer that is tied to the condition semantic pointer by the regularity that the rule expresses. Rules can be innate, acquired through instruction (taught), acquired through generalizing observations (experience), or—for humans—acquired through explanatory inferences as part of scientific investigation (Thagard 2015).

So, how do corvids infer the mental states of conspecifics? I propose the hypothesis that corvids run a series of non-verbal multimodal rules using multimodal representations in the form of semantic pointers. To explain this, let us consider an example. As we saw in the section "[Evidence for mental state attribution in corvids](#)," corvids that cache in the presence of an observing conspecific will selectively recache items that are at high risk of being pilfered. Employing this cache protection strategy results from the running of a rule like: $\langle cache\ location\ compromised \rangle \rightarrow \langle recache\ to\ new\ location \rangle$. What constitutes the representation of the cache location being compromised is a representation of the observing conspecific's knowledge of the cache location. This representation is likely to be largely made up of visual information, but as suggested by Clary and Kelly's (2011) results, it can also be made up of auditory information.

Interestingly, Emery and Clayton (2004) discovered that it was only the individuals who had previous experience as a pilferer (and not just as an observer to pilfering) who employed cache protection strategies when they had been observed by a conspecific while caching. For this reason, Emery and Clayton believe that the jays in their experiments project their own experience onto observing conspecifics. This experience projection is a form of process-driven simulation, whereby the cacher runs a non-verbal multimodal rule (which was gained through their personal experiences) as if they were the observing conspecific. For example, in Emery and Clayton (2001), the non-verbal multimodal rule run by the Western scrub-jays could be: *<knowledge of cache location>* → *<intention to pilfer>*. In running this rule as if they were the observing conspecific, the cacher uses the perceptual information available to the conspecific (i.e. what the conspecific can perceive about the caches being made) and uses that information to run the rule in order to attribute the intention to pilfer to the observer. Put simply, what the cacher is doing is putting itself in the position of the observer, then determining its mental state. In Ostojic et al. (2013) experiment, the non-verbal multimodal rules run by male Eurasian jays when deciding which type of food item to gift to their female partner could be: *<pre-fed specific type of food item>* → *<desire different type of food item>*, and *<desire for specific food item>* → *<gift desired food item>*. In Bugnyar and Kotrschal's (2002) experiment, ravens could run the rule: *<naïve conspecific present>* → *<avoid divulging cache location>*. For all of the experiments discussed in the section “[Evidence for mental state attribution in corvids](#),” the corvids' behaviours can be explained with the running of non-verbal multimodal rules and process-driven simulation.

Alternative explanations for the corvid behaviours discussed in the section “[Evidence for mental state attribution in corvids](#)” primarily rely on observable environmental cues, usually in the form of behavioural cues given by the observing conspecific. The studies discussed here have taken care to rule out a number of alternative explanations. The corvid behaviours are unlikely to be the result of the mere presence of or an aversion to an observing conspecific (Emery and Clayton 2001), behavioural cues given by observing conspecifics (Dally et al. 2006; Bugnyar 2013), stress (Thom and Clayton 2013), an aversion to a light source or the lack of a light source (Dally et al. 2004), or an aversion to noisy substrates (Stulp et al. 2009; Shaw and Clayton 2013). Furthermore, the studies discussed here have also shown that the behaviours are unlikely to be the result of learned associative rules or the projection of the cacher's own mental states onto the observer, e.g. Stulp et al. (2009), Dally et al. (2006), Bugnyar (2013). One particular alternative explanation argues that cachers are sensitive to a conspecific's line of gaze and that cachers engage in cache protection strategies when a conspecific has a direct line of gaze on the caching (Lurz 2011). Though some may wonder whether there is an important difference between direct line of gaze and seeing in some of the studies discussed here, there are simpler reasons for rejecting this behaviour-reading hypothesis. Cachers in the studies with noisy substrates and the gift-giving studies are not required to attribute any *visual* perceptual states to observers. Instead, cachers in these studies attribute *auditory* perceptual states and *desires* based on their partners' physical states. Additional rules that involve sensitivity to “line of sound” (Lurz

2011, pp. 60–61) and other behaviour-reading explanations (Penn and Povinelli 2007) have been suggested, but each is limited in the number of behaviours it can explain. The hypothesis that I have proposed here is easily able to account for all of the behaviours exhibited by corvids and is neurobiologically plausible.

Conclusion

Corvids keep track of who was watching and when and go to great lengths to protect their caches. They cache more food items and recache food items when being observed by a conspecific. They reduce the amount of visual information available to observing conspecifics by choosing caching locations that are further away from the observer, in shadowed areas, or behind obstructing barriers. They reduce the amount of auditory information available to observing conspecifics when they can hear but not see by preferentially caching in quiet substrates. They deceive and confuse observing conspecifics by moving cached items around repeatedly and by making false caches. They selectively recache food items at high risk of being pilfered and avoid divulging information to naïve observers. When giving food items as gifts, they give items for which conspecifics have developed a preference. All of these behaviours are readily explained if corvids attribute mental states to conspecifics, but they are not easily explained otherwise.

I have hypothesized that corvids are able to infer the mental states of conspecifics through process-driven simulation, which is accomplished by the running of non-verbal multimodal rules. These rules are non-linguistic and are composed of multimodal representations called semantic pointers. This explanation eliminates the need for language in order to attribute mental states to conspecifics and is biologically plausible for corvids. Though arguments against the non-human animal ability to attribute mental states to conspecifics are still made (Davidson 1982; Lurz 2011), they are becoming increasingly implausible.

Being able to represent conspecifics as having mental states is an impressive cognitive feat. For a long time, this ability was thought to be uniquely human. The idiom “birdbrain” is a clear example of the expectations humans had for avian cognition. We now have reason to reject this idiom. Corvids are extremely intelligent animals and they are capable of more complex cognition than we ever imagined. They even seem capable of mental state attribution. This gives rise to new and exciting questions for future research. Whether and how the mechanisms responsible for this ability differ among human and non-human animals is already an interesting question. But if we now have reason to believe that the ability to attribute mental states to conspecifics is not an ability that is unique to mammals, we should now wonder whether and how the responsible mechanisms may differ among mammals and non-mammals. Similarly, investigating how this and other cognitive mechanisms develop in corvids may provide an interesting comparison for human development. This is already being done with chimpanzees (Wobber et al. 2014). Finally, we should keep an open mind when considering potential candidates for future mental state attribution research. It is easy for mammalian biases to affect comparative research. Though these biases have practical benefits for determining

starting points, we should not allow them to set unreasonable limits on new research. Like corvids, octopuses, squid, and cuttlefish (members of the Cephalopod sub-class Coleoidea), are highly intelligent and are capable of much more than we ever expected (Ikeda 2009; Mather 2008; Hochner 2008). These animals should not be discluded from future mental state attribution research simply because they are not mammals.

Acknowledgments Thank you to Paul Thagard, John Turri, Chris Eliasmith, Paul Meyer and anonymous reviewers for helpful feedback. This research was supported by the Social Sciences and Humanities Research Council of Canada.

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