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New Caledonian Crows Can Interconnect Behaviors Learned in Different Contexts, with Different Consequences, and After Exposure to Failure

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Interconnection of behaviors is a process that describes how independently acquired behavioral repertoires can be combined together as a new sequence of behaviors. Manipulations of training, training context, and experience of failure in the test situation can hinder this interconnection of previously acquired behaviors. We tested whether wild New Caledonian crows (*Corvus moneduloides*) could perform a sequence of 6 independently acquired behaviors in order to fetch a stone from inside a box in a nearby room and use it to gain food from a stone-dropping apparatus. However, crows were only trained on 3 or 4 of the 6 behaviors required, and these prerequisites were trained in different contexts. One of the crows that learned 4 prerequisites solved the task. Neither of the crows that learned 3 prerequisites solved the task. The crows that learned 4 prerequisites but did not solve the problem were later trained in an additional behavior and then were able to solve the task. These results show that New Caledonian crows are able to produce novel behavioral solutions to new problems by interconnecting behaviors learned in different contexts, with different consequences, and, despite experience of failure, after the first exposure to the task.

Keywords: problem solving, innovation, creativity, insight, comparative cognition

A problem is any situation in which an organism does not have an immediate response to achieve a goal, and, thus, this organism needs to “find a solution” to the problem at hand (Chappell et al., 2015). One way to “find” the solution of a problem is by trial-and-error (i.e., by interacting and learning with the immediate environment until problem solving is gradually reached). Another way is to reorganize previous experiences with components of a problem situation into a new sequence of behaviors that leads to problem solving (Epstein, 2015; Shettleworth, 2012).

Investigating the role of learning on problem solving, Epstein, Kirshnit, Lanza, and Rubin (1984) identified that the training of prerequisite behaviors of a given task facilitated problem solving. The authors trained pigeons (*Columba livia*) to perform two behavioral sequences independently: (1) to push a box towards a green spot and (2) to climb a box located beneath a target and peck this target. In a test situation, later called the box displacement test (Cook & Fowler, 2014), the target and the box were presented, and the box was placed at a distance from the target. To solve the problem, the pigeons had to push the box towards the target, stop when the box was beneath

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the target, climb the box, and peck the target, a sequence of behaviors never directly trained. Subjects trained in all two prerequisite behaviors were able to solve the problem, and the solution was akin to classic "insightful" problem solving, as described by Köhler (1917/1948). This "insightful" performance in pigeons was described as an initial state of "confusion," in which the pigeons stared at the box and at the target, followed by the sudden emergence of responses of pushing the box in the direction of the target and immediately climbing and pecking the target as soon as the box was near it. Pigeons that learned only one of the two behaviors, or had incomplete training (i.e., learned only non-directional pushing) did not solve the problem or solved it in a nondirectional fashion.

Epstein et al.'s (1984) experiment shows that, given a problem situation, independently learned behaviors can come together to form a new sequence that leads to problem solving. Epstein (1985, 2015) called this coming together of independently acquired behaviors the "interconnection of previously acquired behavioral repertoires." This interconnection of behaviors was initially described only by associative processes, such as operant reinforcement, extinction, and resurgence (Epstein, 1985, 2015). However, cognitive mechanisms involved in this process, such as memory and causal reasoning, are currently being investigated (Cook & Fowler, 2014; Neves Filho, Carvalho Neto, Taytelbaum, Malheiros, & Knaus, 2016). The key difference between the interconnection of behaviors and classic behavioral chaining is that, in classic chaining, all behaviors of the chain are trained in succession and the consequence of one behavior is the cue, the discriminative stimulus, for the next one. That is, the links are explicitly trained, so that the cue works in a manner akin to a conditioned reinforcer. In interconnection procedures, this explicit training of chaining behaviors does not occur. Instead, the prerequisites of a given task are trained independently. A classic chaining procedure aims to produce a deterministic and rigid chaining, because all links between behaviors are explicitly trained. In contrast, during interconnection procedures, the animal has to "decide" which behavior it will do after performing the first, which has been shown to be influenced by prior training history. For example, two variables, (1) the contexts of training and testing (Neves Filho, Carvalho Neto, Barros, & Costa, 2014) and (2) whether failure in the test setting has been experienced before training of all prerequisites behaviors (Neves Filho, Stella, Dicezare, & Garcia-Mijares, 2015) seem to interrupt mammals' abilities to interconnect independently acquired behaviors into a longer sequence of coherent behavior.

Context dependent learning has been studied since the 1930s (e.g., Maier, 1931; Spencer & Weisberg, 1986). In most cases, problem solving is facilitated if environmental variables (such as context and consequences) are made stable, rather than variable, during training and testing (Birch & Rabinowitz, 1951; Griffin, Guez, Lermite, & Patience, 2013; Maier, 1940; Neves Filho et al., 2014). In an interconnection task involving two behaviors in capuchin monkeys (*Sapajus* spp.), when one behavior was trained in a different context than the training of the second behavior, interconnection was hindered (Neves Filho et al., 2014). Two behaviors were independently trained: (1) joining two pieces of a tool to manufacture a new tool in an experimental chamber and (2) using one tool to rake food in their living quarters. When tested with the target problem in their living quarters, interconnection did not occur. However, when the same two behaviors were trained in the monkeys' living quarters, they were able to solve the problem by joining two pieces of a new tool into a larger tool that could be used to get out of reach food (Neves Filho et al., 2016). These results suggest that undergoing training and test in the same context is necessary for interconnection to occur.

Experience of failure also appears to have a strong effect on problem solving performances in general (Maier, 1940; Maier & Seligman, 1976). In an interconnection task, albino rats (*Rattus norvegicus*) who learned (1) to dig shavings and (2) to climb stairs were then presented with a problem in which they needed to dig and find a hidden tunnel beneath the shavings that gave access to two flights of stairs, which led to food (Neves Filho et al., 2015). Rats that learned the two behaviors concurrently before the test were able to solve it. Rats who learned only one of the two behaviors did not solve the problem. This second group of rats was then trained in the second behavior after failing in the test, and the problem situation was presented again. Of four rats that received this successive training, only one solved the problem in its second presentation, in a gradual trial-and-error fashion. Once again, merely training the prerequisite behaviors was not enough to guarantee the interconnection in a task. Rats that experienced failure in the test session, in between the training of the two prerequisite behaviors, were not as successful as rats that learned the two behaviors before testing. This result implies another significant restriction on the interconnection of behaviors in mammals: All prerequisite behaviors apparently must be trained before the testing situation for the interconnection to occur reliably.

Recently, research on New Caledonian crows has focused on whether this species is capable of "insightful" problem solving and what cognitive processes might underpin it (Gruber et al. 2019; Taylor, Elliffe, Hunt, & Gray, 2010; Taylor, Hunt, Holzhaider, & Gray, 2007; Taylor, Knaebe, & Gray, 2012; Wimpenny, Weir, Clayton, Rutz, & Kacelnik, 2009). To date, New Caledonian crows have been presented with problems where behaviors were learned sequentially with the same kind of consequence (food) and needed to be interconnected in the same context of training. Taylor et al. (2010), for example, presented a three-stage metatool problem, in which the birds had to pull up a string, remove a short tool attached at the end of this string, take this short tool to a toolbox, extract a long stick from the toolbox, take the long stick to a hole, and extract meat inside of it. In the control group of three crows, the trained prerequisite behaviors were (1) extracting meat from hole with a long stick, (2) withdrawing a long stick from the front of a barred toolbox with the beak and using this stick to obtain meat in a hole, (3) using a nonfunctional 5-cm-long stick to try and extract meat from the 15-cm deep hole, (4) pulling strings, (5) using the short tool to extract the long tool from the toolbox (metatool use), and (6) pulling a string with a tool attached to its end and use this tool to obtain meat in a hole. These behaviors were trained in blocks of trials before the test. The three birds that were trained in these behavioral sequences solved the designed problem with few errors. Additionally, four other birds (the innovation group) were not trained in behaviors (5) and (6), hence, learned only behaviors (1), (2), (3), and (4), and two of these four birds solved the task with the same level of performance as the birds that received the full training.

The other two birds with incomplete training eventually solved the problem after repeated presentations of the task.

It is not yet clear from current research whether interconnection is based on similar cognitive mechanisms in mammals and birds. Comparing the differential effects of training variables upon the interconnection of behaviors across species offers one way to test this. If the interconnection of behavioral repertoires in different species is based on similar cognitive processes (such as planning, causal reasoning, context dependent learning, spatial problem solving, attentional control, memory, etc.), then it follows that procedural changes involved in training should create similar effects on performance. As mentioned above, manipulations of context between training and testing and exposure to failure all interrupt problem solving performances in interconnection tasks in mammals, such as rats (Ellen, Parko, Wages, Doherty, & Herrmann, 1982; Maier, 1931; Neves Filho et al., 2015) and capuchin monkeys (Garber, Gomes, & Bicca-Marques, 2011; Neves Filho et al., 2016). Manipulation of these variables has not yet been carried out in birds in interconnection tasks.

New Caledonian crows use tools in both foraging and nonforaging contexts (Hunt, 1996; Hunt & Gray, 2004; Taylor, Hunt, & Gray, 2011) and have performed impressively across a wide range of problem solving tasks (Auersperg, Von Bayern, Gajdon, Huber, & Kacelnik, 2011; Jelbert, Hosking, Taylor, & Gray, 2018; Jelbert et al., 2019; Jelbert, Taylor, & Gray, 2015; Taylor, Hunt, Medina, & Gray, 2008; Taylor, Hunt, & Gray, 2011; Von Bayern, Heathcote, Rutz, & Kacelnik, 2009). Here, we gave these birds an extractive foraging problem, in which they had to open a door to fly into another cage to retrieve a stone, which could be used to trigger an apparatus in the original cage, containing food. Unlike past work regarding the interconnection of behaviors in birds (Cook & Fowler, 2014; Epstein, 1985, 1987; Luciano, 1991; Taylor et al., 2010), the crows in our experiment learned prerequisite behaviors in different contexts and with different consequences (different magnitudes of food reward or access to a new environment) for the training of each prerequisite. If similar cognitive processes underpin the interconnection of repertories in mammals and these crows, then we expected, based on past research with capuchin monkeys (Neves Filho et al., 2014; Neves Filho et al., 2016), that this should hinder problem solving performance as it does in capuchin monkeys. We trained four prerequisite behaviors for a task that required six behaviors. Following this, we gave birds who were incapable of solving the problem further training on one additional related behavior and then presented the problem situation again. We did not directly train the missing behavior; instead, we trained an independent behavior (searching for stones) that was related to the behavior these birds required to properly solve the task (carrying stones from one cage to another). Based on past work on rats (Neves Filho et al., 2015), if similar cognitive processes are involved in rats and crows as these subjects interconnect behaviors, we expected that this additional training after being exposed to failure would not lead to problem solving. If, however crows did solve the presented tasks, even with this diverse history of training, it would suggest that crows may have different cognitive mechanisms at play during the acquisition of these behaviors or during the process of interconnecting them, compared to mammals such as rats and capuchin monkeys.

Method

Study Subjects and Housing

The subjects were six New Caledonian crows (*Corvus moneduloides*). Three were juvenile males (RWY, D4B, D3B) and the other three were females, two of which were adults (D3R & D4R) and one juvenile (D4G). All subjects were wild crows, brought to temporary captivity in an aviary for the duration of the experiments. In the aviary, birds lived in cages measuring on average 20 m × 20 m × 10.5 m in groups of two or four. The living and experimental areas were constructed out of wood and wire mesh, with the floors covered in sand, and lit exclusively through natural light, thus following a natural day/night cycle. Birds were fed independently of trials twice a day.

All procedures of this study were conducted under approval from the University of Auckland ethics committee (reference no. R602). All birds were caught on private land with permission from the land owners and were released at their site of capture at the end of testing. These crows also participated in experiments involving tool use, self-control, and prosocial behavior (Jelbert, Taylor, & Gray, 2015, 2016; Neilands, Jelbert, Breen, Schiestl, & Taylor, 2016).

Apparatus and Experimental Environment

Experiments were conducted in three adjacent cages (Cage A, 20 m × 20 m × 20.5 m; Cage B, 17 m × 20 m × 20 m; and, Cage C, 20 m × 20 m × 20.5 m), separated by wire mesh, with tarp near the ground level, so the birds could observe the contents of any adjacent cage. In the walls dividing Cages A and B and B and C, near the ceiling, were two 20 cm × 20 cm × 15 cm purple cloth doors (from Cage A to Cage B and from Cage B to Cage C) that could be opened by the birds and, thus, granted access between cages. The cloth doors could only be opened from Cage A and Cage C, both opening a passage to Cage B, by pulling a green iron ring of approximately 4 cm in diameter. A stone dropping apparatus (20 cm × 10 cm × 10 cm) was used in training and testing (similar as the one used by Bird & Emery, 2009). The apparatus consisted of a translucent acrylic box with a hollow tube on top. Inside the box was a mobile platform were held together with magnets in a manner that, when a heavy object was dropped inside the tube, the platform detached and lowered itself, being accessible from an opening at the bottom of the box. Two translucent acrylic boxes (25 cm × 20 cm × 30 cm), with one of the sides being a removable purple cloth door, held by a green metal ring. Ten different man-made clay squares (“stones”) measured approximately 2 cm × 2 cm × 2 cm and weighed between 20 g and 80 g.

All experimental apparatuses were presented on top of one of two wooden tables, measuring 2 m × 1 m × 1.5 m, located in Cages B and C. Two cameras, one GoPro Hero 5 and one Sony Handcam HDr, were used to record test sessions for data analysis.

General Procedure

Four prerequisite behavioral sequences for the designed task were taught to the birds in distinct stages of their stay at the aviary for different experiments (Figure 1). All these behaviors were trained by shaping. Thus, training of these prerequisites occurred in a successive order (i.e., behaviors were learned one after another), with different quantities of training, in different contexts, and with different consequences (i.e., food or access to a new environment) during training. The final test was intended to verify if, even with such a diverse history of training, the interconnection of these behavioral sequences, explicitly trained in the aviary, would occur in a problem-solving situation requiring six behaviors, the four trained behaviors and two that were never trained before the first test. Additional tests and trainings were devised to observe if training of other untrained behavioral sequences after the first exposure to the task would improve the performance of the birds in subsequent presentations of the same task and to observe how these birds were solving the task (i.e., if it is a directed performance or if it is a more explorative performance, as measured by variations of the first test and by the presence of an empty box, without any relevance to the tests, in all its variations).

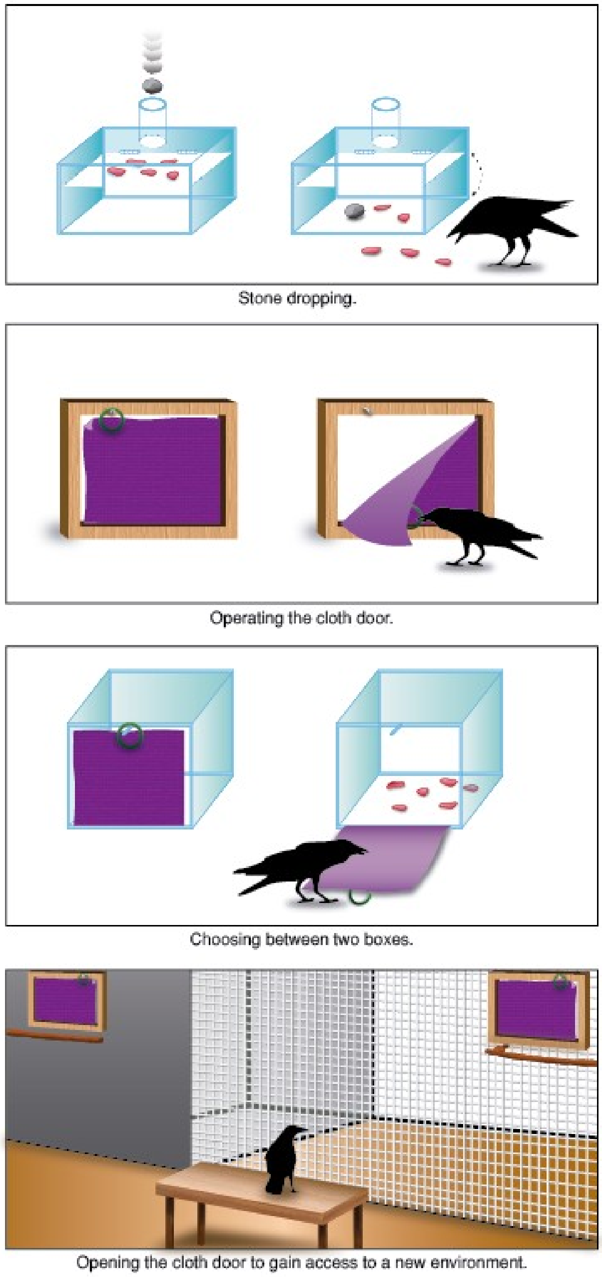

Figure 1. **Illustrations of all prerequisite behaviors trained during the birds' stay at the aviary.** These behaviors were trained during different experiments in which birds participated. Stone dropping is depicted in the first (top) portion of the figure. In this training, the birds learned to drop stones in a tube located in the top portion of the apparatus (the stone, when dropped, gave access to food visibly located in the interior of the apparatus). In the second portion of the figure, operation of the cloth door is depicted. In this training, birds learned to pull a ring in order to open a purple cloth door. In the third portion of the figure, the choosing between two boxes training is depicted, in which birds had to choose between two translucent boxes by operating the cloth door (one box contained food, and the other was empty, in random order). The fourth portion of the figure (bottom) illustrates the opening of the cloth door to gain access to a new environment training. In this training, a crow could operate a cloth door in Cage A

to choose between two new environments, one smaller cage with no direct sunlight or a larger and sunlit cage. Conspecifics (other crows of the aviary) were randomly present in these cages during this training.

Stone dropping training. Birds learned to drop one stone in two identical stone-dropping apparatuses, each containing different kinds of food: high-value meat or low-value dog food (Figure 1). Training occurred until birds dropped the stone in the meat-containing apparatus in 9 out of 10 trials (for a detailed description and results of this study, see Neilands et al., 2016). Before testing, brief retraining occurred. In this retraining, birds had access to the stone-dropping apparatuses and various wood sticks. When poked with the stick, the platform would liberate the food. The birds had a total of five trials with the sticks. All birds used the stick five times to operate the apparatus. After these five trials, the sticks were removed, and ten clay stones were presented. The criterion to end this retraining phase was 10 consecutive stone-dropping responses in less than 10 min.

Operating a cloth door. First, birds were trained to associate a green ring with food. The ring was placed in a stand and baited so that, when the bird picked the bait up, the ring necessarily dropped from the stand. Once the birds became used to the ring dropping and were consistently removing the ring from the stand to consume the bait, the baiting was faded out. Meat was only awarded when the animals removed the ring fully from the stand. Once this behavior was stable, the purple cloth was introduced. First, the birds were made to feed on top of the cloth. Once they no longer showed neophobia, the cloth was hung from the green ring, forming a “door” (Figure 1). At this stage, removing the cloth door by pulling the ring was reinforced with meat. The criterion to end this training was 10 consecutive correct responses in less than 10 min. The cloth door was used both to cover the open end of a box containing food and to open an access between two adjacent experimental cages, as described in details in the following sections.

Choosing between two boxes. This behavior was trained in an experiment that aimed to observe how crows chose different boxes containing different quantities of food in each trial. Two translucent boxes were placed on a table, and only one of the boxes was baited (a piece of meat) on each trial (Figure 1). Both boxes possessed an opening, covered with a purple cloth door, held by a green metal ring placed around a clothespin. To open the box, the bird had to pull the green metal ring off the clothespin, thus making the cloth fall down. Boxes were baited pseudorandomly across trials. The bait could be seen from the back and sides of the box. Once the bird had made a choice (i.e., opened one of the boxes), the trial was over. Each session consisted of 10 trials. Criteria for this training was choosing the baited box at least six consecutive times on each session for two consecutive sessions.

Opening the cloth door to gain access to a new environment. Training was conducted using the cloth door between Cages A and B. The mechanism of the cloth door was identical to the one used in the training of choosing between two boxes. Opening the cloth door had two possible consequences: access to a new environment and access to a new environment containing a conspecific. During the experiment in which this behavior was trained, the birds were presented with two cloth doors, one leading to a large, well-lit chamber and one leading to a smaller, less well-lit chamber (Figure 1). Either could contain a conspecific of varying degrees of kinship, which was assigned in a pseudorandom manner. The birds that underwent this experiment received 36 sessions containing five trials each. D4G and D4R were not part of this experiment; thus, these two crows did not learn how to open a door to have access to a new environment, though they were taught how to operate the cloth door. No learning criterion was used in this training. All birds had the same number of opportunities to open the cloth door to have access to new environments, and all birds that participated in this phase were already trained in how to operate the cloth door. This experiment ended 1 week before the interconnection tests began.

Training Order and Timing

The order in which the crows learned the prerequisite behaviors was as follows: stone dropping, operating a cloth door, choosing one of two translucent boxes, and opening a door to gain access to one of two cages. All behaviors were learned independently from one another. Stone dropping was taught 5 months before testing (a brief retraining was made days before testing); operating the cloth door was trained 3 months before; choosing a box was trained 3 months before and, lastly, choosing a cage was learned 1 week before testing. Subjects D4G and D4R did not participate in the experiment, in which the other crows learned to gain access to a new environment by operating the cloth door. For this reason, these two crows were assigned as a Comparison Group (CG) to test if an incomplete training would, as expected, hinder problem solving, in comparison to other birds that learned more behaviors.

First Test

Tests were conducted in Cages B and C. Each cage had a wooden table in its center. In the first test, subjects started the session in Cage C. The stone-dropping apparatus, containing visible food in its interior, was on top of the table in Cage C. Two translucent boxes (the same as used in training) were on top of the table in Cage B. One of these two translucent boxes contained three different clay stones in its interior; the other was empty. The boxes were placed on the table in a position so to make their interiors visible from Cage C. All three stones could properly activate the stone-dropping apparatus. The translucent box containing stones was randomized for each test. Cages B and C were connected by a purple cloth door, identical to the doors used in the training. The cages were separated by a wire mesh fence, so the birds could see between cages (Figure 2).

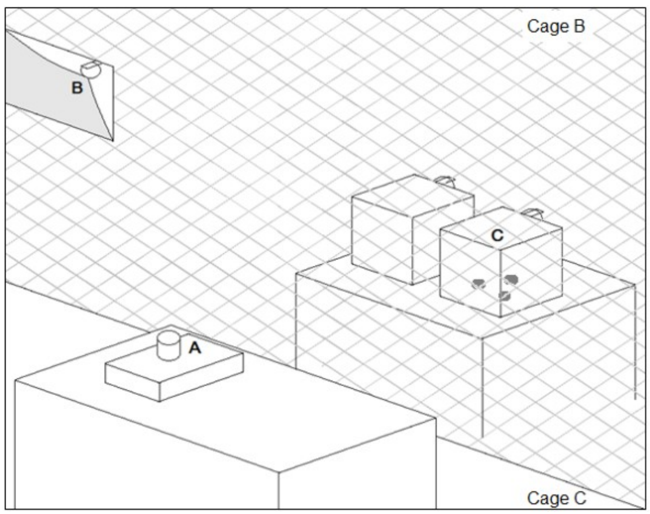

Figure 2. **Diagram of the test situation.** Subjects started the test session in Cage C, separated by a wire mesh from Cage B. The stone-dropping apparatus containing food (A) was presented on a table in Cage C. Cages B and C were connected by a purple cloth door (B) located in one of the top corners of the cage. Cage B had two translucent boxes on top of a table (C). One of these boxes contained three stones in its interior; the other was empty. The interiors of the two boxes were visible from Cage C.

To solve the task, the birds had to (1) open the purple cloth door, (2) cross from Cage B to Cage C, (3) open the translucent box containing the stones, (4) pick one stone up, (5) cross back from Cage C to Cage B while carrying the stone, and (6) drop the stone in the apparatus. This problem-solving performance required the interconnection of behaviors learned in different contexts, with different consequences (1, 3, 4, and 6), and two never explicitly trained behaviors: (2) and (5). Although these crows had experience moving between cages through open doors in their aviary routine, they had never operated the cloth door by themselves to move between these specific cages (from B to C) nor had to go fetch a stone from more than 20 cm away from the apparatus or transport a stone between cages. Test sessions had a maximum duration of 10 min.

The two translucent boxes on Cage B were used as a means to test goal directed behavior during problem solving. Ignoring the empty box and opening only the box containing stones, picking up one stone, and immediately flying back to the stone apparatus in Cage C would be evidence that the bird opened the cloth door and flew to Cage B in order to pick the stone and solve the problem.

Test data were videotaped, and a descriptive analysis of the problem-solving performance of each bird was carried regarding (a) solving or not solving the problem, (b) time required to solve the problem,

(c) order of emission of behaviors related to the task and time between emissions of these behaviors, and (d) ignoring or opening the empty box in the tests. After solving the task for the first time, the same problem situation was immediately presented a second time.

Post-test Training and Re-exposure to the problem Problem Situation

After the first test, birds that did not solve the task in its first presentation received one session of training of *searching for stones*, a behavior related to the never directly trained step (5) of the solution of the problem: crossing from Cage B to cage C while carrying the stone. For this session, 10 different stones were placed in random locations in Cage C. The stone-dropping apparatus was presented in the table at the center of the cage. The bird had to search the room, find the stone, pick the stone, take the stone, and drop the stone in the apparatus to solve the task. Stones used were retrieved by the experimenter so to make the bird search for different stones in each trial. After completing 10 trials, the birds were presented with the same problem as the first test session. All birds that solved the problem in its first presentation or after the post-test training had additional test sessions with variations of the problem.

Variations of the Problem Situation

Two additional tests were made with birds that successfully solved the first problem two consecutive times. These variations were intended to test the behavioral flexibility of the birds by changing the stimuli configuration of subsequent test sessions in order to require a new sequence of behaviors, never directly trained, to properly solve the task. We examined if the birds were simply responding to a series of “smaller”, directly trained problems (e.g., opening the cloth door just because the door is there and not cross to the other cage) or if the birds were responding to the problem situation as a whole (i.e., the sequence of behaviors is goal directed to achieve problem solving).

In Variation 1, birds started the session in Cage C (same as the first test). On the table of this cage was the box containing the stones. The stone-dropping apparatus and an empty translucent box were on the table in Cage B. To solve this variation of the test, the birds had to open the cloth door, take a stone from inside the box, cross from Cages C to B while carrying a stone, and drop the stone in the apparatus located right beside the empty box, a novel, never directly trained behavioral sequence.

In Variation 2, birds started in Cage B (rather than Cage C as in previous tests). Cage B had only the empty box, and both the stone-dropping apparatus and the box containing stones were located in Cage C. To solve this problem, the birds had to open the cloth door, cross from Cage B to Cage C, open the box containing stones, pick up one stone, and drop this stone in the stone-dropping apparatus located right beside the box containing stones, a different sequence of behaviors from the other two sequences that solved the problem in previous configurations (Test and Variation 1). Birds were first exposed to Variation 1 and then to Variation 2 (Table 1).

Table 1

Sequence of Behaviors Required to Solve A ll Tests and the Cages Where Problem Solving Started and Ended

Test	Sequence of Behaviors to Solve the Task	Starting Cage	End of Problem Solving in Cage
First test	(1), (2), (3), (4), (5), and (6)	C	B
Variation 1	(1), (3), (4), (2), and (6)	C	B
Variation 2	(1), (2), (3), (4), and (6)	B	C

Note. (1) Open the purple cloth door, (2) cross from Cage B to Cage C, (3) open the translucent box containing stones, (4) pick one stone up, (5) cross back from Cage C to Cage B carrying one stone, and (6) drop the stone in the apparatus.

Results

Training Stages

Stone dropping. All birds learned to drop one stone to obtain food through shaping in the initial training. In the retraining session, when confronted with the stone-dropping apparatus and stones, all subjects promptly used stones to obtain the food inside the apparatus. All birds correctly dropped all available stones in the apparatus 10 consecutive times in less than 10 min in one session (Table 2).

Operating a cloth door. Birds learned to operate the cloth door in less than 10 sessions of 10 trials each. D3R learned in 20 trials; D4B, 90 trials; D3B, 50 trials; RWY, 30 trials; D4R, 70 trials; and D4G, 10 trials (Table 2).

Choosing between two boxes. Birds took 40 to 140 trials with the two boxes to reach the criteria (i.e., six consecutive correct responses in two consecutive sessions of 10 trials each; Table 2).

Opening the cloth door to gain access to a new environment. D4R and D4G (CG) did not participate in this phase. All other birds had 36 sessions with 5 trials each (180 trials for each bird). Since there was no learning criterion for this phase, we quantified only how many times each bird operated the cloth door and crossed over to Cage B (the new environment). All birds who operated the cloth door to choose cages did so regardless of other conspecifics in the chosen cage. Most of the times, especially in later trials, birds did not operate either door. D3R operated the cloth door and crossed to Cage B 19 times; D4B, 6 times; D3B, 20 times; and, RWY, 10 times (Table 2).

Table 2

Number of Trials Each Crow had for Each Trained Behavior

Subjects	Number of Trials			
	Stone Dropping	Operating a Cloth Door	Chooding Between Two Boxes	Access to a New Environment
D3R	10	20	40	19
D4B	10	90	30	6
D3B	10	50	20	20
RWY	10	30	90	10
D4R (CG)	10	70	120	-
D4G (CG)	10	10	140	-

Tests

D3R solved the problem in the first trial. D4B, D3B, and RWY did not solve the problem on the first trial and so were given the search-for-stones training. D4B solved the task immediately after the additional search-for-stones training, but D3B and RWY required two test sessions to solve the problem for the first time, even after the additional training ofsearching for stones. Birds in the comparison group (D4R and D4G) did not solve the problem on any occasion (Figure 3).

After solving the task, D3R was immediately re-exposed to the same problem situation. In this second presentation of the task, D3R opened the cloth door and crossed to Cage B at 5 s of session time and again opened the two boxes. This time, D3R picked one stone after inspecting both boxes and crossed back carrying the stone to Cage C, solving the problem at 30 s of session time (a video of this performance is available as Supplemental Material 1).

Tests							
Crow	1st	Post-test training	2nd	3rd	4th	Variation 1	Variation 2
D3R	SO	-	SO	-	-	SO	SO
D4B	PS	OK	SO	SO	-	SO	SO
D3B	NR	OK	PS	SO	SO	SO	SO
RWY	NR	OK	PS	SO	SO	NR	NR
D4R (CG)	NR	OK	NR	NR	NR	-	-
D4G (CG)	NR	OK	NR	NR	NR	-	-

Figure 3. **Summarized description of the performance of all crows.** "SO" (black) indicates successful problem solving. "PS" (grey) indicates a partial solution (i.e., opening the cloth door crossing from Cage B to Cage C but not crossing back to Cage B with a stone). "NR" (light grey) indicates no response related to problem solved occurred. D4R and D4G (CG) were the crows that learned only three behaviors in the aviary before the first test. "OK" means that these birds had the post-test training.

All subjects that did not solve the problem in its first presentation, including D4R and D4G, received one training session of the search-for-stones behavior. Here, they had to search for stones in a room and carry these stones to the apparatus. All birds found and dropped the 10 available stones in less than 5 min. After the training of searching for stones, D4B, D3B, and RWY solved the task. D4B solved immediately after learning how to search for stones; D3B and RWY required two test sessions to solve the task. D4R and D4G, the animals that did not have any training in opening the cloth door to gain access to a new environment (CG), did not solve the task, even after learning to search for stones (Figure 3).

Variations of the Problem Situation

Of the four subjects that solved the task, three of them (D3R, D4B, and D3B) solved the two additional variations of the problem (Variation 1, in which birds started in Cage C, and Variation 2, in which the box containing stones and the stone-dropping apparatus were side by side in Cage B). RWY did not solve either of the two variations (Table 3).

Table 3

Time (in minutes and seconds) for Each Subject to Solve the Problem in All Tests

	Test (First Solution)	Test (Second Solution)	Variation 1	Variation 2
D3R	5 min 27 s	0 min 30 s	3 min 19 s	0 min 35 s
D4B	9 min 58 s	2 min 10 s	1 min 0 s	2 min 53 s
D3B	2 min 32 s	0 min 52 s	3 min 42 s	3 min 01 s
RWY	4 min 07 s	1 min 2 s	X	X

Note. "X" indicates that the animal did not emit any response related to the problem.

From all birds that solved the two variations of the tasks, only D3R opened the empty translucent box. All other birds only opened the translucent box containing stones, ignoring the empty box in both variations of the problem situation. RWY did not solve any of the two variations of the problem and did not emit any problem related responses, which suggests that failure was due to a lack of motivation. A detailed description of the performances of all crows in all tests and its variations is available as Supplemental Material 2.

Discussion

We were able observe the interconnection of six behavioral sequences, namely, to open a cloth door, cross from one cage to another, open a translucent box, pick one stone, cross back to the initial cage carrying the stone, and drop the stone in the apparatus after repeated testing. All these behaviors were trained for different experiments conducted during the bird's stay at the aviary (except for D4R and D4G, who learned only three behaviors before the first test). For this reason, for all birds, these behaviors were trained in different contexts with different quantities of training and with different consequences. One bird, D3R, solved the task in the first test presentation after learning four of these six behaviors prior to testing. Other birds had an additional training of a searching-for-stones behavior, after failure to solve the problem in its first presentation. D4B solved the problem right after learning to search for stones; D3B and D4B needed repeated testing. Thus, interconnection of behaviors in New Caledonian crows was not totally hindered by differences in the timing, consequences, and quantity of various experiences or by changes in the context and in the environment in which behaviors were trained and tested. In comparison, in a study with rats (Neves Filho et al., 2015), all subjects that had any exposure to failure before testing failed to solve the programmed task, even after a complete training of prerequisite behaviors for the task. In another study with capuchin monkeys (Neves Filho et al., 2014), the same failure to interconnect behaviors was observed in all subjects when there was a variation of contexts of training and testing. In both these cases, with rats and monkeys, repeated tests did not produce problem solving as it did in the crows.

D3R, who solved the task in its first presentation, interrupted the sequence of problem-solving behaviors, crossing back to Cage C without carrying a stone to inspect the stone-dropping apparatus (see Supplemental Material 2 for a detailed description). Inspection behaviors like these were also observed in past metatool tasks (see Taylor et al., 2010). After inspecting the stone-dropping apparatus and having already opened the two boxes, D3R then solved the problem without interruptions. All other subjects did not solve the task in the first presentation, which was the case in all previous experiments with pigeons, rats, and monkeys in which subjects did not learn all prerequisite behaviors for the given task. Four subjects (D3R, D4B, D3B, and RWY) solved the task after the post-test training of searching for stones. This behavior was identified as the prerequisite that these subjects lacked, since they all failed to solve the task in its first presentation because none had carried the stone while crossing back to the cage where the stone dropping apparatus was located. D4R and D4G, the comparison group, who learned to search for stones after failing the test, did not solve the task, likely because they lacked any training in opening the cloth door to gain access to a new environment. This suggests that opening the cloth door to gain access to a new environment was a crucial prerequisite for the designed task. Searching for stones, however, was probably more prone to emerge as a new behavior in the test situation, given that D3R solved the task even without a specific training of searching for stones.

Individual differences probably played a role in the different performances among our crows. Some aspects of individual differences are known to modulate problem solving, such as previous experience (both in laboratory and in the wild), neophobia, neophilia, curiosity, memory, spatial cognition, social influences, cognitive and motor flexibility, learning, and motivational systems that promote exploration and perseverance (Auersperg, Gajdon, & Von Bayern, 2012; Cole, Cram, & Quinn, 2011; Griffin & Guez, 2014; Kaufman, Butt, Kaufman, & Colbert-White, 2011; Matzel, Wass, & Kolata, 2011; Tebbich, Griffin, Peschl, & Sterelny, 2016). D3R's successful performance of problem solving in the first test is indicative of a more "innovative profile," probably due to specific traits or interactions of these traits (Reader, Morand-Ferron, & Flynn, 2016). Regardless, training of the prerequisite behaviors increased the chance of solving the task as well as its variations.

Animals with little or incomplete training tend to be incapable of coming up with a solution through the interconnection of repertoires, as has been shown in literature (Epstein et al., 1984; Epstein, 1985; Luciano, 1991; Neves Filho et al., 2015), due to the simple fact that they do not possess relevant behaviors to be interconnected. However, in all past experiments in which animals successfully solved a task requiring the interconnection of independently acquired behaviors, all prerequisite behaviors were trained or suppressed only before testing. Our data show that it is also possible to train additional prerequisite repertoires after failure on test, which leads to successful problem solving, at least in crows.

It is interesting that all the birds opened the empty translucent box when solving the task for the first time. This error may be due to past reinforcement: The crows had previously been rewarded for opening boxes with food (of a high reinforcing magnitude) and so may have been unable to inhibit this behavior even when the box was empty. This behavior is also in line with other evidence that crows do not need or show an unequivocal understanding of causality, even when properly solving certain tasks (for a review, see Taylor, 2014). Results in the variations of the test indicate that crows that solved the task with the given prerequisite behaviors were able to later interconnect these behaviors in other new sequences in new and different opportunities to innovate, which indicates that the problem-solving performance was not a case of classic chaining of responses, since these new sequences of behaviors required to solve the variations of the original task were never directly trained. Also, the performance in the variations of the task indicates that the birds were not employing a trial-and-error strategy in these tests. Birds that had the additional training of searching for stones solved the variations of the task without errors (i.e., none of these birds opened the empty translucent box in the variations) and generally solved the problem more quickly (see Table 3). This errorless performance fits into the classic definition of insight, made by Thorpe (1956, p. 100): “the sudden production of a new adaptive response not arrived at by trial behavior or the solution of a problem by the sudden adaptive reorganization of experience”.

Two nonexclusive possibilities may explain why New Caledonian crows were better than rats and capuchin monkeys in interconnection tasks, given that crows interconnected behaviors with a diverse history of training during problem solving. One possibility is that, due to their experiences in the wild, wild crows have an increased general behavioral repertoire, in comparison to laboratory bred rats and captive held capuchin monkeys. The second is that the behavioral and cognitive process underlying the interconnection of behaviors in crows is not the exact same as the ones observed in other studied animals, which would have implications for the study of the convergent evolution of problem solving in different species (Stayton, 2015; Taylor, 2016). Indeed, though the capuchin monkeys tested were captive at the time of testing, all were born in the wild and then acquired considerable behavioral repertoires and experience during their time in captivity (for details, see Galvão, Barros, Rocha, Mendonça, & Goulart, 2002), which provides some support for the different cognitive mechanisms hypothesis.

Regarding the hypothesis of different cognitive mechanisms at play in different species during the interconnection of behaviors, differences between mammalian and avian brains may contribute to the different performances observed in birds and mammals. Though analogous, there are important structural differences between the pallium and neocortex, and a higher neuronal density is seen in birds (Lui, Hansen, & Kriegstein, 2011; Olkowicz et al., 2016). However, to better ascertain this, more comparative research is necessary. One way to investigate this is to employ standardized interconnection tests for different species. Different tasks require different cognitive mechanisms (spatial cognition, memory, attention, etc.), and different brains learn and tackle problems in different ways (Smith & Church, 2018). By standardizing tests and training regimens of prerequisite behaviors for these tests, it is possible to isolate the behavioral and cognitive processes at hand, and thus conduct a proper comparative analysis (Cole et al., 2011). This however has not yet been properly done in interconnection tasks.

Conclusions

There appear to be substantial differences between the performances of New Caledonian crows and mammals in the interconnection of behaviors in a problem solving task after experiencing failure and training in different contexts. To ascertain that a different cognitive process is at hand in birds and mammals during the interconnection of behaviors, more experiments need to be conducted. Specifically, behavioral tasks need to be standardized and applied to more subjects and more species. Manipulating the experiences prior to testing in a standardized test in different species would make it possible to evaluate if the integration of isolated experiences described in the interconnection of behaviors is created by similar cognition in distantly related species. Such a standardized testing approach could allow us to examine more closely how similar or different species are in their problem-solving performances.

On a final note, the acknowledgement of the interconnection of behaviors as a fundamental process in problem solving can stimulate new interpretations and new research on problem solving and innovation, both in captivity and in the wild. Several approaches to animal problem solving and innovation are already mapping and testing cognitive and behavioral processes involved in the occurrence of new behavior and how this behavior can be transmitted among a given group of individuals. The recent growth of the literature about the interconnection of behaviors and the identification of how interconnection occurs provides new tools to trace the behavioral origins of innovation. For example, it is possible that certain individuals and species are more prone to innovation due to a higher pool of available behaviors. By mapping and measuring this pool of behaviors, it is possible to compare different groups of individuals regarding their potential for innovation and also identify if conspicuous innovations do emerge when prerequisite behaviors for these innovations are well established in individuals of the group.

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