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Vertical string-pulling in green jays (*Cyanocorax yncas*)

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Highlights

The cognition of green jays has never been investigated in captivity to the present.

Green jays solve a vertical string pulling problem without the need of any training or shaping.

Green jays seem to neglect string and worm connectivity in a series of discrimination problems.

Abstract

The cognition of green jays (*Cyanocorax yncas*), a non *Corvus* corvid species, was investigated by using the string-pulling paradigm. Five adult green jays performed a vertical string-pulling task in which they had to retrieve a worm attached to the end of a vertical hanging string while sitting on their perch. In the first experiment, three of the subjects managed to retrieve the worm by pulling on the string with their beaks and stepping on the resulting loop, and thereafter repeating this sequence until the worm was accessible. When subjects were given a choice between two strings in subsequent experiments 2 to 4, they chose at random between the string connected to the worm and the one connected to a slice of a wooden dowel. In experiment 5, subjects that had failed the previous discrimination series were able, nevertheless, to solve a more stringent vertical string array in which they had to pull up the whole length of the string without any visual access to the worm at the end. We discuss green jays' performance in comparison with other corvid species in which cognition has been more extensively investigated.

Keywords: *Cyanocorax yncas*, corvids, string-pulling, cognition, insight, means-end understanding.

1. Introduction

When investigating the cognition of nonhuman animals in the laboratory, which thereby allows very careful control of variables, we are left nonetheless with the difficult task of deciding which aspects of the problem the animal has taken into account in order to reach the solution. An apparently “simple” problem, such us pulling from a string to attain a food item attached to the other end, affords an apparently “simple” solution (i.e. pulling), yet the information the animal takes into account before making this seemingly simple action may greatly vary (see Jacobs & Osvath, 2015). The animal could have displayed a wide range of behaviours already in its repertoire until “accidentally” hitting upon the solution, or else could have represented the problem mentally before even probing. This second strategy would reduce considerably the variety of probing behaviours overtly applied to the problem, yet it would still be open to question whether the animal that reached the solution in just one attempt had represented the causal structure of the problem mentally (i.e. string-food connection) or instead its superficial structure (i.e. string-food contact). To add to this complexity we should bear in mind that failing to solve a food-acquisition problem might owe to lack of understanding of critical aspects of it, lack of motivation, or even that the requisite solving strategy worked against the natural predisposition of the species in question (i.e. chimpanzees are not adept at solving problems with their mouths, whereas orangutans are). Therefore, it is not solving the task itself which informs us about the cognition of the animal, but how it approaches the problem and just which information it gathers in order to reach the solution. In this regard, it is essential to take into account whether the animal is able or not to transfer the knowledge acquired from one specific problem to newly encountered problems that share the same causal structure (see Call, 2013 and refs.). String-pulling is a classical means-to-end problem which has been used extensively to investigate the physical cognition of birds (for a review see Jacobs & Osvath, 2015). In the vertical string-pulling task, a string hangs vertically to a bird's perch with its loose end connected to a food reward (e.g., a worm). In order to retrieve the reward the birds cannot fly directly at it but instead need to pull up the length of string that separates them from the reward while sitting on the perch. The task is similar to horizontal string-pulling in that the connection between the string and the reward is the essential causal aspect related to success. However, vertical pulling is affected by gravity and subjects are forced to coordinate their pulls on the string with steps onto it in order to prevent the string and the reward from falling. This sequence of actions makes the task more difficult and calls for sophisticated peck-leg coordination (for more details, see the review by Jacobs & Osvath, 2015).

The vertical task also allows for the presentation of several strings instead of just one. Patterned-strings, in which one of several strings has food attached to the end that is out of reach, have been used to investigate causal understanding. If a subject perceives the means-end connection of the problem it is expected to pull the baited string to access the food. Patterned-string problems vary in difficulty as a function of the number of strings, their orientation (e.g, perpendicular or oblique), and the angles and crossings that they form with each other (Harlow & Settlage, 1934; Heinrich & Bugnyar, 2005; Jacobs & Osvath, 2015; Taylor, Medina, Holzhaider, Hearne, Hunt & Gray, 2010). The most effective strategy for retrieving the reward is to trace the strings back from the perch to the other end where they are connected to the food or the distracter object in order to determine which one to pull. However, several other strategies that do not require any causal understanding, such as pulling the string closest to the desired food item, can bear fruit occasionally. To date, all the studies that employed the string-pulling paradigm to investigate corvid cognition have focused on the genus *Corvus*. The only exception to this is a recent study by Hoffmann, Cheke & Clayton (2016) who investigated the cognition of western scrub jays (*Aphelocoma californica*) using a horizontal string-pulling task. In their study scrub jays were required to pull horizontally on a string connected to a wax worm in order to retrieve it. Several string arrangements were presented to the subjects, including variation in the length of the strings and the proximity between the accessible string ends and the reward. The jays' performance was rather poor as they showed a proximity bias and almost invariably pulled the string end which was closer to the worm, thus neglecting the worm-string connection.

Here we present the second study to investigate the physical cognition of a non-*Corvus* corvid belonging to the genus *Cyanocorax* using a string-pulling task, and the first controlled study conducted with green jays (*Cyanocorax yncas*), a species that is vey difficult to breed in captivity. We chose the vertical string-pulling task to investigate the cognition of green jays because it requires no specific training and because many previous studies with other *Corvus* species have used the same experimental paradigm, thereby allowing for comparison to be made (see Jacobs & Osvath, 2015). We chose green jays as our experimental subjects because there were no previous controlled studies with this species and also because of the existence of one anecdotal observation of two examples of wild green jay (*Cyanocorax yncas*) using twigs to fish for insects (Gayou, 1982), an instance of tool use that is quite exceptional among birds and seems to point towards a high level of understanding of their physical world.

2. Methods

2.1. Subjects

Five green jays (*Cyanocorax yncas*) housed in the zoo at Barcelona (Spain) took part in this study. They were four males (Bernat, Gandalf, Joanot, Konrad), and one female (Penélope), with ages ranging from four months to circa three years at the time of testing. All subjects were captive-born and were lodged in two groups of two and three individuals in separate exhibition cages (both 24.5 m^2 in area and 6.5 m high) (see Table 1 for subjects' details). One month before the experiments started, they were moved to an interior aviary (23 x 13 m) with no public access and lodged in individual cages. Testing adhered to the non-invasive research ethical principles as well as to the Spanish (AIZA), European (EAZA) and World (WAZA) Association of Zoos and Aquariums protocols. The Barcelona Zoo fulfils all the requirements specified under Spanish law (*Orden 28/7/1980*; BOE 219, 11/09/1980) and the Catalan law (*Decret legistaliu 2/2008*; DOGC 5113, 17/04/2008) regarding care and welfare of zoo animals. Subjects were never deprived of food or water experiments. To increase the incentive value of the wax moth larvae (*Galleria mellonella*) used as a reward during testing we removed it from the subjects' diet and replaced it with another species of worm with similar nutritive value.

2.2. Apparatus

Testing (also home)-cages measured 2.04 x 1.02 x 2.04 m and were made of welded wire mesh. Each cage was suspended 1.20 m above the ground and equipped with a wooden perch 2 cm in diameter and 102 cm in length that ran parallel to the front door of the cage, at a depth of 18 cm. A wire mesh barrier 7.5 cm high, fixed at a depth of 40 cm, defined the testing area. A Plexiglas flat ("uncomfortable" to walk on) transparent sheet measuring 50 x 24.5 x 0.5 cm was secured horizontally below the wooden perch in place of the wire-mesh floor of the cage. This encouraged subjects to interact with the strings, while sitting on the perch. This sheet had three round holes 5 cm in diameter and 5 cm from each other, aligned with the perch above. During testing the strings tied to the perch hung vertically through the centre of these holes.

Cotton strings 0.5 cm in diameter and 30 cm in length were used to fasten the rewards. We used two different colours (black and white) to facilitate string discrimination during the discrimination experiments (2 to 4). The colour of the string was pseudo-randomly alternated in experiment 1 to eliminate the possibility that subjects might develop a preference for a specific colour, which then might have influenced subsequent choices. A wooden (opaque) board 50 x 30 x 0.5 cm was used in experiment 5 to eliminate visual information on the progress of the task. Therefore in experiment 5 a longer string (40 cm) was used. The extra 10 cm covering the gap that separated the Plexiglas transparent sheet in the cage from the opaque wooden board below. Thus the length of string they had to pull up before they detected the worm was of the same length (30 cm) as in the previous experiments (1 to 4).

2.3. Procedure

2.3.1. Habituation

Subjects were given one month to become familiarized to the new materials. The experimenter (E) entered the aviary every day (9:00 to 12:00) and spent one hour moving the tripod and camera around the aviary so that they stood for 10 min in front of each of the subjects' cages. He also threw *Galleria mellonella* into the bird feeders. The Plexiglas transparent sheet was fixed in the cages and the black and white strings fastened to the cage walls. This was done to reduce any putative neophobic response to these new materials in the testing phase.

2.3.2. Experiment 1: spontaneous string-pulling

Each session started with E tying to the perch the 30 cm string with a worm attached to its free end. The string fell vertically through the middle hole of the Plexiglas sheet (Fig. 1A). Every session was run on a different day and lasted 15 min if the worm was not recovered before. When a jay obtained its first worm the time limit disappeared and a limitation was placed on the number of worms that could be retrieved, up to four (to avoid satiation). Sessions were repeated daily until subjects accumulated 30 worms. Subjects that failed to pull up the worm spontaneously in ten consecutive sessions of 15 min were removed from the study. Across the entire experiment the string colour was assigned to each trial pseudo-randomly in order that the probability was the same that subjects would encounter the worm connected to a black or a white string.

Sessions comprised a varying number of trials. Each trial started when the jay touched the string and ended when it obtained the worm or else abandonned the area between the front part of the cage and the wire-mesh barrier 40 cm behind. Thus, usually the number of trials did not match the number of worms obtained. Trials so defined allowed comparison with previous studies (i.e. Taylor et al., 2010).

2.3.3. Experiment 2: string discrimination

Two strings of different colours (black vs white) were tied to the perch. One of the strings had a worm attached to it , while the other had attached to it a slice of a wooden dowel rod, 2 mm thick and 3 cm in diameter. The two 30-cm strings fell vertically through the lateral holes in the Plexiglas platform 20 cm apart (see Fig. 1 B). The strings hung at a distance of 10 cm from the middle fixation point used in experiment 1. We avoided tying strings to this spot because it had been associated repeatedly with the reward in experiment

1. Both the colour of the string connected to the reward and the rewarded side were counterbalanced across trials and subjects pseudo-randomly. A trial started when the subject touched one of the strings and ended when: a) it recovered the item connected to that string, b) it touched the other string, or c) it abandonned the testing area. The first string touched by the subject was regarded as its choice. If a subject touched a string first but then dropped it and tried to retrieve the other string, the E would approach and remove the food item in order to start the next trial. A limit of three worms per session was established in order to avoid satiation. The number of worms per session was reduced from four in the previous experiment to three, in order to maintain subjects' interest in the reward in the presence of a competing object. Each session ended when the subject had obtained the three worms or accumulated ten trials (whichever came first). When subjects accumulated 20 trials (and not necessarily 20 worms) they moved to experiment 3.

2.3.4 Experiment 3: slanted strings

The only difference from experiment 2 was the inclusion of two translucent fishing lines that displaced the black and white strings 10 cm laterally from their fixation points (see Fig. 1C). Thus the dowel slice and the worm always would hang 10 cm (right and left) from one of the fixation points on the perch, and the jays would need to track down the strings visually in order to know which string was connected to which item.

2.3.5. Experiment 4: crossed strings.

The only difference from the previous experiment 3 was that the two translucent fishing lines were fixed in order to force the crossing of the black and white strings at the centre of the perch, immediately below the central hole. Hence each item fell vertically to the fixation point of the opposite item on the perch (see Fig. 1D).

2.3.6. Experiment 5: blind string-pulling

We proceeded as in experiment 1 except that this time a wooden (opaque) board 50 x 30 x 0.5 cm was fixed 10 cm below the bottom of the cage in order to provide a visual barrier that concealed the worm from the subjects' sight (see Fig. 1E). A rectangular hole in the platform (10x7.5 cm) sealed with two small pieces of black cardboard eliminated any chance of peering at the worm while sitting on the perch. The string used in this experiment was 40 cm long. Thus subjects had to pull up a 30 cm length of string before recognizing the worm attached to it. Sessions progressed until subjects accumulated 10 worms.

2.4. Data scoring and analyses

All trials were videotaped. To assess inter-observer reliability, SP recorded the string that was touched first by the subject for 20% of the discrimination trials. Inter-observer reliability was excellent (Cohen's kappa = 1, N = 100). In experiments 1 and 5 we recorded whenever subjects obtained the worm and the cumulative time needed to retrieve their first worm. We also calculated the average number of trials as well as the average time required to obtain a worm. To avoid ambiguity, in experiments 2 to 4 the response criterion was the first string touched (and not necessarily lifted). To facilitate comparison with previous studies we calculated subjects' pull-step ratios, as defined in Taylor et al. (2010), which were obtained by dividing the number of steps on the string by the number of pulls, and presented as percentages. Both single pulls and pulls followed by a step were included in this measure. A high pull-step ratio would indicate proficiency in the task. We also calculated the relevant-irrelevant action ratio by dividing the percentage of irrelevant actions directed at the string by the percentage of relevant ones, before obtaining the first worm and afterwards. Contrary to the pull-step ratios, higher values here would indicate poorer performance. We defined relevant actions as those directed at the string that could be included in the chain of actions necessary to lift the string (pulling the string with the beak, stepping over the string with one or both feet and moving sideways over the perch, holding the string with the beak) and irrelevant actions such as those directed at the string that did not contribute to lifting it (e.g., pecking, biting, touching, etc.). We did not consider dropping the string as an irrelevant action because it was presumed to be a result of failing to stop the string from falling, after having lifted a loop of it. Results are expressed as means ± S.E.M in order to facilitate comparison with previous studies (Taylor et al., 2010). Two-tailed binomial tests were used to analyse string preferences in the discrimination experiments 2, 3 and 4. We used the Wilcoxon signed-ranks test (two-tailed) in order to compare the performance of subjects in the standard string-pulling condition of experiment 1 with that of the blind condition of experiment 5.

Owing to a recording problem we missed the videos corresponding to the retrieval of the six last worms for Konrad in experiment 1; therefore this bird's average values were calculated based on 24 worms and not 30. Because Penélope was to be moved from the aviary for breeding purposes shortly after completing experiment 1, we therefore decided to skip the whole discrimination phase (experiments 2, 3 and 4) and move her to the final experiment 5, which could be completed reliably. We are aware that this constitutes a limitation for comparing her data on experiment 5 with that of the other subjects. Because of the small sample size we applied non-parametric statistics in order to detect significant differences in performance. As mentioned above, we present descriptive statistics in the form of means and S.E.M and not medians and inter quartile range (IQR) in order to facilitate comparison with data in Taylor et al. (2010).

3. Results

3.1. Experiment 1: spontaneous string-pulling

Three of our subjects, Joanot, Konrad and Penélope, managed to pull up the 30 cm length of string and obtain the worm connected to it without any help (i.e., shaping) or training from the experimenter. The total cumulative time across sessions until the first successful retrieval was of 104, 3500 and 1938 seconds respectively. Discounting the time in which subjects were outside the testing area (hence not trying to retrieve the worm) the values fell to 76, 477 and 431 seconds. Cumulative trials across sessions until the first successful retrieval were 3, 14 and 8 for Joanot, Konrad and Penélope respectively. The average pull-step ratios for the same trials and subjects were 9 ± 16%, 2 ± 8% and 5 ± 10% and their relevant-irrelevant action ratio values were 8 ± 8%, 197 ± 329% and 117 ± 130% , respectively. Table 2 shows the data corresponding to Taylor's experienced group of New Caledonian NC crows (Taylor et al., 2010) and our green jays in order to allow comparison.

Average solution times when considering only the trials between the first successful retrieval (first successful trial) and the last successful retrieval (that of the 30th worm) were 24.55 ± 30.53, 13.09 ± 7.23 and 28.48 ± 29.71 seconds for Joanot, Konrad and Penélope respectively. The average number of trials required to retrieve the worm for these same trials and subjects was 1.55 ± 2.05, 1.04 ± 0.21 and 1.31 ± 0.54 respectively. Average pull-step ratios when pooling trials from the first to the last successful retrieval were 63 ± 39%, 87 ± 25% and 66 ± 29% for Joanot, Konrad and Penélope and their relevant-irrelevant action ratio values for the same trials and subjects were 5 ± 18%, 2 ± 4% and 4 ± 8% respectively.

The other two birds, Goliat and Bernat, did not manage to solve the task. The average pull-step ratios for these two subjects, until they ceased to participate in the experiments, were 5 ± 16%, 42 ± 42% respectively, and their relevant-irrelevant action ratios were 71 ± 56%, 14 ± 20%.

3.2. Experiment 2: string discrimination

Only Joanot and Konrad took part in this experiment. Bernat and Goliat dropped out after failing to retrieve a single worm in previous experiment 1 and Penélope was directly moved to experiment 5 as there was no time for her to finish the discrimination phase.

Joanot chose the correct string connected to the worm in 70% of the trials, yet his performance was not above chance (binomial choice, $p = 0.115$). Konrad also failed to choose the correct string above chance level (35% of the trials, binomial choice, $p = 0.263$).

3.3 Experiment 3: slanted strings

Joanot chose the correct string attached to the worm in 60% of the trials but his performance was at chance level (binomial choice, $p = 0.503$). Konrad chose the connected string in 65% of the trials; his performance was also at chance level (binomial choice, $p = 0.263$).

3.4. Experiment 4: crossed strings

Joanot displayed a clear preference for the string attached to the dowel slice which he pulled in 90 % of the trials (binomial choice, $p = 0.0004$) and Konrad did the same in 70 % of the trials although his preference lacks statistical significance (binomial choice, $p = 0.115$).

3.5. Experiment 5: blind string-pulling

The total cumulative time until the first successful retrieval for Joanot, Konrad and Penélope was of 536, 563 and 22 seconds respectively. Discounting the time when subjects were not actively trying (i.e., were outside the testing area) the values fell to 12, 33 and 12 seconds. The number of cumulative trials until the first successful retrieval was 11 for Joanot, two for Konrad and one for Penélope. The average pull-step ratios for the same trials and subjects were 9 ± 30%, 27 ± 39% and 100% and their relevant-irrelevant action ratio values of 0 ± 0%, 2 ± 3% and 0± 0% respectively.

The average solution time considering only the trials between the first successful retrieval (the first trial in which they succeeded) and the last successful retrieval (worm number 10) was 18.11± 9.99, 12.89 ± 3.14 and 10 ± 2.83 seconds for Joanot, Konrad and Penélope respectively. The average number of trials required to retrieve the worm for these same trials and subjects was 5.78 ± 2.95, 1.11 ± 0.33 and 1 ± 0 respectively. The average pull-step ratios when counting trials from the first successful retrieval to the last successful retrieval (10th worm) were 18 ± 35%, 60 ± 24%, and 84 ± 13% for Joanot, Konrad and Penélope and their relevant-irrelevant action ratio values for the same trials and subjects were 0.09 ± 0.63%, 1 ± 3% and 1 ± 3% respectively. Table 3 shows the mean (and S.E.M) time and number of trials required to retrieve the last 10 worms in experiments 1 and 5 as well as the pull-step ratios for both experiments. We also present the values reported for New Caledonian crows in Taylor's study (Taylor et al., 2010) to allow comparison. The cumulative time per trial required by our jays to obtain a worm in the standard and the blind string pulling conditions did not differ significantly (Wilcoxon signed-ranks, $z = -0.292$, $p = 0.77$). In contrast, to obtain a worm in the blind condition required more trials (Wilcoxon signed-ranks, $z = -2.63$, $p = 0.008$).

-------------------Table 3 around here------------

4. Discussion

Three of our five subjects (Joanot, Konrad and Penélope) solved the standard string-pulling version in experiment 1 without any help or training. The remaining subjects (Bernat and Goliat) accumulated a total of 150 min exposure to the string and the worm without any success. We cannot be certain why Bernat and Goliat failed to solve the task, though we might offer some tentative explanations based on my own observation of the subjects trying to access the worm and the available data for their pull-step and relevant-irrelevant action ratios. Goliat presented a very low pull-step ratio (5%) as well as a very high relevant-irrelevant action ratio (71%), which suggests that he was having problems at coordinating beak and foot and also that he produced significantly more irrelevant than relevant actions directed at the string. Therefore, it seems as if Goliat failed to identify the important aspects of the problem. Bernat's pull-step ratios, on the other hand, were reasonably high (42%) and he displayed a very low relevant-irrelevant action ratio (14%). Taken together, the results might be interpreted as Bernat having identified the critical aspects related to success in the task, albeit lacking the sufficient motor coordination that would produce the reward before the time run out. We do not think it plausible that lack of motivation was the cause for their failure, because they approached the string and worm in the initial sessions in a way that was indistinguishable from the successful subjects. The only two subjects (Joanot and Konrad) that took part in the discrimination series following experiment 1 (experiments 2 to 4), both performed poorly. Only Joanot displayed a slight preference for the baited string and chose it in 70% of the trials in experiment 2, though nonetheless his preference did not reach statistical significance. Moreover, neither subject chose the baited string above chance levels whenever the strings deviated from a straight, vertical trajectory (experiments 3 and 4). The fact that both subjects displayed a preference for the non-baited string (Joanot: 90% choices; Konrad: 70% choices) in the crossed condition of experiment 4 suggests a proximity bias: that is to say, the subjects pulled the string affixed vertically to the worm and which therefore was closest to the desired food item. This finding supports the results of previous studies with ravens and crows in which a proximity bias was observed when solving a horizontal strip pulling task (Albiach-Serrano, Bugnyar, & Call, 2012). More recently, the same proximity bias has been reported in western scrub jays in a horizontal string-pulling task (Hoffmann, Cheke & Clayton, 2016). In addition to pulling the string closest to the worm, subjects would re-enact the strategy which had been successful and led to reward in experiment 1.

In experiment 5, the three subjects that had been successful in experiment 1 (Joanot, Konrad, Penélope) managed to pull the string up and retrieve the worm attached to it without any visual access to the food item, that is to say, without any visual feedback revealing the effects of their actions on the string above the perch on the worm behind the occluder. Moreover, the average time required to obtain a worm in experiment 1 - considering only worms 21 to 30, i.e. after subjects had gained considerable experience in the task, did not differ from the time taken to retrieve a worm in the blind version of the same task (experiment 5). That they needed more trials to attain each worm in the blind version of the task indicates more instances of dropping the string in absence of visual cues. Their performance in experiment 5 was similar to that of New Caledonian (NC) crows, which also needed more trials to solve the visually-restricted string-pulling condition (Taylor et al., 2010) and achieved only modest performance when a mirror provided them with indirect visual information on the worm's ascent. The visual restriction seemed to affect differently green jays and NC crows because the formers' pull-step ratios hardly changed across conditions whereas those of New Caledonian crows were significantly lower in the visually-restricted condition (see table 3), suggesting that their performance might be more reliant on visual guidance. We must stress however, that our jays had acquired more extensive experience with the standard string-pulling task at the time they faced the visually-restricted variation, which also might account for the differences in performance. Although it remains unclear whether the successful crows in Taylor's study were still able to track the worm-displacement through the gaps that surrounded the string, we are certain that our jays could not see anything. Whilst success in the standard string-pulling task has been understood as “insightful”, it is difficult to apply the same interpretation to performance in the blind condition where no visual perceptual feedback is available (see perceptual feedback explanation, Taylor et al., 2010). It is difficult to reconcile our jays’ performance in experiment 4, in which they ignored the string-worm connection, with that in experiment 5, in which they solved the task without the need for visual feedback. Perhaps visual access is only important until subjects reach proficiency in the task, whereafter they can repeat the appropriate chain of memorized motor actions without the need to peer at the hanging reward. Invoking any sort of mental representation to explain subjects’ behaviour in experiment 5 seems illogical in view of the poor performance that these same jays exhibited in experiments 2 to 4. Unfortunately, we did not have enough subjects to separate them into two groups and thereby allowing us to test certain individuals only in the blind string-pulling condition.

The performance of our subjects in experiment 1 may be regarded as quite good or quite poor depending on which species of bird we choose for comparison. In a classical series of experiments by Vince (1958), all 16 chaffinches (*Fringilla coelebs*) tested failed to solve the string-pulling problem spontaneously. Canaries (*Serinus)* fared better, yet only juveniles solved the problem. Greenfinches (*Chloris chloris*) exhibited a very low success rate: only five (out of 12) juvenile subjects managed to pull up the worm spontaneously. Both Vince’s study (Vince, 1958) and ours used the vertical string-pulling paradigm, and one might be tempted to regard them as equivalent. However, Vince used a shorter string (circa 18 cm) which fell through a vertical cylinder, and the friction with the cylinder sometimes sufficed to stop the string from falling back after being pulled by a bird. Hence it was not always necessary to coordinate beak and foot in order to succeed in lifting the worm. In our task, however, it was well-nigh impossible for the jays to lift the bait without combining a pull on the string with a step onto it. We made sure of this by placing a Plexiglas sheet (they do not like walking over it as it is flat and offers no stable footing) below the perch that forced our jays always to pull the string while sitting on the perch. Unfortunately, the age distribution of our sample is too narrow to throw any light on the relation between age and task success. If we compare the performance of our jays in the standard string-pulling task with that of psittacids, we see how Lears' macaws (*Anodorhynchus leari*), hyacinth macaws (*Anodorhynchus hyacinthinus*), blue-fronted Amazon parrots (*Amazona aestiva*) (Schuck-Paim, Borsari, & Ottoni, 2009), grey parrots (*Psittacus erithacus*) (Pepperberg, 2004) and keas (*Nestor notabilis)* (Werdenich & Huber, 2006) clearly outperformed our subjects as they engaged almost immediately in the correct chain of actions that led to the food reward being lifted. However, they did not fare better when they faced discrimination problems similar to the one presented in experiment 4 (Schuck-Paim et al., 2009). Hence it is possible that solving the standard string-pulling task depends less on subjects' understanding of forces and causal relations inherent in the task (i.e., gravity and connectivity) than on how good they are at coordinating beak and foot, which might be related more closely to their feeding routines and the types of food they specialize in.

If we focus on corvids of the *Corvus* genus, New Caledonian crows (*Corvus moneduloides)* and ravens (*Corvus corax)* have a better understanding of the physical relations between the objects and the natural forces involved in the task, because they solve the classical string-pulling problem in just a few minutes: 3 to 8 in the case of ravens (Heinrich & Bugnyar, 2005) and just 16 seconds in New Caledonian crows (Taylor et al., 2010). Table 2 shows the scale of the differences in performance between NC crows and green jays in the standard string-pulling task; our green jays took around 20 times longer than NC crows solve the same problem spontaneously (i.e. meaning here without receiving any external help or shaping) . Moreover, in discrimination problems identical to those presented in experiments 2 and 3 of the current study, NC crows performed extremely accurately (circa 90% correct choices) whereas our jays failed. In experiment 4 neither NC crows nor green jays were able to trace back the strings. However, while green jays showed a clear preference for the non-baited string and exhibited a proximity bias, NC crows chose at random.

The only string-pulling study to be conducted with corvids from a non *Corvus* genus (*Aphelocoma californica*) has been published recently (Hoffmann et al. 2016). As we already had finished data collection, we were unable to follow the same procedure. However, we shall try to compare the performance of western scrub jays with that of our green jays in so far as protocol differences permit. We shall start by pinpointing the procedural differences between studies in order to focus on the results later on. In the horizontal string-pulling study of Hoffmann et al. (2016) western scrub jays were deprived of food two hours before testing in order to increase their hunger. We tried to increase our birds' drive for the food reward by removing the wax worm used in our experiments from the subjects' diet (replacing it with a less preferred type of worm). Regarding the task, our green jays faced a vertical string-pulling task that, unlike horizontal string-pulling, forces the bird to divide its attention between the string, the reward, and its beak and foot coordination, in order to avoid dropping the string. Another methodological difference between studies is that Hoffmann et al. (2016) used shaping to promote the string-pulling behaviour of their subjects by exposing them to increasingly longer distances between themselves and the worm attached to the string (0, 3 cm and 10 cm, respectively). Our subjects, on the other hand, were exposed to a wax worm that hung at a constant distance of 30 cm below the perch in experiment 1 and never received any type of help from the experimenter. Therefore, they had to work out how to attain the worm without any previous experience or external help. Despite all these methodological differences, we believe that scrub jays did not fare much better than our green jays when facing comparable string arrangements. That is to say, both corvid species performed extremely poorly in discrimination experiments in which they had to choose between two strings only one of which was connected to a worm. More specifically, whenever the two strings deviated from a straight trajectory (slanted and crossed string arrangements) their behaviour seemed to be influenced by a proximity bias. Even when western scrub jays succeeded in a slanted condition, in which the string connected to the worm was not straight, the pulling end of the baited string was also closest to the subject. Our green jays faced a slanted condition in which both strings ends connected to the perch were equidistant to the reward and, therefore, no proximity rule would produce the worm reliably. We believe that green jays might solve the same slanted configuration arrangement that western scrub jays solved by applying the same proximity rule, although this is speculation based on how our subjects seemed to prefer to pull on the end of the string end closest to the reward in the crossed strings condition of experiment 4.

The most interesting result of the current study is perhaps the fact that green jays did not need any visual feedback to solve the blind string-pulling problem variation once they had acquired proficiency with the standard string-pulling task. Having deprived our jays of all visual information and hence, of the rewarding view of the bait coming closer, one might be tempted to attribute success in the task to “insightful” mental representation (Taylor et al. 2010, Taylor, Knaebe, & Gray, 2012). But this explanation does not seem to be supported by our data given the jays' extremely poor performance on all the discrimination tasks that preceded experiment 5. Their success in experiment 5 possibly can be attributed to secondary reinforcement. It is plausible that by having associated pulling up the string with obtaining the worm so many times during the previous experiments the motivation provided by the primary reinforcer (the worm coming closer) was transferred to the pulling action itself. In experiment 5 we increased the string length by 10 cm, which meant that subjects needed to combine three pulls followed by four steps on the string before gaining visual access to the worm, but they succeeded nonetheless.

We end the discussion with some tentative explanations as to why NC crows and ravens on the one hand, and green jays on the other, performed so differently in identical tasks. Differences in rearing history and living environment may have influenced subjects' performance and placed green jays in a worse position to compete with Taylor's NC crows (Taylor et al., 2010) or Henrich and Bugnyar's ravens (Henrich & Bugnyar, 2005). Whereas NC crows and ravens were captured immediately before starting the series of food-retrieval experiments (Henrich & Bugnyar, 2005; Taylor et al., 2010), most of our jays were born in captivity and spent most of their lives in a rather impoverished environment (i.e., a zoo as compared with life in the wild). In addition, no enrichment devices to foster extractive foraging behaviour were present in the green jays' cages, and their food was always provided on a plate. Therefore, the difference in performance may be due to the environment. Supporting this idea, a string-pulling study with goldfinches (*Carduelis carduelis*) and siskins (*C. Spinus)* conducted by Seibt and Wickler (2005) found that 33% of all 52 goldfinches and 24% of all 29 siskins tested only pulled and did not step on the pulled-up string. Interestingly, in the birds that were raised with branches, 11 of 40 goldfinches (27.5%) and 16 of 27 siskins (59.3%) solved the string-pulling problem within one to ten 1-h sessions. Establishing whether it was the rearing history and/or the living environment that constrained green jays' problem solving abilities would require capturing wild adults and administering the same tasks as those given to our captive jays.

Another factor not related to cognitive capacity that might help explain the divergence between the results of the common ravens and NC crows and the green jays is the capacity for food manipulation. Altevogt attributed blue tits' (*Parus Caeruleus*) success in the string-pulling task to an innate behaviour pattern that involved the use of the foot (Altevogt, 1953). Both common ravens and New Caledonian crows are significantly bigger than green jays (60 cm, 40 cm, and 25-29 cm respectively) and this anatomical difference might influence the type, as well as the size, of the food they process. Unfortunately, we have failed to find any systematic report on how these two species process food. We know from our own observation of the green jays that they are quite adept at taking food and objects with their foot, but we do not know whether this might help towards building the sophisticated beak and foot coordination involved in vertical string-pulling. We do know, however, that in the classical string-pulling studies by Vince (1961) those species of birds that normally use their feet for feeding purposes (i.e. tits) are more successful than those that do not (greenfinches and canaries). Even when *Corvus* corvids are more skilled in beak and foot coordination, we cannot use the same argument to explain the superior performance of crows and ravens in the discrimination tasks from experiments 2 to 4, where the string selected was the first string touched (and not necessarily lifted).

We would like to finish our discussion by encouraging further studies in which captive and wild birds are exposed to exactly the same tasks in order to determine how important rearing history may be in explaining subjects' behaviour. The difficulties in breeding captive green jays limited the sample size of the current study considerably, and indeed considerable caution is needed before making any general claim as to what green jays as a species can or cannot achieve. The main strength of this study is that it shows what captive green jays without any enrichment or foraging experience incorporated in gaining their daily food can achieve in a classical physical cognition task. We hope that future studies will shed further light on the behaviour and cognition of this species.

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Table 1.

Demographics of subjects

Name	*Sex*	*Place of Birth*	*Age at the beginning of the study (in years, months and days)*
Bernat	M	Zoo of Barcelona	2Y,9M,4D
Goliat	M	Zoo of Barcelona	1Y,7M,13D
Joanot	M	Zoo of Barcelona	2Y,8M,5D
Konrad	M	Zoo of Barcelona	2Y,8M, 4D
Penélope	F	Zoo of Barcelona	0Y,4M,17D

Table 2.

Mean (and S.E.M) time and average pull-step ratios required to obtain the first reward in green jays (n=3; current study) as compared to NC crows (n=4, experienced group, see Taylor et al., 2010) in the standard string-pulling task.

	Time to solution (seconds)	***Average pull-step ratios***
Green jays cumulative	1847.33±1699.81	4 ± 10%
Green jays active trying	318 ± 219	4 ± 10%
NC crows	16.25 ± 14.24	90.2 ± 2.42%

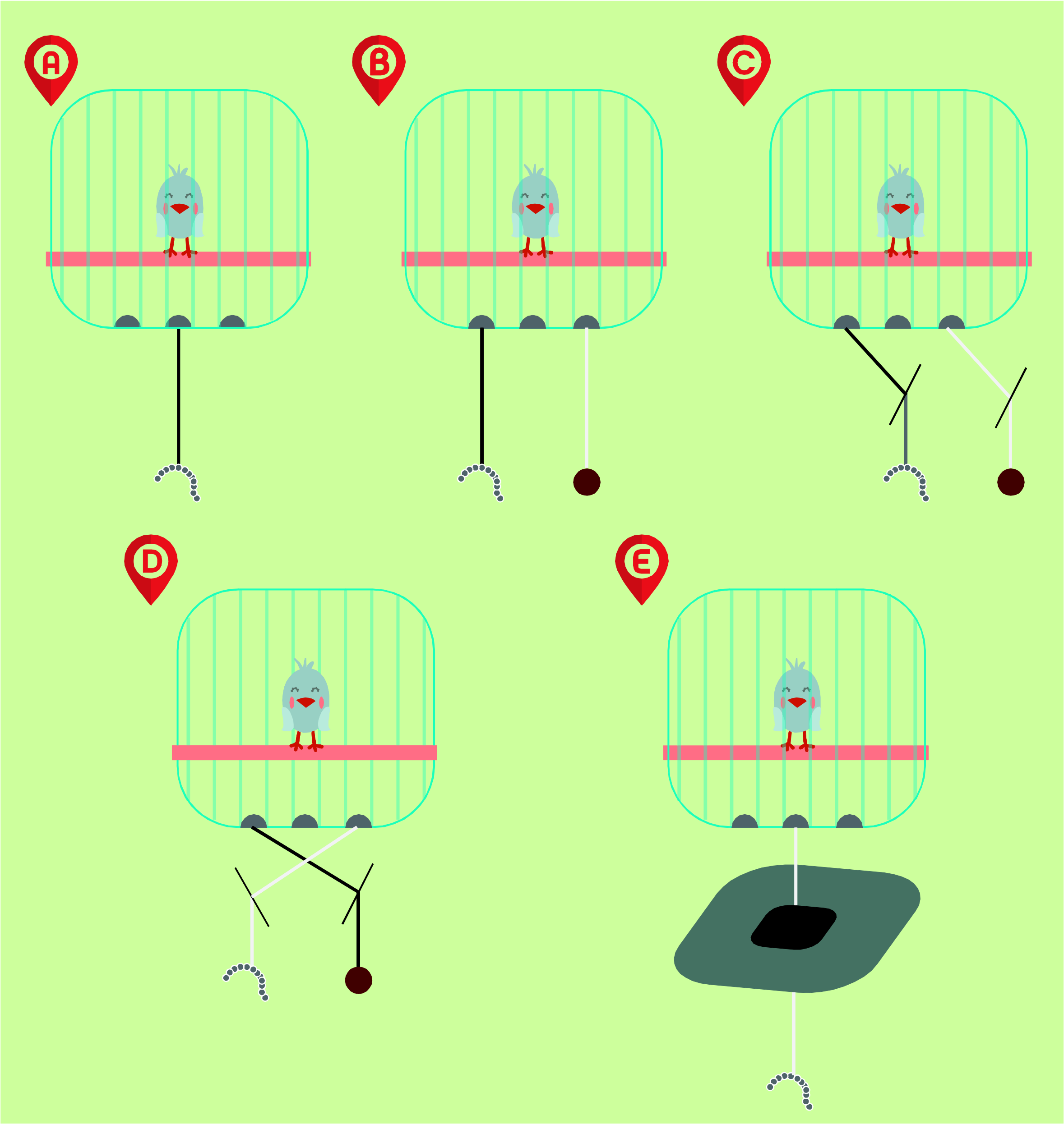
Table 3.

Mean (and S.E.M) time, number of trials and pull-step average ratios required to get the reward in the standard and the blind string-pulling conditions in green jays (n=3; current study) and NC crows (n=4, experienced group, see Taylor et al., 2010). Note that green jay data in the standard string-pulling are the average for the last ten worms (and not ten trials) obtained in experiment 1.

	Green jays		***NC crows***	
Condition	Standard	Blind	Standard	Visually-restricted
Average time to solution (seconds)	14.17 ± 1.30	14.20 ± 1.36	16.25 ± 14.24	Not reported
Average number of trials to solution	1.13 ± 0.06	2.83 ± 0.56	Not reported	3.0 ± 1.08
Pull-step ratio	50 ± 14%	54 ± 24%	90.2 ± 2.42 %	55.7 ± 10.1 %

Figure captions

Fig. 1. The apparatus and string arrangements corresponding to experiment 1 (A), experiment 2 (B), experiment 3 (C), experiment 4 (D) and experiment 5 (E) of the study.


A
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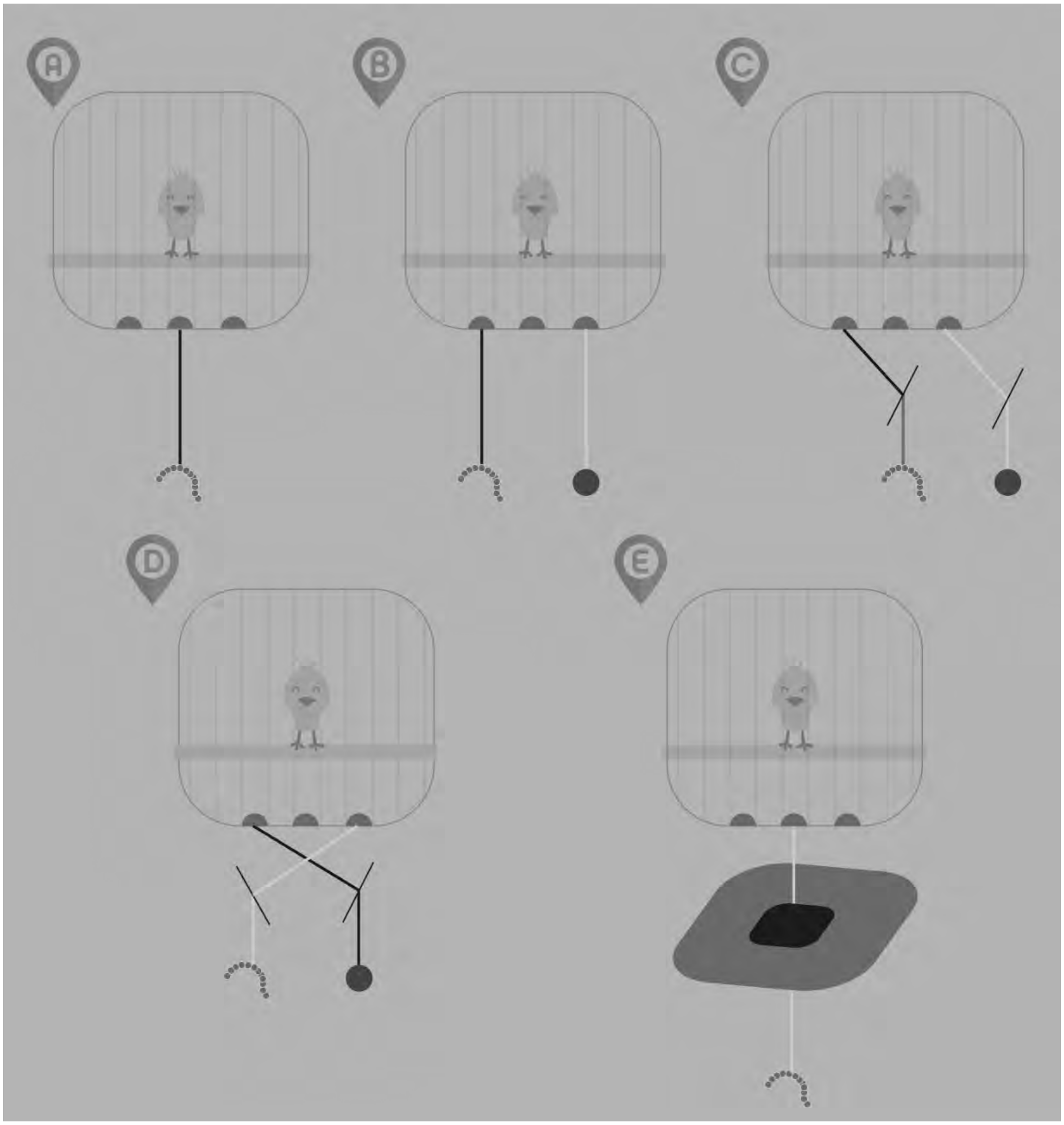
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