



An end to insight? New Caledonian crows can spontaneously solve problems without planning their actions

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Animals rarely solve problems spontaneously. Some bird species, however, can immediately find a solution to the string-pulling problem. They are able to rapidly gain access to food hung on the end of a long string by repeatedly pulling and then stepping on the string. It is currently unclear whether these spontaneous solutions are produced by insight or by a perceptual-motor feedback loop. Here, we presented New Caledonian crows and humans with a novel horizontal string-pulling task. While the humans succeeded, no individual crow showed a significant preference for the connected string, and all but one failed to gain the food even once. These results clearly show that string pulling in New Caledonian crows is generated not by insight, but by perceptual feedback. Animals can spontaneously solve problems without planning their actions.

Keywords: New Caledonian crows; string pulling; insight; perceptual-motor feedback loop; mental scenario building; intermediate cognition

1. INTRODUCTION

How do animals solve complex problems? We currently have little idea exactly what goes through an animal's mind when faced with a cognitively challenging situation. This has led to a number of researchers calling for studies that not only document the behaviour of an animal but also pinpoint the actual cognitive mechanisms used during problem solving [1-3].

One of the most famous examples of spontaneous problem solving in animals is string pulling. When food is hung from a perch by a string, some corvids [4-6] and psittacids [7-9] can, without a single mistake, pull up the string to obtain the food. This is accomplished by the repetition of two actions: pulling up a segment of string and then stepping on it to prevent it from dropping. However, although string pulling was first documented hundreds of years ago [10], we still do not know what cognitive processes are used by birds when they solve this problem.

The 'insight' hypothesis [4,5,11,12] suggests that the birds mentally model their future actions. That is, they imagine the effect that repeatedly pulling and then stepping on the string will have on the position of the food, realize such actions will gain them the food and then execute these actions. The 'feedback loop' hypothesis [6,13] suggests that food moving towards the bird acts as an internal psychological reinforcer that motivates it to repeat pull-step actions. Positive movement of the food following the initial pull drives the bird to first step on the string to prevent it from moving away, and then to repeat the pulling action. Stepping occurs because the animal has learnt from prior foraging experience that positioning objects under the foot allows the beak to be freed for further action.

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Currently, there is no conclusive evidence for either of these hypotheses. The insight hypothesis is supported by a study that presented ravens with a counterintuitive problem where string had to be pulled down in order for the food to move up and towards the bird [5]. Ravens with prior experience of string pulling were able to solve this, but naive ravens were not. The failure to solve a counterintuitive problem where string had to be pulled down to move food up led the authors to suggest that the ravens did understand the cause-effect relationship between string, food and body. However, these results can also be accounted for by the feedback loop hypothesis. The naive crows had no experience with pull-stepping. To spontaneously string pull, these birds needed to both coordinate these novel behaviours and observe how their actions changed the position of the reward. Therefore, they would have had to divide their attention between looking up at the string, down at their feet, and over and down at the food. This need for divided attention could have interrupted the perceptualmotor feedback loop and so prevented spontaneous string pulling. By contrast, the experienced birds had already learnt to coordinate pull-steps and so could have paid sufficient attention to the effects of their actions on the string for the feedback loop to be established.

The feedback loop hypothesis is supported by the finding that New Caledonian crows fail to solve the string-pulling problem when visual feedback is restricted [6]. When naive crows had to pull food up through a small hole in a wooden platform, they failed to produce pull-step sequences, and even experienced crows did not solve the problem immediately. However, not only was sample size low in the study, but also the mechanical difficulties associated with pulling the string through the hole might have interfered with problem solving. Further evidence is needed before we can conclude that perceptual feedback of the reward moving towards a bird does in fact drive string pulling.

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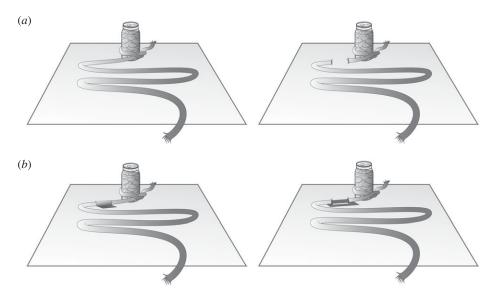


Figure 1. Diagram of the string connectivity problems. (a) The set-up in experiment 1. Humans had to decide if they would pull a money jar with string connected to it or a money jar with string not connected to it. For the crows, the money jar was replaced with meat. (b) The path connectivity control. Humans had to choose between a connected string that had a cloth wrapped around it and a disconnected string that was positioned so that the gap between the two disconnected pieces was spanned by a piece of white tape. Again the jar of money was replaced with meat for the crows.

The insight and feedback loop hypotheses make testable predictions about two aspects of spontaneous string pulling: the role of feedback and the role of causal knowledge. The insight hypothesis predicts that an animal should not need to receive perceptual feedback of the food moving towards it during string pulling because it has already mentally modelled the effect of its actions. It also predicts that the animal must understand the causality of the string (connectivity): that pulling one end of the string will move the other end. An animal cannot mentally model the effect of its future behaviour if it does not understand how the object it is interacting with works. By contrast, the feedback loop hypothesis predicts that an animal's success will be dependent on its observation of the food moving towards itself and that it need not understand how string works.

Here, we created a task with elements from two previous bird studies [9,14], and presented it to humans and New Caledonian crows in order to test these predictions. Crows naive to string pulling had to choose between two coiled horizontal strings, only one of which was connected to the food. This simultaneously tested (i) whether the crows were dependent on feedback from the food moving towards them during string pulling and (ii) whether they were sensitive to the connectedness of the string. The task was presented to humans as a result of work showing that physical cognition tasks used with animals are not always solved by humans, as might be expected [15,16]. Therefore, to ensure the validity of our novel experimental paradigm, we tested whether humans could predict the correct course of action to take when viewing the experimental stimuli from the same perspective as the crows.

2. METHODS

We first tested 50 undergraduate students enrolled at Auckland University with our connectivity task. The humans were shown two photos of a coiled rope attached

to a jar of money. In experiment 1, one photo pictured a continuous rope, and the other a rope divided into two segments separated by a gap of 15 cm (figure 1a; electronic supplementary material, figure S1). Subjects read the statement: 'Please choose the rope you would pull to get the jar full of money'. Subjects received a single trial of this experiment. This experiment tested whether humans could discriminate between a connected and disconnected rope. Success at this experiment would show that humans had used either an understanding of physical connectivity or perceptual continuity to solve the problem. That is, either the subjects understood that pulling one end of the string made the other move because the string was connected to the money, or they had learnt that pulling one end of a perceptually continuous object often led to reward. Experiment 2 tested between these two possibilities. Connection often covaries with perceptual continuity: a string tied to food is both connected and perceptually continuous with the reward. Humans have previously been shown to ignore perceptual features, such as the degree of contact between two objects, and instead attend to physical connection [16]. That is, humans understand that covariation is not the same as causation in regard to connectivity. Here, we examined whether humans showed this same level of understanding with the stimuli used in our experiment by interrupting the correlation between physical connection and perceptual continuity. In this experiment, one photo pictured two rope segments separated by a gap of 20 cm. This gap was spanned by a line of white tape stuck onto a blue cloth. The rope segments were positioned on top of the tape, but were not attached to it. Thus, there was perceptual continuity but no physical connection. The other photo pictured a continuous rope with a blue cloth piece wrapped around it tightly, so that the outline of the continuous rope could be seen (figure 1b; electronic supplementary material, figure S2). Thus, there was physical connection but no perceptual continuity owing to the blue cloth. Again, subjects were given a single trial. If subjects were using perceptual continuity rather than an understanding of string connectivity to make their choice, they should prefer the option that maintained a perceptually continuous path between string and reward. By contrast, if the subjects understood physical connectivity, then they should have rejected the photo of the discontinuous string placed on a segment of tape and instead preferred the photo where the string disappeared beneath the cloth but clearly remained intact. That is, they should have predicted more chance of success when pulling a clearly continuous rope that had a segment perceptually obscured than a clearly cut rope that had been placed on (and so was in contact with) a segment of tape. This study was carried out under the ethics approval of the University of Auckland (reference 2011/433).

We then carried out the experiment with 11 wild crows captured on the island of Maré, New Caledonia. On the basis of sexual size dimorphism [17], four of the crows were female. Eight of the crows were adults more than 2 years old, and three were sub-adults less than 2 years old (two females and one male). The crows were housed in a five-cage outdoor aviary close to the location of capture; the cages varied in size but were all at least 8 m² in area and 3 m high. The crows were first habituated to rope by tying several pieces between two perches in their aviary. To ensure crows were habituated, a rope was put on the edge of a table located outside their aviary, and the crows were allowed to retrieve a piece of meat placed on the segment that protruded into their cage. In the experimental task, the crows were presented with two pieces of rope positioned on the table outside their aviary. The crows had no prior experience of pulling string vertically or horizontally. As in experiment 1 of the human experiments, one piece of coiled rope was continuous, while the second was composed of two rope segments separated by a 10 cm gap (electronic supplementary material, figure S3). Both ropes had meat attached at their end. The rope segments were first presented out of reach of the crows for 20 s to allow the crows to observe both options. After the observation period, the rope ends were placed within reach of the crows. Trials ended once the crows gained the food, interacted with one string and then attempted to interact with the other, or did not interact with the string for 3 min. If a crow failed to interact with the string for the first 2 min of the trial, bait was placed on the perch to determine whether the crow was still sufficiently motivated. If a crow failed to interact for the full 3 min, we reran the habituation procedure outlined earlier. If a crow took the meat from the perch and from the string across three consecutive trials and habituation tests but did not at any point interact with either of the strings in the experimental trials, testing stopped. If birds did respond, the testing ended after 20 trials. To move onto experiment 2, a subject needed to have a significant preference for the connected string. All binomial choice tests were one-tailed, as we were testing a directional hypothesis that crows would perform above chance. All crows were released at their site of capture after testing. This study was carried out under the ethics approval of the University of Auckland (reference R602).

3. RESULTS

In our human study, 49/50 students chose the correct option in experiment 1 (binomial choice p < 0.00001), and 42/50 students chose the correct option in experiment 2 (binomial choice p < 0.00001). The difference between the two experiments does raise the possibility that seven humans (14% of subjects) actually relied on path continuity, rather than on a causal understanding of string connectivity when solving the first task.

In our crow study, 8/11 crows chose the connected string on their first trial (binomial choice p = 0.11). Only one subject completed 20 trials. He scored 13/20 (binomial choice p = 0.13). All the other crows stopped interacting with the string before they had completed 20 experimental trials. In fact, they failed to pull the string sufficiently for the reward to move even once. We analysed the behaviour of these 10 birds as a group. On average, these crows made a choice in 2.5 ± 0.6 trials (mean \pm s.e.) before they then stopped interacting with the string. In the trials where they interacted with a string, the crows chose the connected string on 16/25 trials (binomial choice p = 0.11). Combining the data for the entire group, however, did lead to a significant result, with the crows showing a significant preference for the connected string (binomial choice p = 0.037). Owing to no crow individually showing a significant preference for the connected string, testing ended after experiment 1.

4. DISCUSSION

Adult humans were able to mentally solve a novel stringpulling problem by using a causal understanding of connectivity. String pulling may, however, be a non-trivial task for adults. The failure of the second experiment by 14 per cent of the test subjects raises the possibility that some humans might have relied on the perceptual cue of path continuity, rather than on a causal understanding of the task. Alternatively, these subjects may have had an understanding of connectivity but believed that the tape was connected in some way to the string and thus was a better option than the perceptually discontinuous string. Further testing is required to discriminate between these two possibilities. In contrast to the humans, New Caledonian crows were unable to solve even experiment 1 successfully. In fact, only one crow completed this experiment. The other crows failed to pull the string a sufficient number of times for the reward or string end to begin moving at all. Furthermore, no crow individually attended to the connectivity of the string during string pulling, as evidenced by their lack of preference for the connected string in experiment 1. However, combining together the data from all the crows led us to find a significant preference for the connected string, which raises two possibilities. The first is that this was a statistical fluke created by combining together all the individual data. The second is that the crows did have an understanding of connectivity, but were unable to use this information in a mental scenario to predict that continued string pulling would lead to reward and so motivate themselves to continue pulling the correct string. While it seems likely that the first possibility is correct, given the individual performances of the crows, further work is required to confirm this.

However, this experiment does provide strong evidence against the insight hypothesis. Without perceptual feedback, all but one of the New Caledonian crows tested did not spontaneously pull the string a sufficient number of times to get the reward, a performance very

different to that seen in vertical string-pulling experiments [6]. If the crows had been mentally simulating their interaction with the string, they should have been able to predict the effect of repeated pulling, and so been motivated to carry on string pulling without feedback. Our results clearly demonstrate that such motivation was lacking. The findings here instead provide support for the feedback loop hypothesis, which can also account for the results found in previous studies on string pulling in birds [4-8]. The failure of New Caledonian crows to solve the string-pulling problem when feedback is interrupted [6] or removed (this study), and the failure of chimpanzees to solve a problem highly similar to vertical string pulling without perceptual feedback [18], strongly suggests that such feedback is a key component of this type of problem solving. Testing whether crows discriminate between connected and disconnected uncoiled strings after limited experience would provide further evidence in support of this conclusion.

The findings that New Caledonian crows can spontaneously solve vertical string-pulling problems [6], combined with the findings here, show that spontaneous solutions to novel problems are possible without the behaviours involved being simulated mentally. This brings into question a number of studies purporting to show 'meansend understanding' in humans and other animals. In these studies, it has been suggested that subjects understand that an object such as a cloth is a means to an end (food placed at the end of the cloth). That is, the subjects understand that pulling on one end of the cloth leads to the other end of the cloth, and the food placed on it, moving within reach. Use of path continuity alongside a perceptual-motor feedback loop could account for results where infants [19], elephants [20], monkeys [21] and apes [22] pull an object on a cloth towards them. The positive feedback of an object positioned on a cloth moving towards a subject when the cloth is pulled could drive means-end solutions, rather than an understanding that the object is supported by the cloth such that pulling on one end will lead the other end to move. Testing this possibility may indicate that means-end understanding is less widespread across the animal kingdom than previously thought. Perceptual feedback may also be important to the solution to other types of problems, such as the Aesop's fable task [13,23].

While operant conditioning is a necessary component of the perceptual feedback loop, in that the positive movement of an attractive stimulus towards an animal drives string pulling, it is not sufficient. This is shown by the performances of siskins and goldfinches on string-pulling problems. Both these species use their feet to hold buds, seeds and grass stems, and so possess the necessary behavioural prerequisite for string pulling [24]. However, while they can learn through operant conditioning, they do not spontaneously solve the string-pulling problem [25]. What additional element is required for the establishment of the perceptual feedback loop?

The key to establishing a feedback loop is to note the effect of pulling and stepping: that the food has moved closer. To do this, an animal must pay close attention to the position of the food before and after these behaviours. However, during the execution of the pull-steps, the animal also has to pay attention to its own actions on the string. Formation of a feedback loop therefore

requires attention to be split between the movement of the food and the movement of the animal's own body.

We suggest that there are two ways this problem of split attention could be ameliorated, though there are likely to be others. The integration hypothesis [6] suggests that the faster the information can be integrated between the perceptual and motor pathways, the easier it is for the animal to note the effects of its actions while coordinating pullsteps. That is, animals with more direct routes of connection between specific parts of the brain are able to notice the effects of their action quicker, and so have more time to coordinate the actions of their body. It therefore predicts that species (and individuals) with larger associative brain areas and/or more connected perceptual and motor pathways will be better at string pulling. An alternative laterality hypothesis suggests that the more highly lateralized an animal is, the greater its ability to focus at the same time on both the body's actions and the movement of the food, and so form a stable perceptual-motor feedback loop. This is because one of the advantages of extreme cerebral lateralization is the ability to process several sources of information being received simultaneously [26-29]. The laterality hypothesis therefore predicts that more lateralized species (and individuals) would be better at string pulling.

These hypotheses are intriguing. They suggest that, though the string-pulling task can be solved by a perceptual feedback loop mediated by operant conditioning, it is still a direct test of intelligence. However, it tests for a type of intelligence intermediate between basic learning processes and human-level cognition. While spontaneous string pulling in birds does not require complex cognitive software (i.e. mental modelling of causal relations), it may well require specific neural hardware. As our hypotheses suggest, the structure of the brain, in terms of its level of specialization and/or degree of connectivity between different brain areas, could well explain why some species solve this problem so quickly, and some do not. Testing these hypotheses may therefore open the door for string pulling to be used as a useful behavioural proxy for specific neural capacities.

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REFERENCES

- 1 De Waal, F. & Ferrari, P. F. 2010 Towards a bottom-up perspective on animal and human cognition. *Trends Cogn. Sci.* **14**, 201–207. (doi:10.1016/j.tics.2010.03.003)
- 2 Heyes, C. 2012 Simple minds: a qualified defence of associative learning. *Phil. Trans R. Soc. B* **367**, 2695–2703. (doi:10.1098/rstb.2012.0217)

- 3 Seed, A. & Byrne, R. 2010 Animal tool-use. Curr. Biol. 20, R1032-R1039. (doi:10.1016/j.cub.2010.09.042)
- 4 Heinrich, B. 1995 An experimental investigation of insight in common ravens (Corvus corax). Auk 112, 994-1003. (doi:10.2307/4089030)
- 5 Heinrich, B. & Bugnyar, T. 2005 Testing problem solving in ravens: string-pulling to reach food. Ethology 111, 962-976. (doi:10.1111/j.1439-0310.2005.01133.x)
- 6 Taylor, A. H., Medina, F. S., Holzhaider, J. C., Hearne, L. J., Hunt, G. R. & Gray, R. D. 2010 An investigation into the cognition behind spontaneous string pulling in New Caledonian crows. PLoS ONE 5, e9345. (doi:10. 1371/journal.pone.0009345)
- 7 Pepperberg, I. M. 2004 'Insightful' string-pulling in grey parrots (Psittacus erithacus) is affected by vocal competence. Anim. Cogn. 7, 263-266. (doi:10.1007/s10071-004-0218-y)
- 8 Werdenich, D. & Huber, L. 2006 A case of quick problem solving in birds: string pulling in keas, Nestor notabilis. Anim. Behav. 71, 855-863. (doi:10.1016/j.anbehav.2005.06.018)
- 9 Schuck-Paim, C., Borsari, A. & Ottoni, E. B. 2009 Means to an end: neotropical parrots manage to pull strings to meet their goals. Anim. Cogn. 12, 287-301. (doi:10.1007/s10071-008-0190-z)
- 10 Plinius, C. 1554 Historiae mundi Libri XXXVII. Frankfurt, Germany: Johan Feyerabendt.
- 11 Emery, N. J. & Clayton, N. S. 2004 The mentality of crows: convergent evolution of intelligence in corvids and apes. Science 306, 1903-1907. (doi:10.1126/science.1098410)
- 12 Heinrich, B. 2011 Conflict, cooperation, and cognition in the common raven. Adv. Study Behav. 43, 189-237. (doi:10.1016/B978-0-12-380896-7.00004-6)
- 13 Taylor, A. H. & Gray, R. D. 2009 Animal cognition: Aesop's fable flies from fiction to fact. Curr. Biol. 19, R731-R732. (doi:10.1016/j.cub.2009.07.055)
- 14 Auersperg, A. M. I., Gajdon, G. K. & Huber, L. 2009 Kea (Nestor notabilis) consider spatial relationships between objects in the support problem. Biol. Lett. 5, 455-458. (doi:10.1098/rsbl.2009.0114)
- 15 Silva, F. J., Page, D. M. & Silva, K. M. 2005 Methodological-conceptual problems in the study of chimpanzees' folk physics: how studies with adult humans can help. Learn. Behav. 33, 47-58. (doi:10. 3758/BF03196049)
- 16 Silva, F., Silva, K., Cover, K., Leslie, A. & Rubalcaba, M. 2008 Humans' folk physics is sensitive to physical connection and contact between a tool and reward. Behav. Process. 77, 327-333. (doi:10.1016/j.beproc. 2007.08.001)
- 17 Kenward, B., Rutz, C., Weir, A. A. S., Chappell, J. & Kacelnik, A. 2004 Morphology and sexual dimorphism

- of the New Caledonian crow Corvus moneduloides, with notes on its behaviour and ecology. Ibis 146, 652-660. (doi:10.1111/j.1474-919x.2004.00299.x)
- 18 Völter, C. J. & Call, J. 2012 Problem solving in great apes (Pan paniscus, Pan troglodytes, Gorilla gorilla, and Pongo abelii): the effect of visual feedback. Anim. Cogn. 15, 923-936. (doi:10.1007/s10071-012-0519-5)
- Willatts, P. 1984 The stage-IV infant's solution of problems requiring the use of supports. Infant Behav. Dev. 7, 125–134. (doi:10.1016/S0163-6383(84)80053-3)
- 20 Irie-Sugimoto, N., Kobayashi, T., Sato, T. & Hasegawa, T. 2008 Evidence of means-end behavior in Asian elephants (Elephas maximus). Anim. Cogn. 11, 359-365. (doi:10.1007/s10071-007-0126-z)
- Santos, L. R., Rosati, A., Sproul, C., Spaulding, B. & Hauser, M. D. 2005 Means-means-end tool choice in cotton-top tamarins (Saguinus oedipus): finding the limits on primates' knowledge of tools. Anim. Cogn. 8, 236-246. (doi:10.1007/s10071-004-0246-7)
- 22 Spinozzi, G. & Potí, P. 1993 Piagetian stage 5 in two infant chimpanzees (Pan troglodytes): the development of permanence of objects and the spatialization of causality. Int. J. Primatol. 14, 905-917. (doi:10.1007/ BF02220259)
- 23 Taylor, A. H., Elliffe, D. M., Hunt, G. R., Emery, N. J., Clayton, N. S. & Gray, R. D. 2011 New Caledonian crows learn the functional properties of novel tool types. PLoS ONE 6, e26887. (doi:10.1371/journal. pone.0026887)
- 24 Perrins, C. 1994 Handbook of the birds of Middle East and North Africa, vol. 8. Oxford, UK: Oxford University
- 25 Seibt, U. & Wickler, W. 2006 Individuality in problem solving: string pulling in two Carduelis species (Aves: Passeriformes). Ethology 112, 493-502. (doi:10.1111/j. 1439-0310.2005.01172.x)
- 26 Rogers, L. J. 2000 Evolution of hemispheric specialization: advantages and disadvantages. Brain Lang. 73, 236-253. (doi:10.1006/brln.2000.2305)
- 27 Rogers, L. J., Zucca, P. & Vallortigara, G. 2004 Advantages of having a lateralized brain. Proc. R. Soc. Lond. B 271(Suppl. 6), S420-S422. (doi:10.1098/rsbl.2004.
- 28 Güntürkün, O., Diekamp, B., Manns, M., Nottelmann, F., Prior, H., Schwarz, A. & Skiba, M. 2000 Asymmetry pays: visual lateralization improves discrimination success in pigeons. Curr. Biol. 10, 1079-1081. (doi:10.1016/ S0960-9822(00)00671-0)
- 29 Magat, M. & Brown, C. 2009 Laterality enhances cognition in Australian parrots. Proc. R. Soc. B 276, 4155-4162. (doi:10.1098/rspb.2009.1397)