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SHORT COMMUNICATION

Barriers and traps: great apes' performance in two functionally equivalent tasks

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Abstract Tool-using tasks that require subjects to overcome the obstacles to get a reward have been a major component of research investigating causal knowledge in primates. Much of the debate in this research has focused on whether subjects simply use certain stimulus features or instead use more functionally relevant information regarding the effect that certain features may have on a moving reward. Here, we presented two obstacle tasks, a trap platform and a barrier platform, to 22 great apes. Although perceptually similar, these two tasks contain two perceptually different but functionally equivalent obstacles: a trap and a barrier. In a pre-exposure phase, subjects either experienced an obstacle task or a task without any obstacle. In the transfer phase, all subjects were presented with an obstacle task, either the trap platform or the barrier platform. Our results show that those subjects who received an obstacle task prior to the second task performed better than those who first received a non-obstacle task. The type of obstacle task that subjects received first did not have any effect on their performance in the transfer phase. We suggest that apes possess some knowledge about the effects that obstacles have on slow-moving unsupported objects.

Keywords Tool use · Trap tasks · Great apes · Causal knowledge

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Introduction

Much of the work on causal knowledge in non-human animals has focused on tool use (Fujita et al. 2003; Povinelli 2000; Tomasello and Call 1997). One of the tasks that has received most attention within this field is the trap-tube task (Visalberghi and Limongelli 1994; Limongelli et al. 1995). In this task, subjects are presented with a transparent tube from which they have to extract a reward with a tool without pushing the reward inside a trap situated in the center of the tube. Monkeys, apes and birds find this task difficult (Liedtke et al. 2011; Limongelli et al. 1995; Povinelli 2000; Seed et al. 2006; Teschke and Tebbich 2011; Visalberghi and Limongelli 1994), although recent research has shown ways in which the subjects' performance can be improved. In particular, allowing subjects to choose whether they can rake or push the reward out of the tube (the original studies only allowed subjects to push the reward out of the tube) (non-human primates: Mulcahy and Call 2006; Martin-Ordas et al. 2008; birds: Tebbich and Bshary 2004) or eliminating the need to use a tool (Seed et al. 2009) substantially improves their performance. Although these studies reveal that subjects are capable of solving the tasks, the degree to which they use sophisticated strategies to do so, as opposed to forming a solution based on trial-and-error learning, is a matter of controversy (Call 2000). Solving a task after a few trials (even if not on the first trial) can potentially be explained by high-level as well as low-level explanations (Bluff et al. 2007; Penn et al. 2008; Penn and Povinelli 2007; Taylor et al. 2009; Visalberghi and Tomasello 1998). Subjects may have knowledge about the causal relations between the elements of the problem (e.g., their function and the effect that certain features of the problem may have on other elements of the tasks), but mechanisms such as innate predispositions to avoid a trap or leaned hnseuristics can also lead to high proficiency. Using transfer tasks has been a useful approach to disentangle these two alternative explanations.

There are two approaches to transfer tasks. The first is based on administering an original task and then implementing some critical modifications to that task. The inverted trap-tube task (Visalberghi and Limongelli 1994), the two trap-tube tasks (Liedtke et al. 2011; Seed et al. 2006; Tebbich et al. 2007; Teschke and Tebbich 2011) and the fake trap tube (Martin-Ordas and Call 2009) fall into this approach. The second approach consists of presenting subjects with an original task and later assessing them with a second task that differs in appearance and response but is functionally equivalent to the original task. The trap-table (Povinelli 2000; Girndt et al. 2008), the trap-platform (Martin-Ordas et al. 2008), the trap-box (Seed et al. 2009) and the gap-table (Martin-Ordas and Call 2009) tasks are functionally equivalent to the trap-tube task.

Despite the fact that transfer tasks seem to be one of the most compelling ways to rule out low-level explanations, it is true that they are still vulnerable to criticism. First of all, changing the functional properties of the trap either involves a change in its configuration (e.g., inverted trap-tube task) or introduces new functional elements (e.g., bungs in the two trap tubes). This makes it hard to decide whether subjects' performance is due to a change in the configuration or the function of the elements of the task. Likewise, presenting subjects with tasks that require different motor responses (e.g., trap table) might mask any knowledge that subjects possess about critical features of the task. However, a recent study with apes has shown that subjects were able to generalize (their ability to solve a problem?) across different trap tasks, although they did not generalize to the trap-platform task (Martin-Ordas and Call 2009; see Taylor et al. 2009 for similar results with corvids).

Secondly, although all trap tasks differ in their appearance, the traps in each task are formed by a discontinuity on the surface where the reward is placed. This means that subjects could be using such a perceptual feature to generalize from one type of trap to another and thus exhibit impressively high performances in the transfer tasks.

The goal of the study presented here was to investigate whether subjects could transfer across tasks when the obstacles they experienced were perceptually different but functionally equivalent. We presented subjects with two tasks in which they had to use a tool to get a reward placed on an inverted U-shaped platform while avoiding an obstacle. In order to access the reward, subjects were required to move the reward along the platform away from the obstacle located in one of the platform's sides. One task was the trap-platform problem (Martin-Ordas et al. 2008) in which the platform had a hole in one of its sides. The other task was the barrier-platform problem in which the platform had no holes but a barrier prevented displacement of the reward in a certain direction to get access to it. Thus, the obstacles in each task were perceptually distinct but functionally equivalent.

We investigated whether subjects who had mastered one of the tasks were proficient at solving the other task compared to subjects that had not previously faced either of those tasks. One group of subjects was presented first with a platform without any obstacle (obstacle-free platform) followed by a platform with an obstacle, either the trap platform or the barrier platform. The other group received both obstacle tasks in succession. We predicted that if subjects saw both obstacles as functionally equivalent, those subjects who first received a platform with an obstacle would perform better in the next task than those subjects who received an obstacle-free platform first.

Materials and methods

Subjects

Twelve chimpanzees (*Pan troglodytes*), five bonobos (*Pan paniscus*), four orangutans (*Pongo pygmaeus*) and one gorilla (*Gorilla gorilla*) housed at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo participated in this experiment (see Table 1). There were 15 females and 7 males. All subjects had participated in a variety of cognitive tests, some of which included tasks involving tools and traps; however, 8 subjects had not experienced the trap platform before (see Table 1). There were two experimental groups: obstacle-free group, which was formed of 6 chimpanzees, 2 bonobos and 2 orangutans, and obstacle group, which was formed of 6 chimpanzees, 3 bonobos, 2 orangutans and 1 gorilla (see Table 1). All subjects lived in social groups of various sizes, with access to indoor and outdoor areas that were furnished with natural vegetation, climbing structures and enrichment devices to foster extractive foraging activity during the day, including the use of tools. Subjects were not food or water deprived.

Apparatus

There were three apparatuses: the obstacle-free platform, the trap platform and the barrier platform. The three platforms were U-shaped and consisted of a 70 cm wide × 31 cm long plastic platform surrounded on three sides by a 2-cm border to prevent the reward from falling off the platform. There was also a border on the front side of the platform to prevent the reward from falling into empty space. The obstacle-free platform consisted of a flat continuous surface without any obstacle (see Fig. 1). In the

Table 1 Name, gender, age, rearing history, experimental group in the present study and previous experience of the subjects in tool using in trap tasks

Subject	Gender	Age (years)	Rearing history	Experimental group	Previous experience in trap tasks[a]
Chimpanzee					
Frodo[N]	M	16	Mother raised	Obstacle	2, 4, 5
Patrick[N]	M	13	Mother raised	Obstacle free	2, 4 ,5
Alex[N]	M	9	Mother raised	Obstacle	2, 4, 5
Lome[N]	M	8	Mother raised	Obstacle free	–
Fraukje[F]	F	33	Nursery raised	Obstacle free	2, 3, 4, 5
Jahaga[P]	F	17	Mother raised	Obstacle	2, 3, 4
Fifi[P]	F	17	Mother raised	Obstacle free	1, 2, 3, 4
Sandra[F]	F	17	Mother raised	Obstacle	2, 3, 4, 5
Pia[P]	F	10	Mother raised	Obstacle free	2, 3, 4, 5
Annett[N]	F	10	Nursery raised	Obstacle free	2, 4, 5
Alexandra[N]	F	10	Nursery raised	Obstacle	2, 4, 5
Tai[N]	F	7	Mother raised	Obstacle	–
Bonobo					
Joey[P]	M	31	Nursery raised	Obstacle free	1, 2, 3, 4
Limbuko[P]	M	14	Nursery raised	Obstacle free	2, 3, 4
Kuno[P]	M	13	Nursery raised	Obstacle	2, 3, 4
Ulindi[F]	F	16	Mother raised	Obstacle	1, 2, 3, 4
Yasa[F]	F	12	Unknown	Obstacle	2, 3, 4
Orangutan					
Dokana[P]	F	21	Mother raised	Obstacle	1, 2, 3, 4
Padana[P]	F	12	Mother raised	Obstacle	2, 3, 4
Kila[F]	F	10	Mother raised	Obstacle free	3
Raaja[N]	F	6	Mother raised	Obstacle free	–
Gorilla					
Viringika[F]	F	15	Mother raised	Obstacle	1, 2, 3, 4

[a] *1* trap-tube task (Mulcahy and Call 2006), *2* trap table (Girdnt et al. 2008), *3* trap tube/trap platform [*F* subjects who failed the trap platform, *P* subjects who passed the trap platform, *N* Naïve subjects without previous experience with the trap-platform task (Martin-Ordas et al. 2008)], *4* fake trap tube/gap task (Martin-Ordas and Call 2009), *5* trap box (Seed et al. 2009)

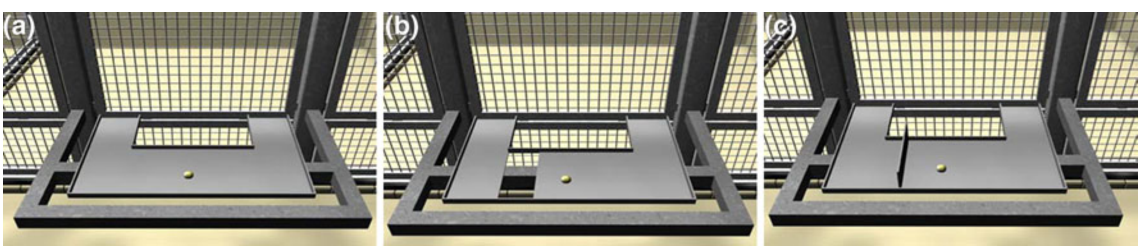

Fig. 1 Experimental setup for the obstacle-free platform **a** the trap-platform **b** and the barrier-platform **c** tasks

trap-platform task, the front part of the platform was cut to create a trap (8 cm wide × 15 cm long) that prevented subjects from getting the reward from its starting position (see Fig. 1). In the barrier platform, we placed an opaque plastic piece exactly the same size as the trap (8 cm wide × 15 cm long) on the front part of the platform in order to prevent subjects from getting the reward from its starting position (see Fig. 1). The distance between the reward and the obstacles was identical in both tasks: 8 cm. The tool consisted of a 50-, 0.5-cm straight wooden dowel for all the three platforms. We used grape halves as rewards.

Procedure

Subjects were individually tested in their indoor cages after being separated from their groupmates. Young infants stayed with their mothers while the test took place. There were three conditions corresponding to the three apparatuses. We followed the same procedure for the three conditions. The experimenter (E) placed the platform outside the cage against the mesh and deposited half of a grape on a predetermined spot in the center of the platform equidistant to the retrieval areas (Fig. 1). E gave the tool to the subject through the mesh at a point located just above the reward so that no side bias was induced. To retrieve the reward, the subject had to take the tool, insert it through the mesh and move the reward toward her through either side of the platform (obstacle-free condition) or away from the trap or barrier (obstacle conditions).

There were two different phases, the pre-exposure phase and the transfer phase, and subjects received one task in each phase. Subjects were distributed into two groups defined by which task they received in the pre-exposure phase:

Obstacle-free group

Subjects received the task without any obstacle in the pre-exposure phase and a platform with an obstacle in the transfer phase (half of the subjects received the trap-platform task, and the other half received the barrier-platform task).

Obstacle group

Subjects received both the trap-platform task and the barrier-platform task in succession with half of the subjects receiving the trap platform in the pre-exposure phase and half of the subjects receiving it in the transfer phase. The order of the presentation of the tasks was counterbalanced across subjects.

In all three conditions, the trial ended after the subject retrieved the reward or the reward fell into the trap. However, in the trap-platform condition, half of the subjects were given the opportunity to retrieve the reward when it fell into the trap. In these trials, E retrieved the fallen reward and placed it back in the predetermined initial position on the platform. E did this as many times as necessary for the subjects to retrieve the reward (all but one subjects needed only between 1 and 2 attempts to get the reward; the exceptional subject needed 15 attempts in one trial to retrieve the reward).

All subjects participated in three 12-trial sessions in each condition (72 trials in total). The position of the obstacle was counterbalanced across trials within a session so that it appeared the same number of times to the left and to the right of the subject.

Data scoring and analysis

We videotaped all trials. Trials were scored as correct if subjects successfully retrieved the food reward and as incorrect if the food fell into the trap or touched the barrier. Those trials in which the E placed back the reward on the trap platform were also scored as incorrect independently of the subject getting the reward after later attempts.

We calculated the percentage of trials in which subjects obtained the reward. We used nonparametric tests because the data were not normally distributed. We used Mann–Whitney tests to analyze the effect of the pre-exposure phase on subjects' performance in the transfer phase and to analyze subjects' performance in the pre-exposure phase. We used the Kruskal–Wallis test to investigate differences between chimpanzees, orangutans and bonobos and the effect of previous experience on performance. We did not include gorillas in this analysis because there was just one representative of this species. We used the Friedman test to investigate learning effects across sessions and Wilcoxon tests to run post hoc comparisons (exact p values were calculated in this case) and to assess whether subjects performed above chance levels in each condition (with 50 % the expected chance value). We used the binomial test to assess the subjects' performance in the first trial. All tests were two-tailed.

Results

There were no significant differences between the trap platform and the barrier platform in the pre-exposure phase [Mann–Whitney test: $U = 9.50$, $P = 0.180$, $N = 12$ ($N_{Trap} = 6$, $N_{Barrier} = 6$)]. Overall, subjects were above chance in all sessions of the pre-exposure phase (Wilcoxon tests: $T = 0.00$, $P < 0.01$, $N = 12$ in all cases). Subjects were also above chance in each obstacle task in the pre-exposure phase (trap platform: Wilcoxon test, $T = 0.00$, $P = 0.031$, $N = 6$; barrier platform: Wilcoxon test, $T = 0.00$, $P = 0.031$, $N = 6$, Table 2). There were no significant differences among orangutans, bonobos and chimpanzees in the transfer phase (Kruskal–Wallis: $X^2 = 0.49$; $P = 0.97$, $N = 21$; Fig. 1). Therefore, we pooled together the data from the various species. Subjects performed significantly better in the first session of the transfer phase when they were presented with an obstacle task in the pre-exposure phase than when they had only experienced a platform without obstacles [Mann–Whitney test: first session $U = 31$, $P = 0.044$, $N = 22$ ($N_{Obstacle} = 12$, $N_{No\ obstacle} = 10$), Fig. 2]; this effect was not significant for the second [$U = 38.5$, $P = 0.126$, $N = 22$, ($N_{Obstacle} = 12$, $N_{No\ obstacle} = 10$) Fig. 2] or third session [$U = 46$, $P = 0.296$, $N = 22$, ($N_{Obstacle} = 12$, $N_{No\ obstacle} = 10$) Fig. 2]. Subjects performed equally well in the transfer phase regardless of which task they had faced in the pre-exposure task [Mann–Whitney test: $U = 57.5$, $P = 0.841$, $N = 22$ ($N_{Obstacle} = 12$, $N_{No\ obstacle} = 10$)].

Note that in the barrier platform, subjects always got the reward and this experience could have positively affected their performance. However, providing subjects with more opportunities to retrieve the reward either in the pre-exposure phase or in the transfer phase of the trap-platform condition did not affect subjects' performance in the pre-exposure phase [Mann–Whitney test: $U = 3.5$, $P = 0.812$, $N = 6$

Table 2 Percentage of correct responses in both tasks in the pre-exposure and transfer phase, significance levels on binomial tests and session in which subjects are above chance

Subject	Pre-exposure phase						Transfer phase					
	Barrier			Trap			Barrier			Trap		
	%	*P*	Ses.	%	*P*	Ses.	%	*P*	Ses.	%	*P*	Ses.
Chimpanzee												
Frodo	86.1	<0.001	2							72.2	0.011	2
Patrick							77.8	0.001	2			
Lome										66.7	0.065	–
Alex	91.7	<0.001	2							97.2	<0.001	1
Fraukje										94.4	<0.001	1
Jahaga				88.9	<0.001	2	94.4	<0.001	1			
Fifi										94.4	<0.001	1
Sandra	75.0	0.029	3							97.2	<0.001	1
Pia							97.2	<0.001	1			
Annet							91.7	<0.001	1			
Alexandra				94.4	<0.001	1	91.7	<0.001	2			
Tai				58.3	0.405	–	94.4	<0.001	1			
Bonobo												
Joey							83.3	<0.001	2			
Limbuko										83.3	<0.001	2
Kuno	88.9	<0.001	2							100	<0.001	1
Ulindi	100	<0.001	1							94.4	<0.001	1
Yasa				80.6	0.004	3	91.7	<0.001	1			
Orangutan												
Dokana				94.4	<0.001	1	91.7	<0.001	1			
Padana	94.4	<0.001	1							97.22	<0.001	1
Kila							94.4	<0.001	1			
Raaja										72.22	0.011	2
Gorilla												
Viringika				100	<0.001	1	100	<0.001	1			

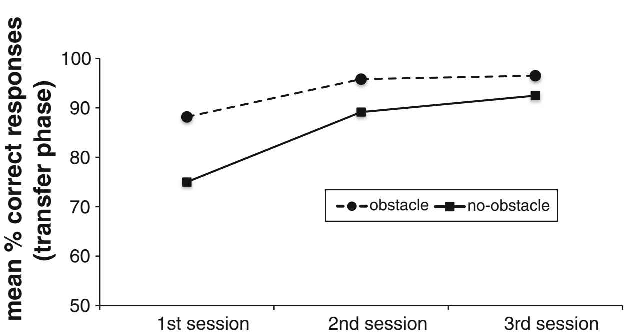

Fig. 2 Mean percentage of correct responses in the transfer phase across sessions as a function of the condition received in the pre-exposure phase (obstacle vs. no obstacle)

($N_{\text{grape back}} = 3$, $N_{\text{no grape back}} = 3$)] or the transfer phase [Mann–Whitney test: $U = 8$, $P = 0.195$, $N = 11$ ($N_{\text{grape back}} = 6$, $N_{\text{no grape back}} = 5$)].

Subjects' performance varied significantly across sessions (Friedman test: $X^2 = 17.51$, $P < 0.001$, $N = 22$, see Fig. 2). Subjects performed better in the second (Wilcoxon test: $T = 3$, $P = 0.002$, $N = 22$) and third session (Wilcoxon test: $T = 6.50$, $P < 0.001$, $N = 22$) than in the first session of the transfer phase. There were no significant differences between the second and third session (Wilcoxon test: $T = 17.50$, $P = 0.150$, $N = 22$). Subjects' performance across sessions was not dependent on which obstacle task they received in the transfer phase [Mann–Whitney test: first session $U = 48.50$, $P = 0.438$; second session $U = 49.00$, $P = 0.478$; third session $U = 42.00$, $P = 0.243$ $N = 22$ in all cases ($N_{\text{trap}} = 11$, $N_{\text{barrier}} = 11$)]. Additionally, the type of prior experience with the trap-platform task did not have any effect on subjects' performance (pre-exposure phase: Kruskal–Wallis, $X^2 = 0.746$, $P = 0.689$, $N = 12$; transfer phase: Kruskal–Wallis, $X^2 = 4.44$, $P = 0.108$, $N = 22$).

Overall, subjects were above chance in all sessions of the transfer phase (Wilcoxon tests: $T = 0.00$, $P < 0.001$, $N = 22$ in all cases). Subjects were also above chance in each obstacle task in the transfer phase (trap platform: Wilcoxon test, $T = 0.00$, $P = 0.001$, $N = 11$; barrier platform: Wilcoxon test, $T = 0.00$, $P = 0.001$, $N = 11$). However, subjects were not above chance in the first trial of the transfer session (binomial test, $P = 0.286$, 14/22 correct). The same was true in both the trap-platform (binomial test, $P = 1$, 5/11 correct) and barrier-platform conditions (binomial test, $P = 0.065$, 9/11 correct). Receiving an obstacle task did not significantly affect subjects' performance in the first trial of the transfer phase (obstacle group: binomial test, $P = 0.146$, 9/12 correct; obstacle-free group: binomial test, $P = 1$, 5/10 correct).

Table 2 presents the subjects' individual performance in each task in both phases. All 6 subjects solved the barrier task, and 5 solved the trap task in the pre-exposure phase. In the transfer phase, 11 subjects solved the barrier task, and 10 solved the trap task. Table 2 also presents the speed at which subjects reached above chance performance.

Discussion

Apes were able to solve both the trap-platform and the barrier-platform tasks within the first session. More importantly, our results show that subjects who received an obstacle task prior to the other obstacle task performed better than those who had previously received an obstacle-free task despite subjects' previous experience with similar trap tasks. The type of obstacle task that subjects received first had no effect on their performance in the transfer phase.

The difference between the obstacle-free and obstacle groups indicates that apes are able to transfer knowledge between two tasks even though the obstacles were perceptually different yet functionally equivalent. One could argue that having experience with an obstacle in the pre-exposure phase allowed subjects to extract a rule of the type: only one side of the platform is correct. This would not require subjects to encode the functional properties of the obstacles, but it would give them an advantage over those subjects who had not experienced obstacles before. However, if this interpretation were correct, one should also expect that having experience from a previous experiment with the trap-platform task would have affected subjects' performance, at least, in the pre-exposure phase. But this was not the case. Therefore, experience with an obstacle in pre-exposure phase rather than previous experience with similar trap tasks affected subjects' performance in the transfer phase.

However, we also found a learning effect in the transfer phase; that is, subjects' performance improved across sessions. In fact, our results show that this improvement was dependent on the type of pre-exposure experience that subjects received; that is, those subjects who received an obstacle task in the pre-exposure phase performed better in the first session of the transfer phase than those subjects who did not experience an obstacle task in the first place.

Although we found evidence of transfer across tasks, apes were still not above chance in the first trial of the transfer phase. This result was independent of the type of pre-exposure or task received in the transfer phase. One could argue that this result indicates a lack of transfer. However, subjects' better performance in the obstacle group than in the obstacle-free group weakens this explanation. It is conceivable that subjects failed to meet this demanding criterion for reasons unrelated to an inability to represent the functional properties of the obstacles (see Seed et al. 2009), especially when one considers that adult humans make a number of mistakes on similar tasks (Silva et al. 2005; Silva and Silva 2006).

Previous research with non-human primates using the trap table has concluded that subjects' high performance in the transfer task could merely be due to an association between a "solid and continuous" surface and rewards, which subjects could have learned during training (Povinelli 2000; Fujita et al. 2003; Cunningham et al. 2006). Interestingly, the obstacle-free group's worse performance in the transfer phase does not support this explanation. If subjects had learned to associate a solid surface with the reward, then those subjects who were presented with a platform without any obstacle in the pre-exposure phase should have performed at least as well as those who received a platform with an obstacle.

In line with other previous studies on trap tasks (Mulcahy and Call 2006; Girdnt et al. 2008; Martin-Ordas et al. 2008; Martin-Ordas and Call 2009; Seed et al. 2009), subjects solved both platform tasks particularly fast in both phases (see Table 1) and they did so independently of the type of obstacle task that they faced. Additionally, subjects' performance did not differ between the trap-platform and the barrier-platform tasks. This result is particularly revealing because it weakens the idea that apes' performance in the trap platform is driven only by an innate predisposition to avoid holes (see Martin-Ordas and Call 2009 for similar results). Instead, it seems more plausible to argue that apes possess a more general knowledge about the effects that perceptually different obstacles (barrier and trap) that are functionally equivalent (both block food from retrieval) have on slow-moving objects on an horizontal solid surface. Such knowledge was relevant to both tasks because in both, subjects had to displace the objects while avoiding the two different obstacles.

One possible limitation of the study presented here could be the level of difficulty of the tasks. Subjects were able to solve both tasks independently of their previous experience with the problem and independently of the type of pre-exposure they received; they already did so in the first session of the transfer phase. It is worth mentioning that a long history of research on causal understanding has indicated that non-human animals seem to find trap tasks extremely difficult (Visalberghi and Limongelli 1994; Limongelli et al. 1995; Povinelli 2000; Fujita et al. 2003; Cunningham et al. 2006), and subjects' performance has tended to be explained by associative learning. Interestingly, the results presented here show that apes were able to solve two obstacle tasks and more remarkably naïve subjects were also able to do so relatively fast.

Another limitation of this study is that other aspects of experience with trap tasks might have facilitated subjects' performance, for example, learning to inhibit certain disadvantageous responses. However, we think that such effects of previous experience are not likely to explain the difference in performance between the obstacle group and the obstacle-free group because all subjects had been extensively tested on a large number of tasks in which inhibition was required. It is true that three of our naïve subjects had no previous experience with any trap tasks and their performance was lower than those subjects with previous experience in trap tasks. However, these three subjects were also the youngest in our sample. Future studies should include older naïve subjects lacking any experience with trap tasks to disentangle the effect of age and experience.

Our results suggest that the apes were sensitive to causal elements of the tasks. The apes may have abstracted rules based on observable features of the task, such as inability of objects to pass through barriers or discontinuous surfaces. Following Seed and Call (2009), the evidence presented here suggests that apes are not only able to form arbitrary associations between elements of tasks (perceptual knowledge) but also able to understand the functional properties of an obstacle (structural knowledge). Having this knowledge would allow them to generalize between two functionally equivalent tasks.

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