New Caledonian crows reason about hidden causal agents

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The ability to make inferences about hidden causal mechanisms underpins scientific and religious thought. It also facilitates the understanding of social interactions and the production of sophisticated tool-using behaviors. However, although animals can reason about the outcomes of accidental interventions, only humans have been shown to make inferences about hidden causal mechanisms. Here, we show that tool-making New Caledonian crows react differently to an observable event when it is caused by a hidden causal agent. Eight crows watched two series of events in which a stick moved. In the first set of events, the crows observed a human enter a hide, a stick move, and the human then leave the hide. In the second, the stick moved without a human entering or exiting the hide. The crows inspected the hide and abandoned probing with a tool for food more often after the second, unexplained series of events. This difference shows that the crows can reason about a hidden causal agent. Comparative studies with the methodology outlined here could aid in elucidating the selective pressures that led to the evolution of this cognitive ability.

evolution of intelligence | causal cognition | corvids

Imagine a bird looking down on a monkey moving through a forest canopy. Generally, the bird will be able to observe both the monkey moving and the canopy shaking at the same time. Sometimes, however, when the canopy is thick overhead, the bird may only observe that, against a background of stationery leaves, there are waves of moving leaves that can start and stop abruptly. Humans are able to imagine why the leaves are moving when the monkey is out of sight. They can hypothesize that there is a hidden causal agent that must be moving the leaves because when the wind is not blowing, the canopy does not shake on its own. We make such inferences from a very early age. Between 7–10 mo of age, infants begin to show surprise if a bean bag is thrown from behind a screen and the screen is then lifted to show an inert object, rather than a causal agent such as a hand (1, 2). The use of such causal reasoning underpins not only scientific (3) and religious thought (4, 5) but also our sophisticated tool-using abilities (6) and understanding of social interactions (7–9). However, we currently have little idea how such cognition evolved.

One way to increase our knowledge would be to study the evolution of this type of causal reasoning in other species. Unfortunately, there is no evidence to date that any nonhuman animal has the ability to make inferences about hidden causal mechanisms (10–14). However, no studies have attempted to recreate ecological situations, such as the canopy problem outlined above, where the ability to make inferences about hidden causal agents would be highly adaptive. To solve the canopy problem an animal must infer the presence of a hidden causal agent from the movement of an inanimate object. We presented eight New Caledonian crows, a species that has produced behavior suggestive of complex causal cognition (15–23), with the hidden causal agent (HCA) problem. This experimental paradigm mirrored the canopy problem by creating a situation where an animal had to infer what caused an inanimate object to move. The crows were first given experience extracting food with a tool from a box. The box was then placed close to a novel hide that had been setup in the crows' aviary. The entrance to the box faced the hide, so crows had to turn their heads directly away from the hide to pull the food out of the tube with the tool. Testing began once the crows were able to extract the food when the box was 20 cm from the hide. The crows were first given three trials of the hidden causal agent (HCA) condition. Here, they observed two humans walk into the aviary. One, the agent, walked into the hide and so became hidden from the crows. A wooden stick was then probed in and out of a hole in the hide wall 15 times toward the baited hole. The agent then exited the hide and left the room. At this point the second human, who had stood 1.5 m from the hide in the corner of the room with closed eyes and hands held in front of the body, also left the room. The crow was now free to come down to the table, pick up a tool, and use it to extract the food from the box. The crows were then given three trials of the unknown causal agent (UCA) condition. Here, one human entered the cage and stood in the far corner, with closed eyes and hands held in front of the body as before. The tool was then probed through the hole in the hide 15 times. The human then left, and the crows again were free to come down to extract food. In both the HCA and UCA conditions, the stick moved in the same way because it was actually moved by an experimenter pulling on a string that could be pulled either from within the hide or from outside the testing room.

The movement of the probing stick was a novel stimulus and, thus, likely to elicit neophobic responses from the crows. The movement of the stick was also likely to be an aversive stimulus for the crows as it moved into the space where the crows would put their heads when they attempted to extract the food from the box. When the crows used a tool in the hole, they had to face away from the hide and, thus, could not easily monitor whether the stick was being moved. Thus, a repetition of the sticks' movement was likely to result in the stick hitting the crows in the back of the head. (Of course, in reality, there was no chance of the stick hitting the crows because the experimenter never pulled the string when the crows were on the table.) For the crows to extract food in this situation, they needed to minimize the perceived risk of being hit by the stick emerging from the hide during tool use. There were two potential ways they could do this. First, they could be very cautious after seeing this stick being probed for the first time. The level of caution would then be progressively reduced each time the crows used a tool in the box and the stick did not appear. That is, the crows would initially show a neophobic response and then gradually habituate (24, 25). An alternative way for the crows to minimize risk would be for the crows to predict the stick's movement by reasoning about why the stick was moving. In the first condition, the crows

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observed the human enter the hide, the stick move, and the human leave both the hide and cage. If the crows could attribute the stick's movement to the hidden human, they could infer that when the human left the room, the stick would not move again. In contrast, in the second, unknown condition, if the crows were capable of causal reasoning, they would predict that the stick might move again because they had not observed a potential causal agent leave the hide. This "causal reasoning hypothesis," therefore, made the opposite prediction from the "habituation hypothesis" outlined above. In the hidden agent condition, the crows should show similar levels of caution to those in the final trial of habituation to the hide. In the unknown condition, the crows should show a high level of caution, despite the movement of the stick no longer being a novel stimulus.

To test between these hypotheses, we measured the degree of caution in the crows' behavior. We examined the number of times the crows both inspected the hide and abandoned probing across our experiment. Hide inspections were defined as a crow orientating its head toward the hole and then moving its head toward the hide, so that one or both eyes was/were in line with the hide. Orientations to the hide were not scored if the crow was not first looking toward the baited hole or if the crow looked at an area of the cage other than the hide after looking at the hole. An abandoned probe was defined as a crow inserting the tool into the hole and then leaving the testing area without extracting the food.

Results and Discussion

Our results provide strong support for the causal reasoning hypothesis. Inspection rates were higher in the three trials of the UCA condition than in the human agent (HCA) condition (Wilcoxon signed rank test; $n = 8$; $Z = 3.171$; $P = 0.002$) (Fig. 1 and Movie S1). Every crow also had a higher inspection rate on the first trial of the UCA condition than the HCA condition (Wilcoxon signed rank test; $n = 8$; $Z = 2.521$; $P = 0.008$). The overall difference between conditions was not solely attributable to differences in inspection rate on the first trial. Inspection rates were also higher in the unknown condition in the second trial condition (Wilcoxon signed rank test; $n = 8$; $Z = 2.521$; $P = 0.008$), although not the third trial (Wilcoxon signed rank test; $n = 8$; $Z= 0.70$; $P = 0.547$) (Fig. 1). In contrast to these results, there was no difference in inspection rate between the last habitation trial and the first HCA condition trial (Wilcoxon signed rank test; $n = 8$; $Z = 0.14$; $P = 0.945$) (Fig. 1). Individual differences in inspection rate were not significantly different for crows of different sex (Mann–Whitney rank sum test; $n = 8$; $U = 3$; $P = 0.2$) or age (adults vs. subadult and juvenile) (Mann–Whitney rank sum test; $n = 8$; $U = 6$; $P = 0.786$).

The differences in inspection rate between the two conditions were mirrored in other aspects of the crows' behavior. No crow abandoned probing in the HCA condition or during the final trial of habituation. However, in the UCA condition, four birds stopped probing and left the table at least once (mean ± SE, 2.75 ± 1.03) (Fig. 2). Of the four crows that abandoned probing, two were male and one was juvenile, which suggests that neither sex nor age were strong predictors of this response type either.

These results show that New Caledonian crows, like humans, can attribute an observable event to a hidden causal agent. When the stick moved while a potential agent was in the hide, and that agent then departed, the crows had a relatively low inspection rate. All of the crows we tested, however, increased their inspection rates after observing the stick move when no potential causal agent was present. In fact, inspection rates were far higher in the first trial of the unknown agent condition than in the first human agent trial. This was despite the human trial being the first time the crows had observed the novel stimuli of a stick emerging from the hide and a human entering and exiting the hide. Similarly, no crows abandoned probing and left the table when the stick emerged from the hide for the first time, but some did when the stick's movement could not be attributed to a causal agent. Given the probing stick was a novel, aversive stimulus to the crows, a purely associative account would struggle to explain why the crows reacted to this stimulus in the unknown causal condition but not in the human condition. This pattern of

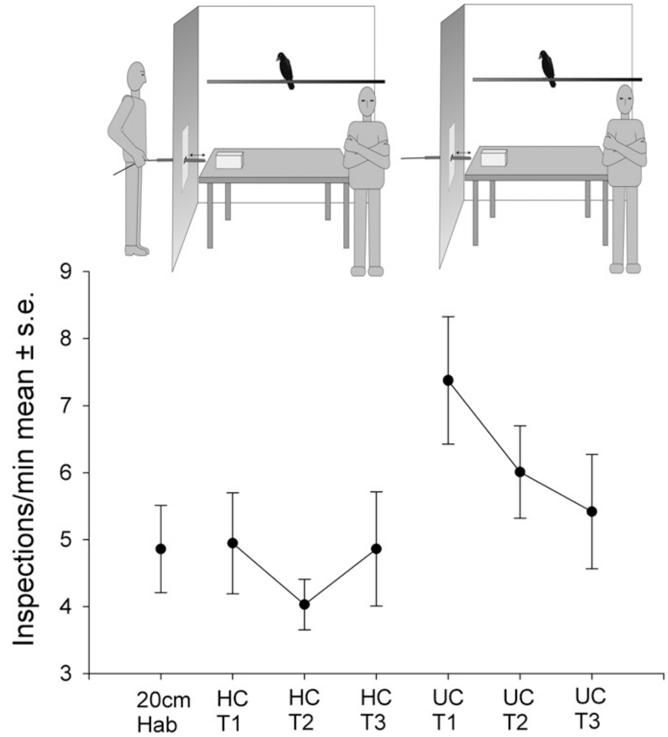

Fig. 1. Inspection rate across conditions. Final habituation trial before testing is indicated by 20cm hab. (*Upper Left*) Diagram of the HCA condition. (*Upper Right*) Diagram of the UCA condition. In the HCA condition, one human walked into the hide and one stood in the corner of the room. A wooden stick was then probed from the hide. The agent then exited the hide. Both humans then left the room. In the UCA condition, one human entered the cage and stood in the corner. The tool was then probed through the hole. The human then left.

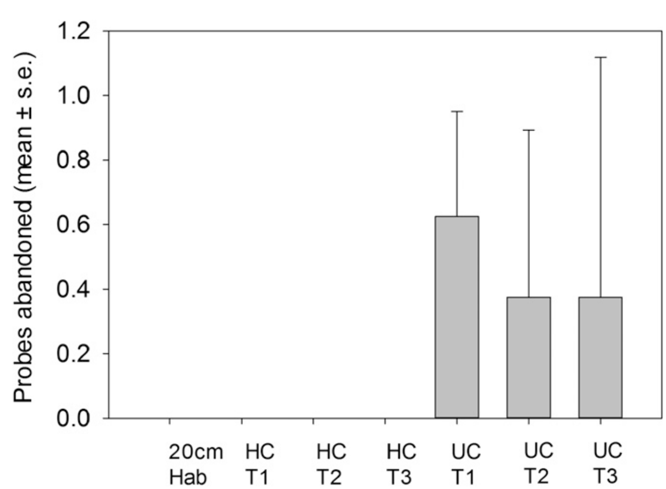

Fig. 2. Average probes abandoned across conditions. Final habituation trial before testing is indicated by 20cm hab. An abandoned probe was defined as a crow inserting the tool into the hole and then leaving the testing area without extracting the food.

results is, however, predicted by a causal account of the crows' actions: the crows attributed the movement of the stick in the human condition to the agent inside the hide and, so, inferred that the stick was unlikely to be probed again once the human had left the hide. In the unknown condition, there was no recently departed causal agent to attribute the movement of the stick to, so the crows reasoned the stick could be probed again.

Darwin himself speculated that a dog barking at a parasol moving slightly in a breeze might be because the dog reasoned that "movement without any apparent cause indicated the presence of some strange living agent" (26). There is also evidence of crows reacting differently to the presence of hunters remaining within versus vacating a hide (27). Our results suggest that these animal behaviors may be underpinned by complex cognition. The ability to make inferences about why an inanimate object is moving would be highly adaptive in many ecological situations, such as the canopy problem outlined above. It is, therefore, possible that the ability to reason about hidden causal agents is far more widespread in the animal kingdom than has been thought previously. Alternatively, additional selective pressures may be required to scaffold the evolution of this ability, such as those created by extractive foraging (28), tool use, tool manufacture, and complex social interactions (29). Future comparative tests presenting the HCA methodology to animal species with different levels of sociality, tool use, and predation should help in understanding the type of selective pressures that led to the evolution of this ability.

Methods

We carried out the experiment with eight wild crows captured on the island of Maré, New Caledonia. Five of the crows were adults, and three were subadults. Based on sexual size dimorphism (30), four were females. The crows were housed in a five-cage outdoor aviary; the cages varied in size but were all at least 8 m^2 in area and 3 m high. All crows were released at their site of capture after testing. Birds were not deprived of food before testing.

Habituation to the blue hide (200 cm × 50 cm × 50 cm) began with the crows being given trials extracting food from a box (15 cm × 5 cm × 2 cm) facing away from the hide and positioned 100 cm away. Once the crows had reached a criterion of extracting food in two consecutive 3-min trials, the box was positioned 100 cm away but facing the hide. Once criterion was again reached, the box was then put 50 cm and then 20 cm away. Once crows again reached criterion, the box was positioned 20 cm away from the hide. Criterion at this point was changed to extracting food within one trial of 60 s. If crows did not reach criterion, the box was placed at the last distance the crows reached criterion. Crows had to reach criterion again to move to the closer distance. Once the 20-cm criterion was passed, the crows received the HCA condition and then the UCA condition. Trial 1 of the HCA condition was, therefore, the first time the crows had observed a human enter or exit the hide. In both conditions, the same experimenter pulled the string. The presence of the second human in both conditions was to ensure the crow did not interact with the apparatus when the stick was moving. A trial started when the crow landed on the table and ended when the crow got food or after 2 min. Inspection rate was calculated as the number of hide inspections over the latency between a crow picking up a tool and extracting the food. Data were coded by two observers. Interreliability was 91%. This study was carried out under the ethics approval of the University of Auckland (reference no. R602).

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