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A reversed-reward contingency task reveals causal knowledge in chimpanzees (*Pan troglodytes*)

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Abstract In the reversed-reward contingency task, subjects are required to choose the less preferred of two options in order to obtain the more preferred one. Usually, this task is used to measure inhibitory skills, but it could also be used to measure how strong the subjects' preferences are. We presented chimpanzees with support tasks where only one of two paper strips could physically bring food into reach. Subjects were rewarded for choosing the non-functional strip. In Experiment 1, subjects failed to pick the non-baited strip. In Experiment 2, subjects failed to pick the broken strip. Chimpanzees performed worse in these tasks than in other similar tasks where instead of paper strips, there were similar shapes painted on a platform. The fact that subjects found the reversed-reward contingency task based on causality more difficult to solve than a perceptually similar task with no causality involved (i.e., arbitrary) suggests that they did not treat real strips as an arbitrary task. Instead, they must have had some causal knowledge of the support problem that made them prefer functional over non-functional strips despite the contrary reward regime.

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Introduction

Inhibitory control has been defined as the ability to suppress the activation, processing, or expression of information that would otherwise interfere with the efficient attainment of a cognitive or behavioral goal (Christ et al. 2001). Therefore, it allows individuals to suppress a prepotent response when, for whatever reason, this response is not useful to obtain a goal anymore. This is relevant for problem solving, since such suppression is an important step for finding alternative solutions to a given problem (e.g., Santos et al. 1999). For example, in order to be able to use a tool to obtain otherwise unattainable food, an individual needs first to refrain from trying to reach directly for the food.

One method that has been used to measure non-human primates' inhibitory skills is the reversed-reward contingency task (henceforth reverse contingency task, Boysen and Berntson 1995). In the standard version of this task, a subject is allowed to choose between two different amounts of food but she receives the non-chosen amount. Thus, to net the larger food amount, the subject needs to pick the smaller amount. This problem has proven very difficult for all primates tested, invariably requiring hundreds of trials to master the task (see Albiach-Serrano et al. 2007; Shifferman 2009 for a review). Reaching for the largest food amount, therefore, is hard to inhibit even when the reward contingencies are reversed. Other prepotent responses that have been used to measure inhibitory control in primates include the preference for: (1) larger over smaller food sizes (e.g., Boysen et al. 2001), (2) certain

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food types over others (e.g., Anderson et al. 2008; Genty and Roeder 2007), (3) an immediate over a delayed reward, even when the delayed reward is larger (e.g., Beran and Evans 2006; Beran et al. 1999), and (4) reaching directly for objects instead of making a detour (e.g., Santos et al. 1999; Vlamings et al. 2010). However, as far as we know, no inhibition study has used a prepotent response derived from subjects' knowledge, for example, about tools.

The nature of the knowledge that non-human animals possess about how objects relate to each other is a contentious issue. For example, when given the choice, several species prefer pulling a functional support (that can physically affect the position of the supported food when pulled) over a non-functional support (Auersperg et al. 2009; de Mendonça-Furtado and Ottoni 2008; Herrmann et al. 2008; Irie-Sugimoto et al. 2008; Povinelli 2000; Redshaw 1978; Spinozzi and Potí 1989, 1993; Yocom and Boysen 2010). One possibility is that individuals actually know something about object–object relations (i.e., how an object can affect the shape or position of another object) and therefore are able to recognize a functionally relevant cue in a problem even without having encountered this specific problem before (Causal knowledge hypothesis; e.g., Hauser and Santos 2007; Seed and Call 2009). Alternatively, it is conceivable that individuals' knowledge about objects as tools derives from their ability to associate perceptual features of objects with outcomes, without considering the cause–effect relations between them (Perceptual knowledge hypothesis; e.g., Hauser and Santos 2007; Seed and Call 2009; see also Kummer 1995). Partly, the controversy exists because a successful performance in most studies can fit both a causal and a perceptually based explanation.

To confront the causal and perceptual hypotheses, Albiach-Serrano et al. (2012, submitted) compared chimpanzees' performance in the traditional support tasks with a version in which the support materials (paper strips) were replaced by identical shapes painted on the platform (painted strips). The real and the painted conditions looked very similar, and in both cases, the subject was rewarded for picking the strip that held (or appeared to hold) a functional relation with the reward. Therefore, in principle, both conditions were equally solvable using perceptual knowledge. In contrast, causal knowledge would only help in solving the real condition, where the "correct" strip could physically affect the position of the reward, and not the painted condition, where the "correct" strip was only arbitrarily associated with the reward. We found that chimpanzees performed better in the real than in the painted condition, suggesting that they applied causal knowledge to solve the task. However, one could argue that the richer input obtained from the paper strips (e.g., they could be grabbed) may have enhanced learning in the real compared to the painted condition, and therefore, these same results may be explained with perceptual knowledge ("saliency effect", Albiach-Serrano et al. 2012).

The aim of the current study was to contrast the causal and perceptual (salience version) hypotheses using a reverse contingency (support) task. In Experiment 1, we presented two crossed or parallel paper strips with a food reward placed on the distal end (in relation to the subject) of one of the paper strips. In Experiment 2, we presented a food reward on top of each of two parallel paper strips but one of the paper strips was cut into two pieces. Each experiment included two conditions. In the real condition, to obtain a reward, chimpanzees had to pick the non-functional paper strip, namely the strip not supporting the food (Experiment 1) or the broken strip (Experiment 2). In the painted condition, we replaced the paper strips for painted strips that lacked the functional properties of the former (e.g., one could not pull from them) but were otherwise nearly identical in appearance to paper strips. Similar to the real condition, in the painted condition, chimpanzees were rewarded for choosing the strip without the reward on top of it (Experiment 1) or the strip with a gap in it (Experiment 2).

If subjects' solution of the support problem was based on causal knowledge, we expected that they would perform worse in the reverse compared to the (standard) direct contingency version of the real condition (Albiach-Serrano et al. 2012, submitted). This is so because subjects would need to inhibit their prepotent response of choosing the functional strip. Additionally, we expected that the difference between the reverse and direct contingency versions would disappear in the painted condition, even though both the real and the painted conditions are based on stimuli that are nearly identical in appearance. This is so because the association between any painted strip and the reward is arbitrary from a causal point of view. Finally, we expected that subjects using causal knowledge would perform worse in the real reverse condition compared to the painted reverse condition, since the former but not the latter requires inhibitory control. If, on the contrary, subjects used perceptual information, we expected that they would perform better in the real reverse condition compared to the painted reverse condition, considering that paper strips are more salient than painted strips and may therefore enhance learning (i.e., salience effect). Because subjects using perceptual information would not have prepotent responses based on causality, we did not expect differences between the direct and reverse versions of the tasks, in the real as well as in the painted condition.

In sum, our predictions were as follows. According to the causal knowledge hypothesis, subjects should perform (1) worse in the real than in the painted condition, (2) worse in the real condition with a reverse contingency than

Table 1 Summary of subjects including sex, age at the time of the study, rearing history (mother or hand-reared, although all subjects were born in captivity and have lived in social groups), experience in support or string-pulling studies and group assignment, for Experiments 1 and 2

Experiment	Group	Name	Sex	Age (years)	Rearing history	Experimental experience
1	A	Tai	F	5	Mother	–
		Bunyoro	M	10	Mother	–
		Ulla	F	30	Hand	[a]
	B	Trudi	F	14	Mother	[a]
		Frodo	M	14	Mother	[a]
		Natascha	F	27	Hand	[a]
2	A	Kara	F	4	Mother	–
		Lome	M	8	Mother	[b, c]
		Sandra	F	16	Mother	[a, c]
		Ulla	F	32	Hand	[a, b]
		Riet	F	32	Hand	[a]
	B	Kofi	M	4	Mother	–
		Trudi	F	16	Mother	[a, b]
		Frodo	M	16	Mother	[a, b]
		Jahaga	F	16	Mother	[a]
		Dorien	F	29	Hand	[a, c]
		Natascha	F	29	Hand	[a, b]

[a] Herrmann et al. (2008)

[b] Albiach-Serrano et al. (2012)

[c] Mayer et al. unpublished results

with a direct contingency, and (3) similar in the painted condition with a reverse or a direct contingency. According to the perceptual knowledge hypothesis (with salience effect), subjects should perform (1) better in the real than in the painted condition, (2) similar in the real condition with a reverse or a direct contingency, and (3) similar in the painted condition with a reverse or a direct contingency.

Experiment 1

Introduction

This experiment investigated whether chimpanzees would learn to pick a paper strip not supporting food over one supporting food, in order to obtain the food item from the experimenter. In addition, it compared the chimpanzees' performance in this "real condition," with paper strips, to a "painted condition," where the strips' shapes were painted on a platform and therefore had no physical power to alter the position of the food. The spatial configuration of the strips (crossed and not crossed) allowed us to explore the role played by a proximity bias in this kind of task. In essence, this experiment is the same as Albiach-Serrano et al. (2012) but using a reverse instead of a direct contingency. Since our analyses include comparing the results obtained by chimpanzees in both studies, note that both sets of data were collected by the same experimenter, using the same materials, and simultaneously (2009–2010), so even though each study had different subjects (a within-subjects' design using direct and reverse contingencies may have been affected by order effects), their living and testing conditions were comparable.

Materials and methods

Subjects

Six chimpanzees (*Pan troglodytes*) housed at the Wolfgang Koehler Primate Research Center (WKPRC) in Leipzig Zoo, Germany, participated in Experiment 1. See Table 1 for details on their sex, age, rearing history, experimental experience on related tasks, and group assignment. Apes at the WKPRC live in social groups inside large enclosures with grass, rocks, streams, and natural vegetation. They have trees and other vertical and horizontal structures for climbing and finding shelter. In addition, they have enrichment devices, such as artificial termite mounds. Subjects were tested individually in special observation rooms that they were free to enter or not. Their feeding routines did not change for the present study, and water was always available during testing.

Materials

Brown paper strips (6 × 30 cm), straight and angular, could be placed on top of a dark blue plastic panel (78 × 32 cm) to form the patterns cross and pseudo-cross shown in Fig. 1 plus the single strip pattern of the pretest (see the "Design" section). Other similar panels had the patterns' shapes on them, painted with brown spray (Plasticote 2118/Ral 1019 Grey Beige), which were

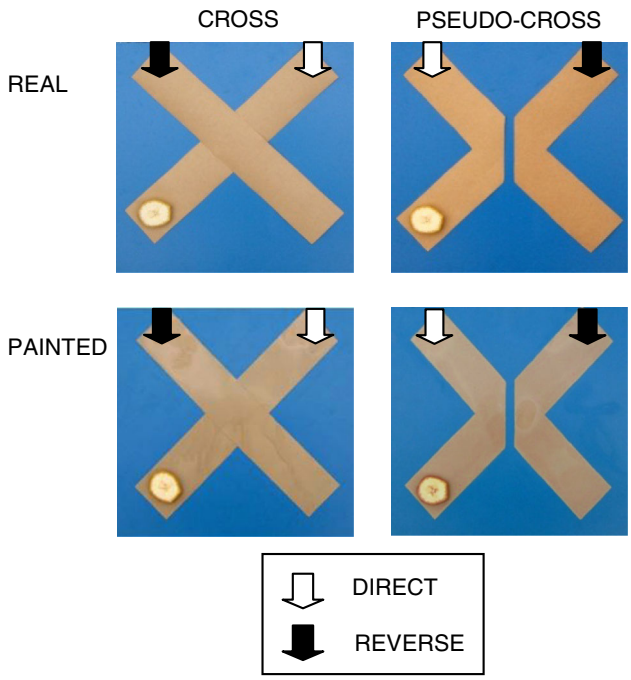

Fig. 1 Patterns, materials, and contingencies. Two patterns, the cross and the pseudo-cross, either made with paper strips (real condition) or painted on a platform (painted condition) were used in Experiment 1. Subjects received *banana slices* (in the picture) or half grapes as reward. *Arrows* show the correct responses (i.e., responses that permitted obtaining the reward) in both the direct and the reverse contingency (Albiach-Serrano et al. 2012 and Experiment 1, respectively)

difficult to distinguish from real strips at first sight (Fig. 1). However, since we did not want to mislead subjects into thinking that painted strips were real ones, the setup of the materials was done in their full view (see the "Procedure" section). The task was presented on a sliding table (80 × 39 cm) fixed to the outside of a mesh testing window (69 × 48 cm). Banana slices (approx. 8 mm thick) or half grapes were used as rewards, depending on the subject's preference.

Design

The pretest consisted of 2 sessions of 12 trials each, in which subjects had to obtain a piece of food placed on a straight strip in the middle of the panel, either by pulling (real condition) or by touching (real and painted condition) the strip. This ensured that subjects knew how to pick a strip. The test consisted of 12 sessions, 6 in the real and 6 in the painted condition, in which subjects had to obtain a piece of food placed on one of two strips, by choosing (touching or pulling) the strip *not* supporting the reward in order to obtain the reward from the experimenter (reverse contingency, Fig. 1). Group A first did the real condition block and then the painted one, while Group B did the reverse. Each session had 12 trials, of which 6 were with the cross-pattern and 6 were with the pseudo-cross-pattern. Patterns and food position (left/right) were counterbalanced within sessions and presented pseudo-randomly, with the only restrictions being that the same pattern could not appear more than twice in a row and that food could not appear more than three consecutive times on the same side, to avoid potential side biases. Note that in the cross-pattern, one strip crossed over the other. Which strip (left/right) was on top was randomized in the real condition, whereas in the painted condition, the side of the apparent "top" and "bottom" strips was not manipulated. Nevertheless, in both conditions, the reward was half of the times placed on the top strip and the other half on the bottom strip, since the reward's position was counterbalanced. We only gave a pretest before the first condition encountered by each subject. This means that subjects in group A received a pretest with real strips whereas subjects in group B received a pretest with painted strips.

Procedure

A session started with the blue plastic panel out of reach from the subject. 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 so that *S* could insert her fingers through it and pull/touch one strip. During the whole trial, *E* maintained a symmetrical body position and stared at a central point on the far wall of the testing room, to avoid possible cueing. When a correct choice occurred (the strip not supporting the reward was chosen), *E* rewarded *S* with the food placed on the other strip. When an incorrect choice occurred (the strip supporting the reward was chosen), *E* removed the food item from the strip and moved the panel backward before *S* could make a second choice. A session ended after the 12 trials had been completed, or after 5 min without *S* choosing, in which case it was continued on the next day. Sessions were held over different, and as far as possible, consecutive days.

Scoring and data analyses

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, while our independent variables were pattern (cross vs. pseudo-cross), material (real vs. painted), and contingency (direct vs. reverse, by comparing with the data from the chimpanzees in Albiach-Serrano et al. 2012, ergo

in this kind of comparison, we used between-subject analyses and our sample size was $N = 12$). Since 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 tests (Mundry and Fischer 1998). When sample sizes were smaller than 6, we did not conduct within-subject tests of significance because such small sample sizes make it impossible to reject the null hypothesis and therefore render the tests uninformative (Siegel and Castellan 1988). These cases are indicated in the "Results" section. A total of 20 % of sessions were randomly selected, and a second observer coded them to assess inter-observer reliability, which was excellent (Cohen's $\kappa = 0.98$; $p < 0.01$).

First, we analyzed the effect of each of the independent variables on the percentage of correct responses. Next, we investigated in more detail the subjects' performance by matching the various direct and reverse conditions depending on the response (with regard to space) that subjects were required to produce to get the reward. Note that the two different contingencies required subjects to execute opposite responses when faced with the same stimuli. For instance, if the food was on the left side on a cross-pattern, they had to pull the strip on their right in the direct contingency but the strip on their left in the reverse contingency. Conversely, subjects had to execute identical responses when faced with different patterns in different contingencies. For instance, they needed to pull the strip on their left both when facing a cross baited on the right in the direct contingency and when facing a pseudo-cross baited on the right in the reverse contingency. We contrasted those conditions that required pulling the same side to obtain the reward. In addition, we analyzed the data separately for the first and the last sessions to assess changes in performance across sessions.

Results

All chimpanzees starting with the real condition pulled the single strip of the pretest spontaneously. Also, all chimpanzees starting with the painted condition readily learnt to touch the painted strip to get the reward in the first trial(s) of the first session.

Figure 2 presents the median percentage of correct trials in each condition of the test. Overall, chimpanzees performed significantly better in the cross than the pseudo-cross-pattern, and this happened both in the real and the painted conditions (Wilcoxon tests: $T = 21$, $N = 6$, $p = 0.03$ in all cases). In fact, subjects performed above chance in both cross-conditions and below chance in both pseudo-cross-conditions (Wilcoxon tests: $T = 21$, $N = 6$, $p < 0.03$ in all cases). More specifically, all six

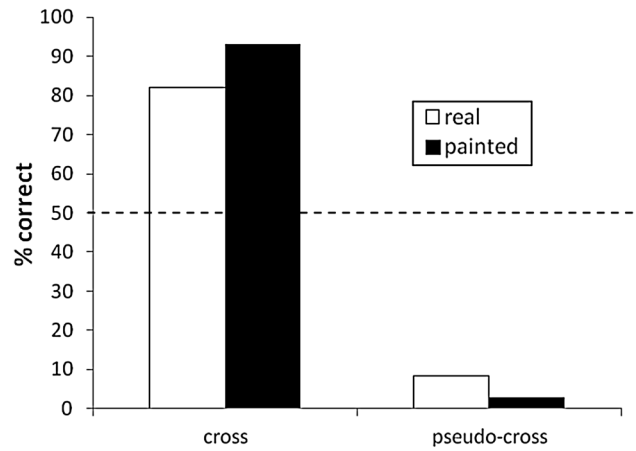

Fig. 2 Median percentage of correct trials as a function of pattern and material in Experiment 1. All results differed significantly from chance ($p < 0.03$)

chimpanzees solved the painted cross (they responded correctly at least in 5 out of 6 trials in two consecutive sessions), and half of them did so in the minimum number of sessions possible (i.e., the first two sessions). Similarly, all chimpanzees except one solved the real cross, three of them from the start. In contrast, none of the chimpanzees solved any of the pseudo-cross-conditions. Overall, subjects picked the strip end aligned with the food more often than the alternative (median 92.36, IQR 0.09). Also, overall they did not differ significantly between the real and the painted condition (Wilcoxon test: $T = 12.5$, $N = 6$, $p = 0.75$). This could not be computed within patterns due to small sample sizes ($N < 6$ in both cases).

Figure 3 presents the median percentage of correct trials as a function of contingency, material, and pattern. Overall, subjects performed significantly better in the direct than the reverse contingency in the real condition (Mann–Whitney test: $U = 0$, $N = 12$, $p < 0.01$). In contrast, there was no difference between the direct and reverse contingencies in the painted condition (Mann–Whitney test: $U = 9.5$, $N = 12$, $p = 0.20$). Also, chimpanzees performed significantly better in the direct than the reverse contingency in the pseudo-cross and the other way around in the cross (Mann–Whitney tests: $U = 0$, $N = 12$, $p < 0.01$ in both cases). Of particular interest was the comparison of the effect of contingency and material within each of the patterns. Chimpanzees performed better in the real cross than the painted cross when the contingency was direct but the other way around when the contingency was reverse, as indicated by a significant interaction between contingency and material ($F1, 10 = 6.82$, $p = 0.03$).

Figure 4 presents the median percentage of correct trials as a function of pattern, contingency, and material in the first and in the last session of the test (Fig. 4a, b). Chimpanzees did not change their performance significantly

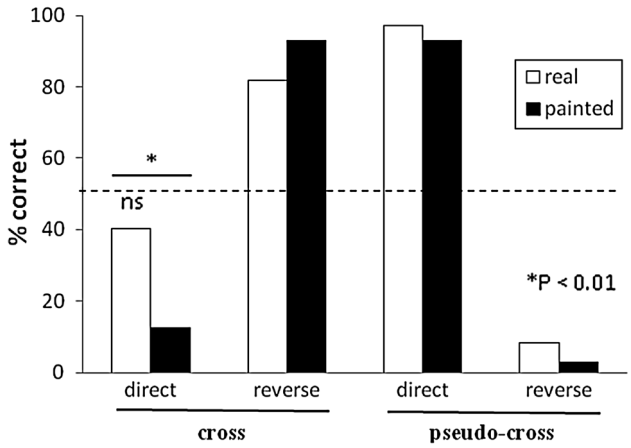

Fig. 3 Median percentage of correct trials as a function of pattern, contingency, and material in Experiment 1 (Albiach-Serrano et al. 2012 is the source of the direct contingency data). All results differed significantly from chance ($p < 0.05$) except for the real cross-direct condition (*ns* non-significant)

across sessions in any of the two conditions, real and painted, of the reverse contingency (Spearman r: $ps > 0.07$). Also in the reverse contingency (and in contrast to the direct contingency), performance did not change from session 1 to session 6 in the real cross-condition (Wilcoxon test: $T = 12$, $N = 6$, $p = 1.00$), whereas for the other conditions, this could not be computed due to small sample sizes ($N < 6$ in all cases). When comparing those conditions from the direct and the reverse contingency tasks requiring similar responses from the subjects (i.e., direct cross vs. reverse pseudo-cross and reverse cross vs. direct pseudo-cross, both real and painted), we found no significant differences between any of the four pairs of conditions in the first session (Mann–Whitney tests: $U < 15$, $N = 12$, $p > 0.15$). In contrast, subjects performed better in the real cross-direct than the real pseudo-cross-reverse in the last session (Mann–Whitney test: $U = 3$, $N = 12$, $p = 0.02$). All other comparisons were non-significant (Mann–Whitney tests: $U < 19$, $N = 6$, $p > 0.18$).

Discussion

Our results support the causal hypothesis, which predicted (1) that chimpanzees would obtain worse results in the real condition with a reverse contingency than with a direct contingency and (2) that they would perform similarly in the painted conditions, regardless of the contingency. However, the causal knowledge hypothesis also predicted (3) worse results in the real than in the painted condition within the reverse contingency task—whereas the perceptual hypothesis predicted the opposite—and although an interaction effect actually showed worse results in the real than the

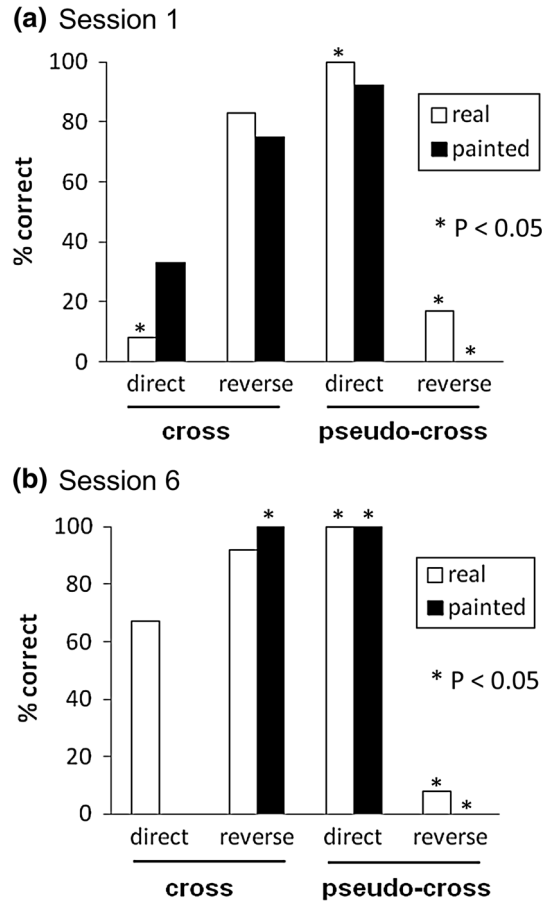

Fig. 4 Median percentage of correct trials as a function of pattern, material, and contingency in the first and the last sessions in Experiment 1 (Albiach-Serrano et al. 2012 is the source of the direct contingency data). *Asterisks* show deviation from chance

painted condition for the cross-pattern, this was not true for the pseudo-cross-pattern and, overall, we did not find differences between the real and the painted conditions.

One possible explanation is that subjects used a spatial rule based on proximity, which raised and lowered success in the cross and the pseudo-cross-patterns, respectively, masking the effect of material. In fact, most of the time chimpanzees picked the strip with its closer end aligned with the food. This may explain why they performed better in the cross-pattern, where the correct response was closer to (and aligned with) the food, than in the pseudo-cross-pattern, where they had to pick the strip end further away from the food. Indeed, they only solved the cross-pattern, independently of the material, and half of the subjects did so from the start. Further evidence of a proximity bias is shown by chimpanzees in the pseudo-cross-pattern performing better in the direct than the reverse contingency, and the other way around with the cross-pattern.

Nevertheless, proximity alone cannot explain the results of Experiment 1, since chimpanzees obtained worse results in the real condition with a reverse contingency than with a

direct contingency, which can only be explained if a mechanism other than proximity was at play. Actually, subjects obtained worse results in the real pseudo-cross with a reverse contingency compared to the real cross with a direct contingency, although both conditions involved performing against the predominant proximity bias. Moreover, subjects' performance did not improve over trials and no subject managed to solve the real pseudo-cross-reverse, contrary to the real cross-direct (Albiach-Serrano et al. 2012). This difference can be explained by subjects having causal knowledge of the task: Whereas both conditions required choosing against proximity bias, the real pseudo-cross-reverse, in addition, required choosing against causality rules and may have posed, therefore, more inhibition problems to subjects.

Experiment 2

Introduction

In Experiment 1, we found some evidence that chimpanzees have causal knowledge about support problems, although subjects seemed to rely strongly on proximity. Experiment 2 tested whether chimpanzees would learn to choose a broken paper strip over an intact one, when both support a similar food item. Therefore, instead of focusing on the chimpanzees' knowledge of the relation between food and strip (whether a strip has food on top of it or not), we shifted our attention to their knowledge of the functional features of the strip (the continuity of the strip). Moreover, since both strips presented were baited and they were straight and parallel to each other, we prevented any possible reliance of the subjects on proximity. This allowed us to better contrast the perceptual and the causal knowledge hypotheses, again by using a real and a painted version of the task. In essence, this experiment is similar to that reported by Albiach-Serrano et al. (unpublished data) but with a reverse instead of a direct contingency. We compared the results obtained by chimpanzees in both studies which, as in Experiment 1, were fully comparable (data were taken between 2011 and 2012).

Materials and methods

Subjects

Eleven chimpanzees housed at the WKPRC took part in Experiment 2. They were divided in two groups (A, B) equivalent as far as possible in sex ratio, ages, rearing histories, and experience in related tasks (Table 1). See Experiment 1 for a description of their living and testing conditions.

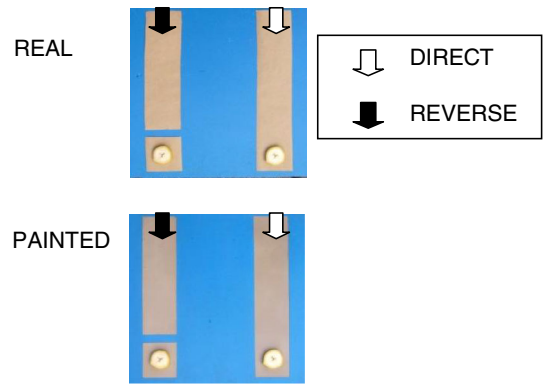

Fig. 5 Pattern, materials, and contingencies. Two parallel strips, one continuous and one discontinuous, either made with paper strips (real condition) or painted on a platform (painted condition) were used in Experiment 2. Subjects received *banana slices* (in the picture) or half grapes as reward. *Arrows* show the correct responses (i.e., responses that permitted obtaining the food) in both the direct and the reverse contingency (Albiach-Serrano et al. unpublished data and Experiment 2, respectively)

Materials

The materials used in Experiment 2 were similar to those in Experiment 1, except that there was only one strip pattern (Fig. 5) consisting of two parallel strips, one continuous (6 × 30 cm) and one discontinuous (same measures except for one 1.5-cm gap at 6.5 cm from the further end, which divided the strip in two pieces).

Design

Since Experiment 1 had shown that chimpanzees solved the single strip pretest from the first trial(s), we only presented six pretest trials conducted right before the first test session. The test consisted of six sessions, three in the real and three in the painted condition, in which subjects had to choose (pull/touch) the discontinuous strip in order to obtain the reward from the experimenter (reverse contingency, see Fig. 5). Each session had 12 trials. The position of the discontinuous strip (left/right) was counterbalanced within sessions and randomly presented, with the restriction that it could not be in the same side in more than two consecutive trials. For more details, see the "Design" section in Experiment 1.

Procedure

The basic procedure was the same as in Experiment 1 except that here *S* was rewarded for choosing the discontinuous strip. When a correct choice occurred (discontinuous strip chosen), *E* rewarded *S* with the food placed on that same strip. When an incorrect choice occurred

(continuous strip chosen), *E* quickly removed the food item from the strip.

Scoring and data analyses

We used the same scoring method, dependent variable and analyses as in Experiment 1. Our independent variables included material and contingency (comparing with the data in Albiach-Serrano et al. unpublished, where the sample size was $N = 12$). We randomly selected 20 % of the sessions, and a second observer coded them to assess inter-observer reliability, which was excellent (Cohen's $\kappa = 0.97$; $p < 0.01$).

Results

All chimpanzees starting with the real condition pulled the single strip in the pretest spontaneously. Also, all chimpanzees starting with the painted condition readily learnt to touch the painted strip to get the reward in the first trial(s) of the pretest.

Figure 6 presents the median percentage of correct responses by chimpanzees in the real and the painted conditions both in the direct and the reverse contingency. Chimpanzees performed significantly worse in the reverse than the direct contingency in the real condition (Mann–Whitney test: $U = 14$, $N = 23$, $p < 0.01$). In contrast, they performed at the same level in the reverse and the direct versions of the painted condition (Mann–Whitney test: $U = 42.5$, $N = 23$, $p = 0.15$). Finally, although chimpanzees performed at chance levels both in the real and the painted condition of the reverse contingency (Wilcoxon tests: $T < 35$, $p > 0.29$), with no subject solving any of the two conditions, their results were worse in the former than the latter (Wilcoxon test: $T = 55.5$, $N = 11$, $p = 0.04$). The chance level performance was not due to side biases. Both overall and individually, subjects did not deviate from chance in their choices to the left and right (Wilcoxon test: $T = 9$, $N = 6$, $p = 0.81$; Binomial tests: $p > 0.08$, $N = 144$). We found no compelling evidence of learning throughout the 36 trials of testing in any of the two conditions (Spearman r: real: $r = 0.26$, $N = 36$, $p = 0.12$; painted: $r = 0.10$, $N = 36$, $p = 0.55$).

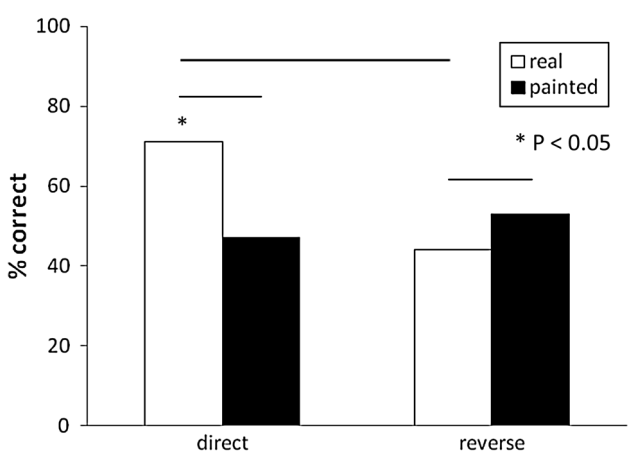

Fig. 6 Median percentage of correct trials as a function of contingency and material in Experiment 2 (Albiach-Serrano et al. unpublished data are the source of the direct contingency data). The *asterisk* shows deviation from chance, and *lines* show significant differences between conditions, with the p value set at 0.05

Discussion

Chimpanzees did not learn to pick a discontinuous strip over a continuous strip in the 36 trials provided, neither in the real nor in the painted condition. Instead, they performed at chance levels in both conditions. This was not due to the development of side biases but to what seemed random performance. However, subjects performed worse in the real than in the painted condition. Moreover, subjects in the real condition performed worse than those who received the real condition in the direct contingency. In contrast, the results in the direct and the reverse versions of the painted condition were similar. So, once we removed the proximity bias present in Experiment 1, all three predictions of the causal knowledge hypothesis were confirmed. This suggests that chimpanzees had expectations regarding the outcomes of pulling one or the other paper strip, independent of the actual reward regime, something that can be best explained by chimpanzees having some causal knowledge of the problem.

General discussion

We presented chimpanzees with two reverse contingency tasks designed to test for causality, where subjects needed to pick the non-functional of two paper supports in order to obtain food resting on top of them. In Experiment 1, this involved picking the strip not supporting the reward. In Experiment 2, this involved picking the broken strip. Subjects found these problems difficult to solve, especially compared to the standard tasks in which subjects are rewarded for picking the functional support (direct contingency tasks). Indeed, except for one condition in Experiment 1 where proximity bias was sufficient to find the solution, not a single subject solved any of the two tasks in the 36 trials given. Moreover, their results were worse in the real, causally counterintuitive, than in the painted, causally arbitrary, condition, even if these conditions looked very similar. These data suggest that subjects had some causal knowledge of the support problem that resulted in a prepotent response—the preference to use a functional over a

non-functional support to bring food resting on top of it. In addition, the fact that chimpanzees performed at chance levels in the painted condition and showed no improvement across trials further supports the idea that learning from perceptual, arbitrary cues is not always easy for non-human great apes (Call 2006; Hanus and Call 2008, 2011). Studies have shown that primates can solve reversed-reward contingency tasks when food is replaced by arbitrary symbols (e.g., Boysen et al. 1996; Genty and Roeder 2011). Perhaps in the present study, the visibility of the food rendered the learning process more difficult.

Of course, one could always argue that chimpanzees' knowledge is perceptual, just more refined than what we have considered until now. When confronted with a support problem, chimpanzees may only pay attention to the functionally relevant features (the contact between the food and the strip or the presence of a gap along the strip) if simultaneously they perceive certain tactile and multisensory inputs. These inputs may include the covariation of the movement of the hand, the strip and the food (to explain why they solve the real but not the painted conditions with a direct contingency), although only if this covariation is positive (to explain why they solve the direct but not the reverse contingency even though both involve paper strips). But this notion of perception-based causality is quite different from the simple notions that have been entertained to explain results of the support problem and other related tasks involving physical causality, like the idea that the chimpanzees' choices are based simply upon visual contact or perceptual containment (see Povinelli 2000). Note that there is evidence that humans perceive certain situations as causal based just on the co-occurrence of events in space and time (e.g., Leslie 1984; Michotte 1963). However, little is known about how subjects recognize static aspects of causality, such as the functional relevance of object's perceptual features, and how this relates to the recognition of dynamic aspects of causality. It seems plausible that the flexible manipulative behavior of some animal species is underpinned by more abstract (and less purely perceptually driven) knowledge of objects than previously thought. Clarifying this question will require further research, and perhaps new paradigms.

Experiment 1 revealed a proximity bias that helped chimpanzees obtain food in some cases but hindered their performance in others (see also Albiach-Serrano et al. 2012). Reaching for food in straight line is probably a good default strategy to save time and effort and avoid competitors and risks during foraging. However, sometimes one may need to take more indirect approaches to the food, like in this experiment, and then the inhibition of such prepotent responses becomes advantageous (see also Santos et al. 1999; Vlamings et al. 2010). Chimpanzees in this study found difficult inhibiting their proximity bias, and in fact the strongest evidence of them having causal knowledge appeared in Experiment 2, when the strips' disposition did not allow reliance on proximity. This may exemplify how inhibitory control is important, since it allows individuals to suppress prepotent responses in favor of more sophisticated solutions derived from subjects' knowledge (e.g., Boysen et al. 1996). The reverse contingency task, usually employed to assess inhibition in primates (e.g., Amici et al. 2008), was used here to assess causal knowledge in chimpanzees. In the future, this and other types of knowledge might serve, in turn, to obtain new measures of inhibitory control. The combined study of inhibitory skills and causal knowledge can be extremely fruitful, especially given that the vast majority of inhibitory tasks used with non-human animals (and human infants) have been based on relatively simple sensorimotor schemas. Ultimately, the ability to refrain from using previous knowledge (causal or otherwise) in order to find solutions to novel problems is an aspect of cognition that may have been crucial to our species—and perhaps other species—for adaptation to changes throughout evolution.

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Conflict of interest The authors declare that they have no conflict of interest.

Ethical standards This study strictly adhered to the legal requirements of the country in which it was conducted.

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