Apes (*Gorilla gorilla, Pan paniscus, P. troglodytes, Pongo abelii*) Versus Corvids (*Corvus corax, C. corone*) in a Support Task: The Effect of Pattern and Functionality

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Apes (*Gorilla gorilla, Pan paniscus, P. troglodytes, Pong abelii*) and corvids (*Corvus corax, C. corone*) are among the most proficient and flexible tool users in the animal kingdom. Although it has been proposed that this is the result of convergent evolution, little is known about whether this is limited to behavior or also includes the underlying cognitive mechanisms. We compared several species of apes (bonobos, chimpanzees, gorillas, and orangutans) and corvids (carrion crows and common ravens) using exactly the same paradigm: a support task with elements from the classical patterned-string tasks. Corvids proved able to solve at least an easy pattern, whereas apes outperformed corvids with respect to the complexity of the patterns solved, the relative number of subjects solving each problem, and the speed to reach criterion. We addressed the question of whether subjects based their choices purely on perceptual cues or on a more abstract understanding of the problem. This was done by using a perceptually very similar but causally different condition where instead of paper strips there were strip shapes painted on a platform. Corvids' performance did not differ between conditions, whereas apes were able to solve the real but not the painted task. This shows that apes were not basing their choices just on spatial or arbitrary perceptual cues. Instead, and unlike corvids, they must have had some causal knowledge of the task.

Keywords: apes, corvids, patterned-strings, support, causality

Many animals manipulate objects to find shelter, build nests, access food, catch prey, fight competitors, or attract potential mates (e.g., Boesch & Boesch, 1990; Byrne & Byrne, 1993;

Hansell, 2005; Madden, 2003). In some cases they use objects as tools to act on other objects, and they even modify objects to produce such tools (Beck, 1980). These behaviors suggest that animals know something about the physical affordances of the objects that they manipulate. However, the nature of this knowledge is still a matter of debate (e.g., Hunt, 2005; Povinelli, 2000). This is mainly because nonverbal organisms' knowledge can only be inferred from behavior, and behavior is often difficult to interpret (e.g., Kacelnik, Chappell, Weir, & Kenward, 2006). Furthermore, convergent evolution of behavior does not necessarily imply convergent evolution of cognition (Seed, Emery, & Clayton, 2009). According to this, two very similar behaviors, such as the extraction of prey from crevices with sticks by both chimpanzees and crows (e.g., Hunt, 1996; McGrew, 1974), might stem from different types of knowledge about the physical world (see Kummer, 1995).

One of the tasks typically used to assess causal knowledge in comparative studies is the patterned-string task, where one of several strings has food attached to the end that is out of reach. The assumption is that a subject that perceives the means-end connections of the problem will pull the baited string to get the food. Patterned-string problems vary in difficulty as a function of the number of strings, the strings' orientations toward the subject (i.e., perpendicular or oblique), and the angles and crossings that they form with each other (Harlow & Settlage, 1934; but see Warden, Koch, & Fjeld, 1940). Most nonprimate mammals can solve sim-

ple patterns, although they require learning (Hobhouse, 1915; King & Witt, 1966; Michels, Pustek, & Johnson, 1961; Osthaus, Lea, & Slater, 2005; Whitt, Douglas, Osthaus, & Hocking, 2009). In contrast, primates, corvids, and parrots can solve simple problems spontaneously and more complex ones with some practice (Dücker & Rensch, 1977; Finch, 1941; Harlow & Settlage, 1934; Hobhouse, 1915; Pepperberg, 2004). One common raven even solved the cross pattern spontaneously (Heinrich, 1995), although this pattern proved difficult for the other ravens in that same study and for various other species (e.g., Balasch, Sabater Pi, & Pedrosa, 1974; Dücker & Rensch, 1977; Schuck-Paim, Borsari, & Ottoni, 2009; Werdenich & Huber, 2006).

There have been several suggestions regarding the type of information that subjects may use to solve patterned-string tasks. These include the proximity of the strings' ends to the food and the general direction of the strings (Harlow & Settlage, 1934), the path of the strings (Huber & Gajdon, 2006), and the perceptual configuration of the display (Dücker & Rensch, 1977). Strikingly, no systematic study has been conducted to clarify this issue or to assess potential differences between species in this respect. And yet, this is an important question, because it could be that primates and some birds outperform other species because they are basing their choices on more causally relevant cues. For example, reliably tracing the path of the baited string (e.g., Riesen, Greenberg, Granston, & Fantz, 1953) would lead to a better general performance than always choosing the string end that is closer to the food.

Some prior work has assessed whether animals attend to causally relevant over arbitrary cues, but has led to mixed results, both in corvids and primates (Bluff, Weir, Rutz, Wimpenny, & Kacelnik, 2007; Hanus & Call, 2011; Santos, Miller, & Hauser, 2003; Visalberghi & Limongelli, 1994). Hauser and colleagues, for example, used the support task (Piaget, 1952) to address this issue in cotton-top tamarins (Hauser, Kralik, & Botto-Mahan, 1999; Hauser, Santos, Spaepen, & Pearson, 2002). First, they found that tamarins preferred to pull a cloth supporting a reward over a cloth placed near a reward (on/off problem), and a complete cloth over a broken cloth when both supported a reward (broken cloth problem). Similar results have been reported for human infants and other primates (Herrmann, Wobber, & Call, 2008; Povinelli, 2000; Redshaw, 1978; Spinozzi & Potí, 1989, 1993; Willatts, 1984; Yocom & Boysen, 2010) and also for some birds (Auersperg, Gajdon, & Huber, 2009; but see de Mendonça-Furtado & Ottoni, 2008; Schmidt & Cook, 2006). However, critically, the tamarins transferred their good performance to new conditions in which functionally irrelevant features such as the color, the shape, and the size of the cloths had been changed. This suggests that, even though subjects may have based their choices on perceptual cues such as the contact between the food and the cloth and the presence of a gap along the cloth (Povinelli, 2000; Spinozzi & Potí, 1989), this may have been the result of attending to functionally relevant, as opposed to arbitrary, cues.

Attending to the adequate cues of a problem (e.g., contact, absence of a gap), however, does not necessarily imply knowledge about the physical relations between the objects in the problem (e.g., support, connection) (Penn & Povinelli, 2007). Indeed, the way perceptual information is interpreted constitutes a critical component of causal knowledge. Individuals may represent causal information in a form very similar to the actual perception of that information (i.e., a percept). Alternatively, subjects may interpret causal information in a way such that its final representation is detached from its original perceptual form (i.e., a concept) (e.g., Hauser & Santos, 2007). The degree of abstraction of causal representations is important, as it determines to a great extent the flexibility of the causal knowledge (e.g., Seed & Call, 2009; Tomasello & Call, 1997). For example, in a patterned-string task, a subject learning to follow the path of the baited string based just on its visual continuity might have difficulties if the string attached to the food were replaced by a big star-shaped cushion. In contrast, a subject learning to follow the path of the string based on abstract concepts, like connection or tension, would find the new problem easier to solve. Therefore, studies on causal knowledge should implement the appropriate controls to differentiate between abstract and perceptual knowledge.

In the present study, we wanted to investigate causal knowledge in great apes and corvids, two taxa that seem to have converged in their ability to solve physical problems (Emery & Clayton, 2004a, 2004b; Emery, 2006; Lefebvre, Reader, & Sol, 2004; Seed, Emery, & Clayton, 2009). To our knowledge, only two parallel studies have directly compared one species of corvid, the rook, and one species of ape, the bonobo, using a version of the trap-tube task (Helme, Call, Clayton, & Emery, 2006; Helme, Clayton, & Emery, 2006). Overall, neither species showed understanding of physical contact, although bonobos slightly outperformed rooks in this task. We presented bonobos, chimpanzees, gorillas, orangutans, carrion crows, and ravens with a task that combined elements of a patterned-string problem (cross and pseudocross patterns) and the support problem (involving paper strips) (see Figure 1a). Specifically, we wanted to know (1) whether subjects could solve this novel task, (2) which cues they attended to, (3) to what extent subjects relied on the perceptual features of the task or on the more abstract information about support, and (4) whether there were differences between apes and corvids or between species within each group.

The cross and the pseudocross strip patterns allowed us to explore the cues that were being attended to by subjects in this task. Based on previous literature, there were three possibilities:
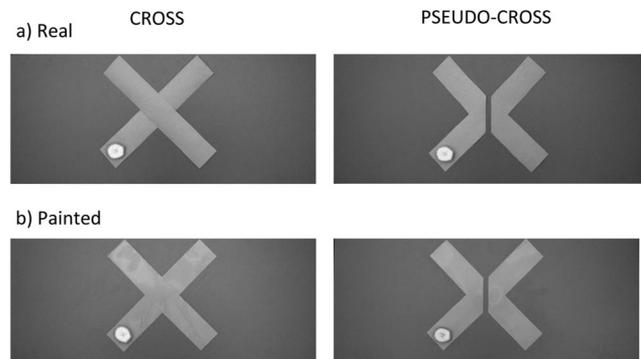

Figure 1. Patterns and conditions. Two patterns, the cross and the pseudo-cross, either made with paper strips (real condition) or painted on a platform (painted condition) were used in this study. Apes received banana slices (in the picture) or half grapes as reward whereas corvids got cheese bits.

One possibility was that subjects would pick the strip of paper whose proximal end was closer to the reward, which would result in the solution of the pseudocross, but not the cross, pattern (Proximity hypothesis). A second possibility was that subjects would follow the general direction of the baited paper strip, which would result in the solution of the cross, but not the pseudocross, pattern (Direction hypothesis). Finally, subjects may follow the path of the baited paper strip or respond to the overall configuration of food and strips, which would afford the solution of both patterns (Path/Configuration hypothesis).

The question of whether subjects had perceptual or more abstract knowledge of the task was addressed by using two conditions that were similar in appearance but that differed in the causality present. Specifically, we used strips of paper placed on a board in the Real (causal) condition and stripes (that were very similar in appearance to the paper strips) painted on the board in the Painted (arbitrary) condition (Figure 1a and 1b, respectively). In both cases, subjects had to select the baited strip to get the reward. This allowed us to investigate two subhypotheses of the Path/Configuration hypothesis: whether subjects merely used the appearance of the strips to get the reward (Perceptual hypothesis), or, whether they additionally used information about the physical relationship between the strips and the reward (Causal hypothesis). Subjects relying on purely perceptual cues should perform similarly in both the real and the painted conditions, or at the very least, should transfer their knowledge from the former to the latter. In contrast, subjects relying on more abstract knowledge of the support problem should perform better in the real than in the painted condition, and they should not transfer their knowledge between conditions. Figure 2 shows our different hypotheses and their predictions.
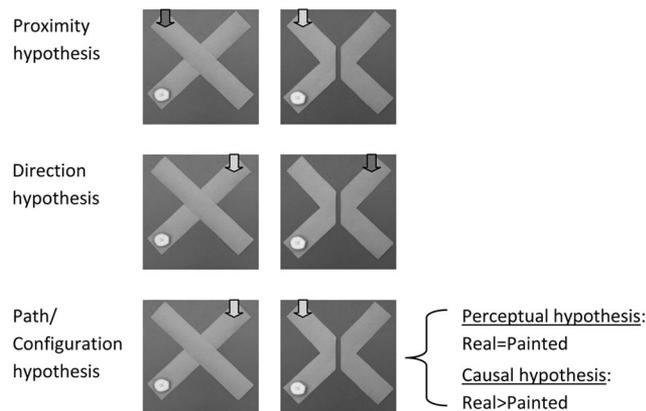

Figure 2. Hypotheses and predictions. Arrows show the choice expected from a subject choosing (1) the strip end closer to the food (Proximity hypothesis), (2) the strip end in line with the general direction of the baited strip (Direction hypothesis), and (3) the strip actually holding the reward (Path/Configuration hypothesis). Green arrows mean the choice would allow getting the food whereas red arrows mean the choice would be incorrect. If subjects solved both patterns based just on perceptual cues, they would succeed both in the real and the painted condition and they would transfer the solution from one condition to the next (Perceptual hypothesis). If, on the contrary, their performance was based on object relations, they would perform better in the real than in the painted condition and they would not transfer knowledge between the two conditions (Causal hypothesis).

Method

Subjects

Five bonobos (*Pan paniscus*), six chimpanzees (*Pan troglodytes*), four gorillas (*Gorilla gorilla*), and eight orangutans (*Pongo abelii*), housed at the Wolfgang Koehler Primate Research Center in Leipzig Zoo, Germany, and eight common ravens (*Corvus corax*) and six carrion crows (*Corvus corone*), housed at the Konrad Lorenz Research Station in Grünau im Almtal, Austria, participated in this study (see Table 1 for subjects' sex, age, and rearing histories). Both the apes and corvids live in social groups inside big enclosures with earth ground, rocks, streams and natural vegetation. They have trees and other vertical and horizontal structures for climbing or perching, and for finding shelter. In addition, they have enrichment devices, such as artificial termite mounds for the apes and small plastic toys for the corvids. Their feeding routines did not change for the present study, and water was always available during testing. Subjects were tested individually; the apes in special observation rooms and the corvids in a division of their enclosure. Most of the apes had some experience with support tasks but those never involved crossing strips (Herrmann et al., 2008). Also, most of the apes had experience with tasks in which they had to use a tool to obtain an out-of-reach reward. One of these studies involved selecting tools based on features such as length, rigidity or hollowness (Mulcahy, Call, & Dunbar, 2005). Other studies involved using tools while avoiding a trap where the food may fall (Girndt, Meier, & Call, 2008; Helme, Call, et al., 2006; Martín-Ordás, Call, & Colmenares, 2008; Mulcahy & Call, 2006; Seed, Call, Emery, & Clayton, 2009). Table 1 presents each subject's experience on each of these tasks. Most of the ravens and half of the crows had experience with string-pulling tasks in different set-ups, that is, acquisition of pulling up food on vertical string (Bonechi, 2005; unpubl. data by Wascher), choice of strings in individual and social conditions (Bonechi, 2005; Gattermayr, 2007; unpublished data by Munteanu) and with or without blockers (Pfuhl, 2009). The majority of patterned string problems concerned parallel strings, but four birds had some experience with vertically crossed strings (total of 12 trials/bird; Bonechi, 2005). The members of each species were divided into two groups (A, B) and, as far as possible, age and gender of the groups were matched (see Table 1).

Materials

Two types of brown paper strips (i.e., straight and angular; apes: 6 × 30 cm, corvids: 4 × 19 cm) could be placed on top of a deep blue plastic panel (apes: 78 × 32 cm, corvids: 50 × 20 cm) to form the patterns shown in Figure 1, namely, *cross* and *pseudocross*, plus the (straight) *single-strip* pattern of the pretest. Other plastic panels had the patterns' shapes on them, painted with brown spray (Plasticote 2118/ Ral 1019 Gray Beige). The similar color, plus the perimeter thin shadows drawn with pencil, made it difficult for the human eye to distinguish between the painted and real strips at first sight (Figure 1a and 1b). However, we did not want to mislead our subjects into thinking that the painted strips were real ones

Table 1

Summary of Subjects Including Sex, Age at the Time of the Study, Rearing History, Experience in Support or String-Pulling Studies and in Other Physical Tasks, and Their Group Assignment

Group	Subject	Sex	Age (years)	Rearing history	Experience in pulling tasks	Experience in other tool tasks
Bonobos (*Pan paniscus*)						
A	Kuno	M	11	hand	1	8, 9
	Ulindi	F	14	mother	1	7, 8, 9
B	Yasa	F	10	mother	1	8, 9
	Limbuko	M	12	hand	1	8, 9
	Joey	M	25	hand	1	7, 8, 9
Chimpanzees (*Pan troglodytes*)						
A	Alex	M	6	hand	1	9, 11
	Alexandra	F	8	hand	1	9, 11
	Fraukje	F	31	hand	1	9, 10, 11
B	Lome	M	6	mother	—	9, 11
	Annett	F	8	hand	1	11
	Fifi	F	14	mother	1	7, 9, 10, 11
Gorillas (*Gorilla gorilla*)						
A	Viringika	F	12	mother	1	6, 7, 9, 10
	Gorgo	M	26	hand	1	6, 9, 10
B	Kibara	F	3	mother	—	—
	Bebe	F	28	mother	1	6, 9
Orangutans (*Pongo abelii*)						
A	Pagai	M	4	mother	—	—
	Kila	F	7	mother	—	10
	Dokana	F	18	mother	1	6, 7, 9, 10
	Dunja	F	34	mother	1	6, 9, 10
B	Raaja	F	4	mother	—	—
	Padana	F	10	mother	1	9, 10
	Pini	F	19	mother	1	6, 7, 9, 10
	Bimbo	M	27	hand	1	6, 7, 9, 10
Crows (*Corvus corone*)						
A	Hugo	M	20	hand	5	
	Petra	F	2	hand	5	
B	Baerchen	M	2	hand	—	
	Klaus	M	<1	hand	—	
	Toeffel	F	1	hand	—	
	Gabi	F	2	hand	5	
Ravens (*Corvus corax*)						
A	Hugin	M	14	hand	2	
	Dora	F	5	hand	2, 3, 4	
	Gerti	F	<1	mother	—	
	Cassandros*	M	5	hand	2	
	Columbo*	F	5	hand	3, 4	
	Mojo	F	1	hand	5	
B	Ilias	M	5	hand	2, 3, 4	
	Rumo	M	1	hand	5	

Note. (1) Herrmann et al., 2008; (2) Bonechi, 2005; (3) Gathermayr, 2007; (4) Pfuhl, 2009; (5) Unpubl. data by Munteanu (2009) and Wascher (2008); (6) Mulcahy et al. 2005; (7) Mulcahy & Call 2006; (8) Helme et al. 2006; (9) Girndt et al. 2008; (10) Martín-Ordás et al. 2008; (11) Seed et al. 2009.
* These subjects only completed the real condition, for lack of motivation.

(because they should be able to discriminate the causal and noncausal structure of each problem). To this effect, the materials were set up in full view of the subjects. Likewise, we chose to paint the strips rather than glue paper strips on the platform because we wanted to avoid potentially misleading the subjects into thinking that they could actually pull the (glued) strips. In the case of apes, the task was presented on a sliding table (80 × 39 cm) that was fixed to the outside of a mesh testing window (69 × 48 cm). In the case of corvids, the task rested on a wooden platform that was situated at ground level outside of the enclosure mesh. Banana slices (approx. 8 mm high) or half grapes were used as rewards for the apes, whereas bits of cheese (approx. 7 × 5 × 2 mm) were used for the corvids.

Design

The present study had two phases: the *pretest* and the *test*. The pretest consisted of two sessions of 12 trials each, although this could be extended, provided subjects failed to solve the task in this amount of trials. Group A was presented with one paper strip placed in the center of the platform, baited with a piece of food on the out-of-reach end of it. Group B received the painted version of this. By the end of the pretest, A-subjects should have learned to pull the paper strip to get the food resting on top, whereas B-subjects should have learned to touch the painted strip to get the food from the experimenter (criterion of success: touching or pulling the strip in all 12 trials of 2 consecutive pretest sessions).

The test consisted of 12 sessions, six in the real and six in the painted condition. Group A first did the real condition block and then the painted one, whereas Group B did the reverse. Each session had 12 trials, six of which were with the cross pattern and six with the pseudocross pattern. Both pattern (cross/pseudocross) and food position (left/right) were counterbalanced within sessions. Moreover, these factors were presented randomly, with the only restrictions being that the same pattern could not appear more than two times in a row and that food could not be in the same position on more than three consecutive occasions.

Procedure

A session started with the blue plastic panel out of the subject's reach. In the case of the real condition, the experimenter (E) placed the paper strips onto the panel in full view of the subject (S). Subsequently, E baited one strip on its far end (with respect to S) and, when S was paying attention (i.e., within approximately 3 m from the panel, facing toward it), E pushed the panel toward the mesh. Pulling or touching a strip in the real condition, and touching a stripe in the painted condition, were considered choices. When pulling the correct strip, the subject could retrieve the reward on its own, although E would provide help if the food fell off the strip. In cases of touching the strip, E gave the food to the subject. When S's choice was incorrect, E moved the platform away before S could make a second choice. A session ended after the 12 trials had been completed or after 5 minutes without S choosing. Sessions were held over different and, as far as possible, consecutive days.

Two aspects of the real cross pattern deserve special mention, because the crossed strips could potentially affect each other's position and also the stability of the food. When the subject made a correct choice (pulled the baited strip) the food very rarely fell off the strip, given its flat shape, its weight, and the fact that both banana and cheese generally stuck to the paper. In case it fell, as said above, the experimenter provided the food to the subject. Note that given a correct choice it was unimportant if the nonchosen, empty strip (situated either above or below) moved or not (dragged by the chosen, baited strip) because the key issue was whether the subject obtained the reward. When the subject made a wrong choice (pulled the empty strip), however, dragging the nonchosen, baited strip could have been a problem. Fortunately, this did not happen often, because the weight of the food usually kept the baited strip in place both when it was above or below the other strip. Yet, when it did happen, the experimenter removed the food before the subject could retrieve it.

Scoring and Data Analysis

We videotaped all trials and scored subjects' responses in situ on data sheets. Our main dependent measure was the percentage of trials in which subjects selected the correct alternative, whereas our independent variables were species, pattern (cross vs. pseudocross) and material (real vs. painted). Because some of our data did not meet the normality and homogeneity assumptions for parametric tests, we used nonparametric statistics. All tests were two-tailed. When sample sizes were small, we used exact probability tests (Mundry & Fischer, 1998).

We did not conduct within-subject tests of significance for bonobos and gorillas separately because their small sample sizes ($n < 6$) made it impossible to reject the null hypothesis and therefore rendered the tests uninformative (Siegel & Castellan, 1988). When small sample sizes occurred as a result of tied observations, we simply indicated this in the results section. Twenty percent of sessions of apes and corvids were randomly selected and a second observer coded them to assess interobserver reliability, which in both cases was excellent (Cohen's $\kappa = 0.96$, $p < .01$).

The data were analyzed in two steps: First, we analyzed the effect of each of the independent variables on the percentage of correct responses for apes and corvids separately. Moreover, we investigated whether responses to the different conditions changed over time by correlating session number with the median percent success for each species and session. Additionally, we tested whether subjects responded at above chance levels in the first and last sessions of each condition. In the case of apes, and just for the cross pattern, we compared the last session of the first condition received with the first session of the second condition received, to assess for any possible transfer between conditions. Second, we combined the data for apes and corvids to compare their performance in the various conditions. In this section, we classified subjects as successful based on their individual performances in each condition - that is, if they responded correctly in at least five of six trials in two consecutive sessions. Finally, we classified subjects using a cluster analysis based on their performance in the following four variables: cross real, cross painted, pseudocross real, and pseudocross painted. The sum of the squared Euclidean distance across the four variables for each pair of individuals was calculated, and we used the resulting matrix to perform the cluster analysis based on the average linkage between groups. This technique allowed us to visualize how much overlap in performance existed between the different taxa and between the different species.

Although our initial intention was to discard the data from any unfinished sessions to ensure that all subjects displayed a similar degree of motivation to get the rewards, because of time restrictions with the corvid testing, this could only be done for the apes. This meant that 1% of sessions undertaken with the apes (including 4 sessions from 2 chimpanzees, 1 bonobo and 1 gorilla) were dropped and replaced by complete sessions, whereas 15% of sessions undertaken with the corvids (mainly ravens) were stopped and continued at a later time, either on the same day or on the next day.

Results

Apes

All apes that started with the real condition pulled the single strip presented in the pretest phase spontaneously. Moreover, all apes, except one orangutan, that started with the painted condition readily learned to touch the painted stripe to get the reward in the first trial(s) of the first session. The orangutan needed four sessions of pretest before starting the test.

Table 2 presents the median percentage of correct trials by ape species and condition. Overall, apes performed significantly better with the pseudocross pattern than with the cross pattern (Wilcoxon's test: $T = 276$, $n = 23$, $p < .01$). Additionally, subjects performed significantly better in the real condition than in the

Table 2
Median Percentage of Correct Trials as a Function of Species, Condition, and Pattern in the Test

			Condition					
			Real			Painted		
Species	N		Cross	Pcross	Total	Cross	Pcross	Total
Apes								
	Bonobos	5	83.3^{na}	100^{na}	88.9	16.7^{na}	100^{na}	58.3
	Chimpanzees	6	40.3	97.2^{*}	69.4	12.5^{*}	93.1^{*}	51.4
	Gorillas	4	41.7^{na}	88.9^{na}	65.3	37.5^{na}	90.3^{na}	57.6
	Orangutans	8	79.2^{*}	97.2^{*}	88.2	5.6	98.6^{*}	52.1
	Total	23	66.7	97.2	79.2	16.7	97.2	52.8
Corvids								
	Ravens	8	51.4^{na}	50.0	51.4	47.2	52.8^{na}	49.5
	Crows	6	34.7	76.4^{*}	55.6	37.5^{na}	70.8^{na}	52.8
	Total	14	50.0	61.1	54.2	42.3	56.2	51.4

Note. The strips could be real or painted (condition) and they could form either a cross or a pseudo-cross (pattern). Correct trials were those where subjects chose the baited strip. Asterisks show those medians that significantly differed from chance. "Na" stands for non-applicable computations, as a result of small sample sizes.

painted condition (Wilcoxon's test: T = 263.5, n = 23, p < .01). However, this difference depended on the stimulus pattern that was presented. Whereas apes performed significantly better with the real cross than with the painted cross (Wilcoxon's test: T = 255, n = 23, p < .01), their performance did not differ between the real and the painted pseudocross (Wilcoxon's test: T = 90.5, n = 23, p = .24).

There were significant differences between ape species in the real cross and the painted pseudocross conditions (Kruskal-Wallis tests: real cross: χ^2(3, n = 23) = 8.38, p = .04; real pseudocross: χ^2(3, n = 23) = 5.80, p = .12; painted cross: χ^2(3, n = 23) = 3.17, p = .37; painted pseudocross: χ^2(3, n = 23) = 7.84, p = .05). However, pairwise Mann–Whitney U tests, with the Bonferroni-Holm correction (Holm, 1979), revealed only that orangutans significantly outperformed chimpanzees in the real cross condition (U = 0.0, n = 14, p < .01).

Table 2 also shows performance of chimpanzees and orangutans against chance levels for each of the four conditions. Both species were above chance in both the real and the painted pseudocross conditions (Wilcoxon's tests: ps <0.05 in both cases). Orangutans further exceeded chance levels in the real cross condition (Wilcoxon's test: T = 36, n = 8, p = .01). Chimpanzees performed significantly below chance in the painted cross condition (Wilcoxon's test: T = 21, n = 6, p = .03).

Figure 3a presents the median percentage of correct trials in the real cross and pseudocross conditions for each ape species across sessions. In the real cross condition, orangutans significantly improved their performance across sessions and chimpanzees also showed a trend in this direction (Spearman r: bonobo: r = −0.31, p = .56; chimpanzee: r = .83, p = .06; gorilla: r = −0.46, p = .35; orangutan: r = .99, p < .01). In the first session, orangutans were at chance levels (Wilcoxon's test: T = 18.5, n = 7, p = .59) whereas chimpanzees responded at below chance levels (Wilcoxon's test: T = 21, n = 6, p = .03). By the last session, orangutans had exceeded chance levels (Wilcoxon's test: T = 36, n = 8, p = .01) and statistics could not be computed for chimpanzees due to their small sample size (Wilcoxon's test: *ns* (n = 5)).

In the real pseudocross condition, by contrast, there was no significant change in performance across sessions for any ape species (Spearman r: bonobo: r = −0.49, p = .40; chimpanzee: r = .51, p = .40; gorilla: r = −0.52, p = .35; orangutan: r = .54, p = .27). Chimpanzees and orangutans performed at above chance levels in the first session and maintained this performance in the last session (Wilcoxon's tests: ps <0.04 in all cases).
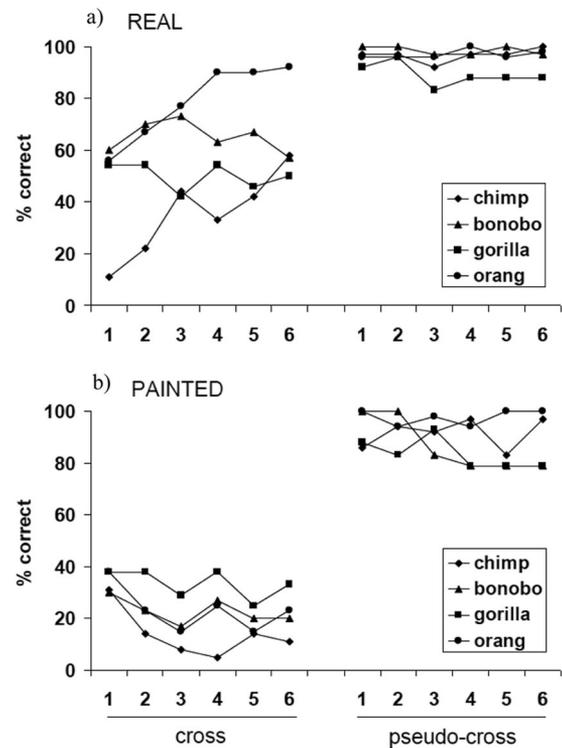

Figure 3. Percentage of correct responses across sessions for both patterns, in the real condition and in the painted condition, by the apes.

Figure 3b presents the median percentage of correct trials in the painted cross and pseudocross conditions for each ape species across sessions. In the painted cross condition, none of the species changed their performance significantly across sessions (Spearman r: bonobo: r = −0.52, p = .30; chimpanzee: r = −0.46, p = .37; gorilla: r = −0.58, p = .25; orangutan: r = −0.44, p = .41). Orangutans performed at chance levels in both the first and last sessions (Wilcoxon's tests: orangutans: n = 7, ps >0.06 in both cases), whereas statistics could not be computed for chimpanzees because of their small sample size (n < 6 in both cases).

In the painted pseudocross condition, there were no significant changes in performance across sessions, except for gorillas whose performance decreased (Spearman r: bonobo: r = −0.51, p = .33; chimpanzee: r = .32, p = .54; gorilla: r = −0.93, p = .03; orangutan: r = .28, p = .60). In the first session, orangutans performed at above chance levels (Wilcoxon's test: T = 36, n = 8, p = .01) whereas statistics could not be computed for chimpanzees because of their small sample size (n = 5). In the last session, both chimpanzees and orangutans performed at above chance levels (Wilcoxon's tests: ps <0.04 in both cases).

Figure 4 shows the percentage of correct responses in the cross pattern condition across sessions, split by those apes that started with the real condition and those that started with the painted condition. The apes that received the real condition first performed significantly better in the last session of the real condition than in the first session of the painted condition. In contrast, the apes that received the painted condition first performed worse in the last session of the painted condition than in the first session of the real condition (Wilcoxon's tests: n = 8, ps < 0.03 in both cases).

Corvids

All corvids starting with the real condition pulled the single strip presented in the pretest spontaneously. Furthermore, all corvids but one crow starting with the painted condition readily learned to touch the painted stripe to get the reward in the first trial(s) of the first session. The crow needed three sessions of pretest before starting the test.

Table 2 presents the median percentage of correct trials as a function of corvid species and condition. Overall, subjects performed significantly better with the pseudocross than with the
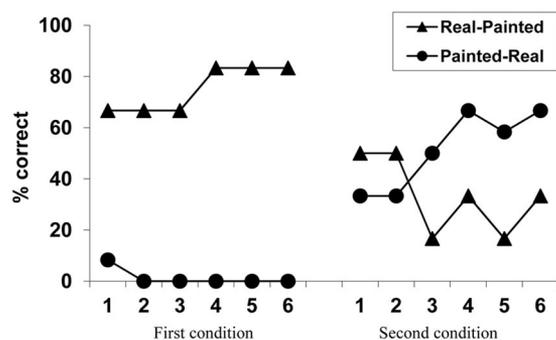

Figure 4. Percentage of correct responses across sessions in the cross pattern by the apes that started in the real and then got the painted condition and the apes that started in the painted and then got the real condition.

cross (Wilcoxon's test: T = 242.5, n = 23, p < .01). However, this difference depended on the material. Whereas corvids performed significantly better with the painted pseudocross than with the painted cross (Wilcoxon's test: T = 54, n = 10, p < .01), there was a marginally significant difference between the real pseudocross and the real cross (Wilcoxon's test: T = 72, n = 13, p = .07).

There was no overall significant difference between the real and the painted conditions (Wilcoxon's test: T = 190.5, n = 24, p = .25), and this was true both for the cross pattern (Wilcoxon's test: T = 60.5, n = 12, p = .09) and for the pseudocross (Wilcoxon's test: T = 39, n = 12, p = 1.00).

Ravens outperformed crows in the real cross condition (Mann–Whitney test: U = 5.0, n = 14, p = .01), whereas the reverse was true in the real pseudocross (Mann–Whitney test: U = 4.0, n = 14, p = .01). There were no significant differences between species in the other two conditions (Mann–Whitney tests: painted cross: U = 7.5, n = 12, p = .09; painted pseudocross: U = 6.0, n = 12, p = .06).

Table 2 also shows each species' performance against chance levels for each of the four conditions. Ravens responded at chance levels both in the real pseudocross and in the painted cross (Wilcoxon's tests: p > .12), whereas in the other conditions the sample size did not allow statistical computations (n < 6 in both cases). Crows responded at above chance levels in the real pseudocross condition (Wilcoxon's test: T = 21, n = 6, p = .03) and at chance levels in the real cross condition (Wilcoxon's test: T = 20, n = 6, p = .06), but no statistical computations could be done with the other conditions because of small sample sizes (n < 6 in both cases).

Figure 5a presents the median percentage of correct trials in the real cross and pseudocross conditions for each corvid species across sessions. In the real cross condition, neither species significantly changed their performance across sessions (Spearman r: raven: r = .03, p = 1.00; crow: r = −0.71, p = .14). Crows were at chance levels in the last session (Wilcoxon's test: T = 20, n = 6, p > .06). None of the remaining comparisons could be done because of small sample sizes (n < 6 in all cases).

In the real pseudocross condition, there was no significant change in performance across sessions for the ravens, and a marginally significant improvement for the crows (Spearman r: raven: r = −0.03, p = 1.00; crow: r = .82, p = .07). No statistical analyses could be done with regard to their performance in the first and last sessions of this condition because of small sample sizes (n < 6 in all cases).

Figure 5b presents the median percentage of correct trials in the painted cross and pseudocross conditions for each corvid species across sessions. In the painted cross condition, neither species significantly changed their performance across sessions (Spearman r: raven: r = .52, p = .35; crow: r = −0.25, p = .67). No statistical analyses could be done with regard to their performance in the first and last sessions of this condition because of small sample sizes (n < 6 in all cases).

Likewise, in the painted pseudocross condition, there was no significant change in performance across sessions (Spearman r: raven: r = −0.09, p = .87; crow: r = .29, p = .60). Statistical analyses cannot be computed for the first session because of small sample sizes (n < 6), but in the last session both species were at chance levels (Wilcoxon's tests: n = 6, ps > 0.24).

Comparing Apes and Corvids

Figure 6 presents the median percentage of correct trials for all species as a function of material and pattern. There were significant differences between species in all dependent variables (Kruskal-Wallis tests: real cross: $\chi^2(5, n = 23) = 17.19, p < .01$; real pseudocross: $\chi^2(5, n = 23) = 27.48, p < .01$; painted cross: $\chi^2(5, n = 23) = 14.29, p = .01$; painted pseudocross: $\chi^2(5, n = 23) = 27.23, p < .01$). Pairwise Mann–Whitney U tests (Bonferroni-Holm corrected) revealed that all four ape species outperformed the two corvid species in both pseudocross conditions, except the gorillas, that only outperformed the ravens in these conditions ($p < .02$). In addition, orangutans outperformed both crows and ravens in the real cross condition ($p < .02$). Interestingly, ravens and crows outperformed chimpanzees, and ravens outperformed orangutans, in the painted cross condition ($ps < 0.02$).

Table 3 shows, for each condition, the number of subjects of each species that responded correctly in at least five of six trials in two consecutive sessions, and those that attained this level of performance in the minimum number of sessions. All apes except two (one chimpanzee and one gorilla) solved both pseudocross conditions, and in most cases, they did so from the start. Interestingly, whereas all crows except one solved the real pseudocross condition—two of them from the start—no raven solved this condition. In addition, half of the crows and one raven solved the painted pseudocross condition, although none of them did so from the start. Of the 24 apes, 14 solved the real cross condition, several of them doing so from the start, with each species contributing at least one successful subject and orangutans outweighing all other
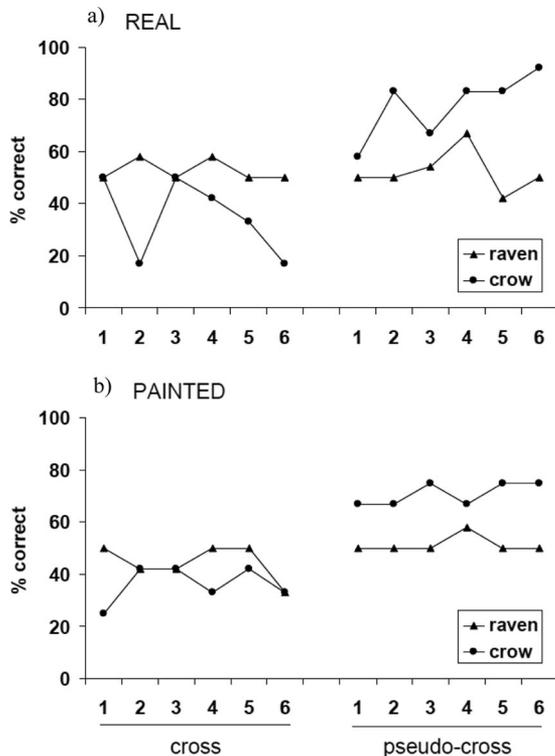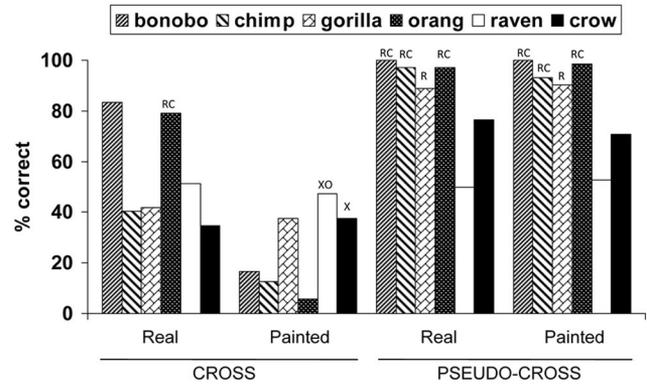

Figure 6. Median percentage of correct trials for all species and conditions. Correct trials are those where subjects picked the baited strip. The capital letters above the bars show those species with respect to which there were significant differences. R=Raven; C=Crow; X=Chimpanzee; O=Orangutan. For example, orangutans outperformed both ravens and crows in the real cross and in the real and painted pseudo-cross conditions but were outperformed by ravens in the painted cross condition.

species in terms of raw numbers. Only one ape (an orangutan) solved the painted cross condition, also from the start. No corvids solved either of the two cross conditions.

Figure 7 presents a cluster analysis based on the four conditions. Two main clusters were apparent. The first cluster was almost entirely formed by corvids, with the exception of two gorillas. The second cluster included all the remaining apes and one crow. Within the first main cluster, we found two subclusters, one formed by all the ravens and one crow, and the other formed by crows and the two gorillas. Within the second main cluster, two subclusters were also apparent. One included four chimpanzees, one gorilla, two bonobos and a crow. The other subcluster was composed exclusively of apes, and included all the orangutans (except one that did not belong to any cluster) and the remaining apes.

Discussion

Both apes and corvids spontaneously pulled a paper strip supporting a reward. They also readily learned to touch a painted stripe to receive a reward from the experimenter. However, when presented with two strips (of which only one was baited), differences between species became apparent. Interestingly, apes readily solved both pseudocross conditions, whereas crows only solved the real pseudocross and ravens did not solve either of the two. Unlike the corvids, the apes reached criterion in the fewest possible sessions. Additionally, a majority of apes, unlike corvids, eventually solved the real cross condition, with orangutans being the most successful species in this regard. In contrast, none of the species was able to solve the painted cross condition. Overall, the pattern of responses in the various conditions clearly separated apes and corvids, with orangutans and ravens occupying opposite poles of the distribution, and crows showing some degree of overlap with the nonorangutan apes. Next, we examine in greater detail the results for each taxon.

Apes showed a strong tendency to pick the strip end closer to the reward (Proximity hypothesis). This allowed them to solve both pseudocross conditions from the first session, but it led to poor

Figure 5. Percentage of correct responses across sessions for both patterns, in the real condition and in the painted condition, by the corvids.

Table 3
Number of Subjects of Each Species That Solved Each Condition in the Test

| | | | Condition | | | | |
| | | | Real | | | Painted | |
Species	n	Cross	Pcross	n	Cross	Pcross
Apes						
Bonobos	6	3 (2)	6 (6)	6	0	6 (6)
Chimpanzees	6	2 (0)	6 (6)	6	0	5 (4)
Gorillas	4	1 (1)	4 (4)	4	0	3 (3)
Orangutans	8	8 (1)	8 (8)	8	1 (1)	8 (8)
Total	24	14 (4)	24 (24)	24	1 (1)	22 (21)
Corvids						
Ravens	8	0	0	6	0	1 (0)
Crows	6	0	5 (2)	6	0	3 (0)
Total	14	0	5 (2)	12	0	4 (0)

Note. The criterion of success was a minimum of two consecutive sessions with at least five (of six) successful trials. The numbers in parenthesis indicate the number of subjects that attained this level of performance in the minimum number of sessions.

performance in the cross conditions, particularly for the chimpanzees. Overall, however, apes performed better in the real cross condition than in the painted cross condition. Moreover, most apes solved the real and not the painted cross condition, and they did not transfer the solution between conditions. This suggests that apes' choices were neither limited to the spatial position of the food (Proximity hypothesis) nor were reliant solely on perceptual information (Perceptual hypothesis). Instead, apes might have attended to the physical relation between the elements in the task (Causal hypothesis).

In the real cross condition, chimpanzees and orangutans improved their performance throughout testing, which allowed most of the orangutans to master the task. In contrast, their performance did not improve in the painted cross condition. In fact, members of all ape species ended up solving the real cross condition, whereas only one orangutan solved the painted cross condition and he did so after having solved the real cross. This suggests that, even though apes' knowledge about object relations was not strong enough to solve the real cross from the start (although two bonobos, one gorilla and one orangutan actually solved it), it at least allowed them to progressively (although relatively fast in the case of the orangutans) overcome their spatial bias. Such causal knowledge could not exist in the painted cross condition, where using visual arbitrary cues was the only means to solve the task. Apes failed to do so. Instead, they based their choices on spatial proximity, which led to reinforcement on half of the trials (the ones with a pseudocross). The combined effect of a strong proximity bias and this reinforcement schedule may very well explain chimpanzees' overall performance below chance levels in this condition.

Turning our attention to corvids, crows solved the real pseudocross condition and half of the subjects also solved the painted pseudocross. In contrast, crows did not solve the cross conditions, showing a proximity bias that was similar (although not as strong) to that of the apes. However, unlike the apes, not a single subject solved the real cross condition and there was no sign of learning in this condition either. This suggests that crows did not use the physical relations or the perceptual cues present in the task. Ravens performed at chance levels in all conditions. Also, they showed no

signs of learning. This suggests that ravens had neither causal knowledge of the task, nor were they able to learn from arbitrary perceptual cues (in the number of trials given), nor did they have a proximity bias. An alternative explanation would be that they found the paper strips rewarding in themselves, to the point that the food became less salient (although they always ate the food when they had the chance). In fact, ravens are known to playfully engage in various kinds of object manipulations, even as adults (Heinrich & Smolker, 1998; Bugnyar, Schwab, Schloegl, Kotrschal, & Heinrich, 2007). Several observations of playful behavior directed toward the paper strips by the ravens in this study support this idea. Such behaviors were almost absent in the crows and were not common in the apes.

One of the most striking differences between the apes and the crows was the fact that several apes solved the real cross condition but none of the crows did. This suggests that although both relied on proximity to some extent, only apes were able to abandon this strategy in favor of a causal strategy. Although a proximity bias is a good default strategy within foraging contexts (because usually the most efficient way to access food is approaching it in a straight line), too strong reliance on it may prevent individuals from attaining their goal when direct access is not possible. Thus, varying degrees of proximity bias (attributable to varying reliance on spatial cues, inhibitory control skills, and/or causal knowledge of the task) could potentially explain the species differences found in the present study.

Support for the crucial role of spatial information in the current task is provided by the superior performance of orangutans compared with chimpanzees in the real cross condition. Several studies have shown that orangutans perform worse than chimpanzees in spatial tasks that involve tracking the relation between containers and rewards (Albiach-Serrano, Call, & Barth, 2010; Barth & Call, 2006). It is conceivable that the orangutans' weaker reliance on spatial information detected in those studies may have protected them against selecting rewards based mainly on proximity in the present study, thus allowing them to more readily use other sources of information. Also, it has been suggested that orangutans, in some tasks, may possess greater inhibitory control than other apes
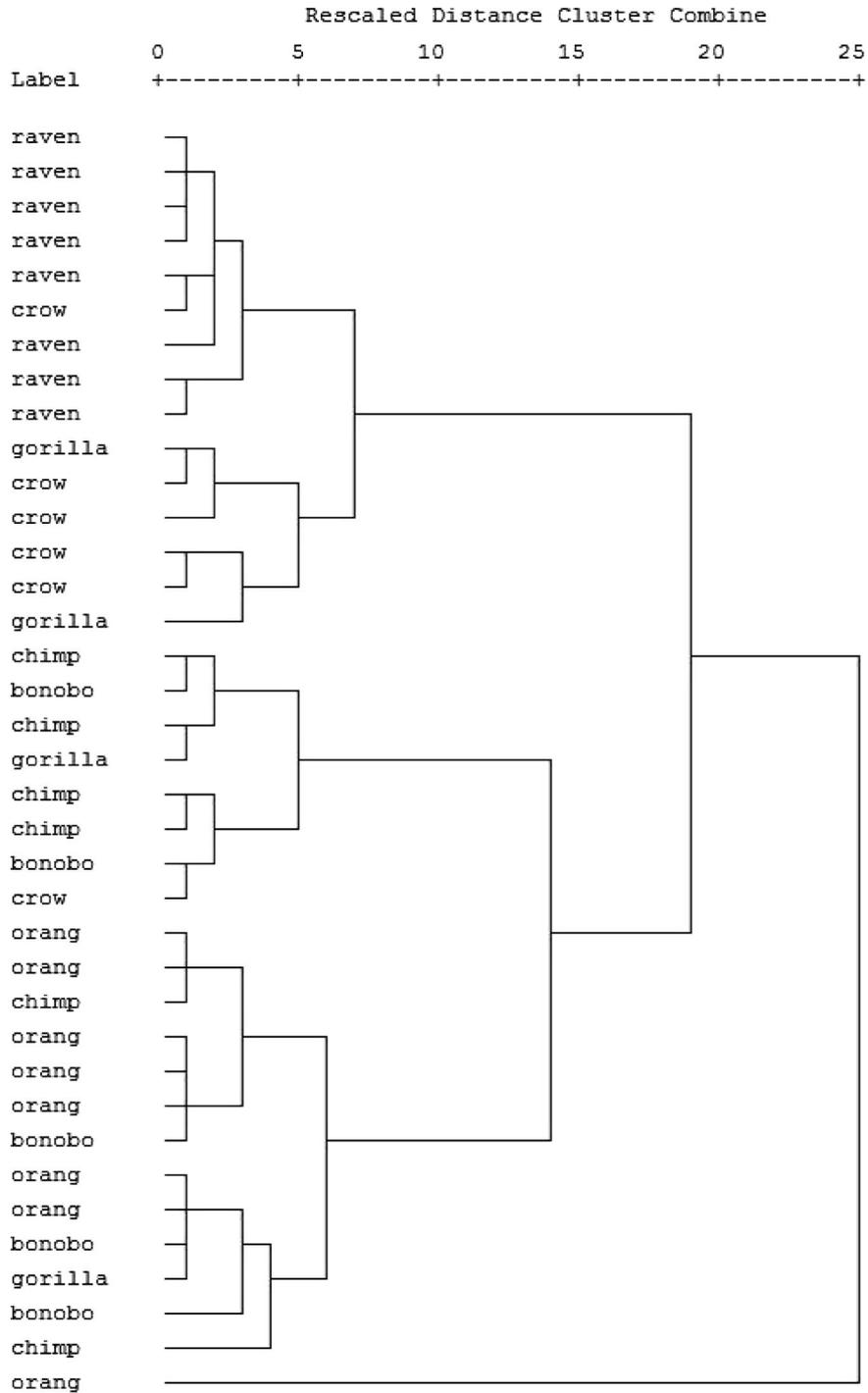
Figure 7. Cluster analysis based on the four conditions in the test (real cross, real pseudo-cross, painted cross, painted pseudo-cross).

(Vlamings, Hare, & Call, 2010). It could be that this skill allowed them to refrain from reaching directly for the food and therefore they attended to the relevant features of the task and solved the problem. However, these do not seem good explanations for the failure of the crows in the real cross condition, because crows showed a weaker proximity bias compared to apes in this task and

nevertheless they failed to solve the real cross problem. Thus, the most plausible explanation seems to be that crows simply lacked the knowledge necessary to solve this problem.

In summary, apes outperformed corvids with respect to the complexity of the patterns solved, the relative number of subjects solving each problem, and the speed to reach criterion. The pattern

of responses of both groups suggests that they share some cognitive features but also differ in others. On the one hand, both of them showed a proximity bias—although this varied both between groups and within species in each group—and both also found it difficult to learn from the arbitrary perceptual cues available in the task (see Call, 2006)—although it is likely that given more trials they might have learned. On the other hand, only apes showed a certain level of causal knowledge of this support problem. These results contrast with those of a previous study where bonobos and rooks did not substantially differ in their performance in one version of the trap-tube task, with both species showing little evidence of causal knowledge regarding contact (Helme, Call, et al., 2006; Helme, Clayton, & Emery, 2006). Also, they differ from those in other studies where corvids performed successfully in different causal tasks (e.g., Bird & Emery, 2009a, 2009b; Seed, Tebbich, Emery, & Clayton, 2006; Taylor, Hunt, Holzhaider, & Gray, 2007; Taylor, Hunt, Medina, & Gray, 2009). Future studies will have to clarify whether the differences found between apes and corvids in the present study correspond to species differences or whether they are the result of sampling, motivational differences concerning the type of reward, or the different previous experience in each of the groups.

Unfortunately, the current data are also insufficient to determine why crows marginally improved their performance in the real pseudocross condition but not in the painted pseudocross (although subjects succeeded in both). It could be argued that crows had causal knowledge (very weakly, because it only helped to solve the simpler pattern), but it is more probable that something in the real condition facilitated learning of this task by making it more attractive to the subjects. The real and the painted conditions were visually very similar (they were both two-dimensional and had similar shapes, similar color and similar "shadows"). Therefore, most likely the key difference between the two conditions lay either on the tactile information provided (the texture, the possibility to grab the strips, the sense of effort when pulling a strip), or the motion perceived (movement of strip and reward, covariation of the movement of body and strip plus reward). Also, it could be a combination of both. This "salience effect" should not be confounded with either perceptual or causal knowledge, because more rapid learning in a task resulting from higher attention level does not necessarily mean that the information learnt is perceptual or causal. In fact, in the case of the crows, it apparently promoted the learning of spatial information. The question remains open to what extent such a salience effect could also have affected apes' performance in the present study. It could well be that the saliency effect is a precursor in the evolution (and development) of causal knowledge. By increasing the amount of attention that a subject directs toward causally relevant cues, the probability of the subject solving a causal problem naturally increases—even if the subject does not form abstract representations of the problem. Future comparative research should explore this possibility by assessing the role of the salience effect in nonhuman animals performing in physical tasks.

References

Albiach-Serrano, A., Call, J., & Barth, J. (2010). Great apes track hidden objects after changes in the objects' position and in subject's orientation. *American Journal of Primatology, 72,* 349–359.

Auersperg, A. M. I., Gajdon, G. K., & Huber, L. (2009). Kea (*Nestor notabilis*) consider spatial relationships between objects in the support problem. *Biology Letters, 5,* 455–458. doi:10.1098/rsbl.2009.0114

Balasch, J., Sabater Pi, J., & Pedrosa, T. (1974). Perceptual learning ability in *Mandrillus sphinx* and *Cercopithecus nictitans*. *Revista Española de Fisiología, 30,* 15–20.

Barth, J., & Call, J. (2006). Tracking the displacement of objects: A series of tasks with great apes (*Pan troglodytes, Pan paniscus, Gorilla gorilla,* and *Pongo pygmaeus*) and young children (*Homo sapiens*). *Journal of Experimental Psychology: Animal Behavior Processes, 32,* 239–252. doi:10.1037/0097-7403.32.3.239

Beck, B. B. (1980). *Animal tool behavior: The use and manufacture of tools by animals.* New York, NY: Garland STPM Press.

Bird, C. D., & Emery, N. J. (2009a). Insightful problem solving and creative tool modification by captive nontool-using rooks. *PNAS Proceedings of the National Academy of Sciences of the United States of America, 106,* 10370–10375. doi:10.1073/pnas.0901008106

Bird, C. D., & Emery, N. J. (2009b). Rooks use stones to raise the water level to reach a floating worm. *Current Biology, 19,* 1410–1414. doi:10.1016/j.cub.2009.07.033

Bluff, L. A., Weir, A. A. S., Rutz, C., Wimpenny, J. H., & Kacelnik, A. (2007). Tool-related cognition in New Caledonian crows. *Comparative Cognition & Behavior Reviews, 2,* 1–25.

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica; International Journal of Primatology, 54,* 86–99. doi:10.1159/000156428

Bonechi, B. (2005). *String-pulling in ravens (Corvus corax)* (Unpublished bachelor's thesis). University of Trieste, Italy.

Bugnyar, T., Schwab, C., Schloegl, C., Kotrschal, K., & Heinrich, B. (2007). Ravens judge competitors through experience with play caching. *Current Biology, 17,* 1804–1808. doi:10.1016/j.cub.2007.09.048

Byrne, R. W., & Byrne, J. M. E. (1993). Complex leaf-gathering skills of mountain gorillas (*Gorilla g. beringei*): Variability and standardization. *American Journal of Primatology, 31,* 241–261. doi:10.1002/ajp.1350310402

Call, J. (2006). Descartes' two errors: Reason and reflection in the great apes. In S. Hurley, & M. Nudds (Eds.), *Rational animals?* (pp. 219–234). Oxford, UK: Oxford University Press.

de Mendonça-Furtado, O., & Ottoni, E. (2008). Learning generalization in problem solving by a blue-fronted parrot (*Amazona aestiva*). *Animal Cognition, 11,* 719–725. doi:10.1007/s10071-008-0168-x

Dücker, G., & Rensch, B. (1977). The solution of patterned string problems by birds. *Behaviour, 62,* 164–173. doi:10.1163/156853977X00081

Emery, N. J., & Clayton, N. S. (2004a). Comparing the complex cognition of birds and primates. In L. J. Rogers, & G. Kaplan (Eds.), *Comparative vertebrate cognition: Are primates superior to non-primates?* (pp. 3–55). New York, NY: Kluwer Academic/Plenum Press.

Emery, N. J., & Clayton, N. S. (2004b). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science, 306,* 1903–1907. doi:10.1126/science.1098410

Emery, N. J. (2006). Cognitive ornithology: The evolution of avian intelligence. *Philosophical transactions of the Royal Society of London B Biological Sciences, 361,* 23–43. doi:10.1098/rstb.2005.1736

Finch, G. (1941). The solution of patterned string problems by chimpanzees. *Journal of Comparative Psychology, 32,* 83–90. doi:10.1037/h0056785

Gattermayr, M. (2007). *Tolerance between subadult common ravens (Corvus corax): Is it task specific?* (Unpublished master's thesis). University of Vienna, Austria.

Girndt, A., Meier, T., & Call, J. (2008). Task constraints mask great apes' ability to solve the trap-table task. *Journal of Experimental Psychology: Animal Behavior Processes, 34,* 54–62. doi:10.1037/0097-7403.34.1.54

Hansell, M. (2005). *Animal architecture.* New York, NY: Oxford University Press. doi:10.1093/acprof:oso/9780198507529.001.0001

Hanus, D., & Call, J. (2011). Chimpanzee problem-solving: Contrasting the use of causal and arbitrary cues. *Animal Cognition, 14,* 871–878. doi:10.1007/s10071-011-0421-6

Harlow, H. F., & Settlage, P. H. (1934). Comparative behavior of primates. Capacity of monkeys to solve patterned string tests. *Journal of Comparative Psychology, 18,* 423–435. doi:10.1037/h0073305

Hauser, M. D., Kralik, J., & Botto-Mahan, C. (1999). Problem solving and functional design features: Experiments on cotton-top tamarins, *Saguinus oedipus Oedipus. Animal Behaviour, 57,* 565–582. doi:10.1006/anbe.1998.1032

Hauser, M. D., Santos, L. R., Spaepen, G. M., & Pearson, H. (2002). Problem solving, inhibition and domain-specific experience: Experiments on cottontop tamarins, *Saguinus oedipus Animal Behaviour, 64,* 387–396. doi:10.1006/anbe.2002.3066

Hauser, M. D., & Santos, L. R. (2007). The evolutionary ancestry of our knowledge of tools: From percepts to concepts. In E. Margolis, & S. Laurence (Eds.), *Creations of the mind: Theories of artifacts and their representation* (pp. 267–288). Oxford, UK: Oxford University Press.

Heinrich, B., & Smolker, R. (1998). Play in common ravens (*Corvus corax*). In M. Bekoff, & J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 27–44). Cambridge, UK: Cambridge University Press. doi:10.1017/CBO9780511608575.003

Heinrich, B. (1995). An experimental investigation of insight in common ravens (*Corvus corax*). *The Auk, 112,* 994–1003.

Helme, A. E., Call, J., Clayton, N. S., & Emery, N. J. (2006). What do bonobos (*Pan paniscus*) understand about physical contact? *Journal of Comparative Psychology, 120,* 294–302. doi:10.1037/0735-7036.120.3.294

Helme, A. E., Clayton, N. S., & Emery, N. J. (2006). What do rooks (*Corvus frugilegus*) understand about physical contact? *Journal of Comparative Psychology, 120,* 288–293. doi:10.1037/0735-7036.120.3.288

Herrmann, E., Wobber, V., & Call, J. (2008). Great apes' (*Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology, 122,* 220–230. doi:10.1037/0735-7036.122.2.220

Hobhouse, L. T. (1915). *Mind in evolution* (2nd ed.). London, UK: Macmillan and Co.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6,* 65–70.

Huber, L., & Gajdon, G. K. (2006). Technical intelligence in animals: The kea model. *Animal Cognition, 9,* 295–305. doi:10.1007/s10071-006-0033-8

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature, 379,* 249–251. doi:10.1038/379249a0

Hunt, G. R. (2005). Weird and wonderful artefacts. *Trends in Ecology & Evolution, 20,* 655–656. doi:10.1016/j.tree.2005.08.008

Kacelnik, A., Chappell, J., Weir, A. A. S., & Kenward, B. (2006). Cognitive adaptations for tool-related behaviour in New Caledonian crows. In E. A. Wasserman, & T. R. Zentall (Eds.), *Comparative cognition: Experimental explorations of animal intelligence* (pp. 515–528). Oxford, UK: Oxford University Press.

King, J. E., & Witt, E. D. (1966). The learning of patterned strings problems by rock squirrels. *Psychonomic Science, 4,* 319–320.

Kummer, H. (1995). Causal knowledge in animals. In D. Sperber, D. Premack, & A. J. Premack (Eds.), *Causal cognition: A multidisciplinary debate* (pp. 26–39). Oxford, UK: Oxford University Press.

Lefebvre, L., Reader, S. M., & Sol, D. (2004). Brains, innovations and evolution in birds and primates. *Brain, Behavior and Evolution, 63,* 233–246. doi:10.1159/000076784

Madden, J. R. (2003). Bower decorations are good predictors of mating success in the spotted bowerbird. *Behavioral Ecology and Sociobiology, 53,* 269–277.

Martín-Ordás, G., Call, J., & Colmenares, F. (2008). Tubes, tables and traps: Great apes solve two functionally-equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition, 11,* 423–430. doi:10.1007/s10071-007-0132-1

McGrew, W. C. (1974). Tool use by wild chimpanzees in feeding upon driver ants. *Journal of Human Evolution, 3,* 501–508. doi:10.1016/0047-2484(74)90010-4

Michels, K. M., Pustek, J. J., Jr., & Johnson, J. I., Jr (1961). The solution of patterned-strings problems by raccoons. *Journal of Comparative and Physiological Psychology, 54,* 439–441. doi:10.1037/h0043615

Mulcahy, N. J., Call, J., & Dunbar, R. I. M. (2005). Gorillas and orangutans encode relevant problem features in a tool-using task. *Journal of Comparative Psychology, 119,* 23–32. doi:10.1037/0735-7036.119.1.23

Mulcahy, N. J., & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition, 9,* 193–199. doi:10.1007/s10071-006-0019-6

Mundry, R., & Fischer, J. (1998). Use of statistical programs for nonparametric tests of small samples often leads to incorrect p values: Examples from Animal Behaviour. *Animal Behaviour, 56,* 256–259. doi:10.1006/anbe.1998.0756

Osthaus, B., Lea, S. E. G., & Slater, A. M. (2005). Dogs (*Canis lupus familiaris*) fail to show understanding of means-end connections in a string-pulling task. *Animal Cognition, 8,* 37–47. doi:10.1007/s10071-004-0230-2

Penn, D. C., & Povinelli, D. J. (2007). Causal cognition in human and nonhuman animals: A comparative, critical review. *Annual Review of Psychology, 58,* 97–118. doi:10.1146/annurev.psych.58.110405.085555

Pepperberg, I. M. (2004). "Insightful" string-pulling in grey parrots (*Psittacus erithacus*) is affected by vocal competence. *Animal Cognition, 7,* 263–266. doi:10.1007/s10071-004-0218-y

Pfuhl, G. (2009). *Do ravens have a concept of effort?* (Unpublished part of doctoral thesis). Norwegian University of Science and Technology, Norway.

Piaget, J. (1952). *The origins of intelligence in children.* Oxford, England: International Universities Press. doi:10.1037/11494-000

Povinelli, D. J. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works.* Oxford: Oxford University Press.

Redshaw, M. (1978). Cognitive development in human and gorilla infants. *Journal of Human Evolution, 7,* 133–141. doi:10.1016/S0047-2484(78)80005-0

Riesen, A. H., Greenberg, B., Granston, A. S., & Fantz, R. L. (1953). Solutions of patterned string problems by young gorillas. *Journal of Comparative and Physiological Psychology, 46,* 19–22. doi:10.1037/h0057069

Santos, L. R., Miller, C. T., & Hauser, M. D. (2003). Representing tools: How two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool. *Animal Cognition, 6,* 269–281. doi:10.1007/s10071-003-0171-1

Schmidt, G. F., & Cook, R. G. (2006). Mind the gap: Means-end discrimination by pigeons. *Animal Behaviour, 71,* 599–608. doi:10.1016/j.anbehav.2005.06.010

Schuck-Paim, C., Borsari, A., & Ottoni, E. (2009). Means to an end: Neotropical parrots manage to pull strings to meet their goals. *Animal Cognition, 12,* 287–301. doi:10.1007/s10071-008-0190-z

Seed, A. M., Call, J., Emery, N. J., & Clayton, N. S. (2009). Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology: Animal Behavior Processes, 35,* 23–34. doi:10.1037/a0012925

Seed, A. M., & Call, J. (2009). Causal knowledge for events and objects in animals. In S. Watanabe, A. P. Blaisdell, L. Huber, A. Young, & K. G. Daigaku (Eds.), *Rational Animals, Irrational Humans* (pp. 173–188). Tokyo, Japan: Keio University.

Seed, A. M., Emery, N. J., & Clayton, N. S. (2009). Intelligence in corvids and apes: A case of convergent evolution? *Ethology, 115,* 401–420. doi:10.1111/j.1439-0310.2009.01644.x

Seed, A. M., Tebbich, S., Emery, N. J., & Clayton, N. S. (2006). Investi-

gating physical cognition in rooks, *Corvus frugilegus Current Biology, 16,* 697–701. doi:10.1016/j.cub.2006.02.066

Siegel, S., & Castellan, N. J. (1988). *Nonparametric statistics for the behavioral sciences* (2nd ed.). New York, NY: McGraw-Hill.

Spinozzi, G., & Potí, P. (1989). Causality I: The support problem. In F. Antinucci (Ed.), *Cognitive structure and development in nonhuman primates* (pp. 113–119). Hillsdale, NJ: Lawrence Erlbaum Associates.

Spinozzi, G., & Potí, P. (1993). Piagetian stage 5 in two infant chimpanzees (*Pan troglodytes*): The development of permanence of objects and the spatialization of causality. *International Journal of Primatology, 14,* 905–917. doi:10.1007/BF02220259

Taylor, A. H., Hunt, G. R., Holzhaider, J. C., & Gray, R. D. (2007). Spontaneous metatool use by New Caledonian crows. *Current Biology, 17,* 1504–1507. doi:10.1016/j.cub.2007.07.057

Taylor, A. H., Hunt, G. R., Medina, F. S., & Gray, R. D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society of London B Biological Sciences, 276*(1655), 247–254. doi:10.1098/rspb.2008.1107

Tomasello, M., & Call, J. (1997). *Primate cognition.* New York, NY: Oxford University Press.

Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology, 108,* 15–22. doi:10.1037/0735-7036.108.1.15

Vlamings, P. H., Hare, B., & Call, J. (2010). Reaching around barriers: The performance of the great apes and 3–5-year-old children. *Animal Cognition, 13,* 273–285. doi:10.1007/s10071-009-0265-5

Warden, C. J., Koch, A. M., & Fjeld, H. A. (1940). Solution of patterned string problems by monkeys. *The Pedagogical Seminary and Journal of Genetic Psychology, 56,* 283–295.

Werdenich, D., & Huber, L. (2006). A case of quick problem solving in birds: String pulling in keas, *Nestor notabilis. Animal Behaviour, 71,* 855–863. doi:10.1016/j.anbehav.2005.06.018

Whitt, E., Douglas, M., Osthaus, B., & Hocking, I. (2009). Domestic cats (*Felis catus*) do not show causal understanding in a string-pulling task. *Animal Cognition, 12,* 739–743. doi:10.1007/s10071-009-0228-x

Willatts, P. (1984). The stage-IV infant's solution of problems requiring the use of supports. *Infant Behavior & Development, 7,* 125–134. doi:10.1016/S0163-6383(84)80053-3

Yocom, A. M., & Boysen, S. T. (2010). Capuchins (*Cebus apella*) can solve a means-end problem. *Journal of Comparative Psychology, 124,* 271–277. doi:10.1037/a0019369

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