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ORIGINAL ARTICLE

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How great apes perform on a modified trap-tube task

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Abstract To date, neither primates nor birds have shown clear evidence of causal knowledge when attempting to solve the trap tube task. One factor that may have contributed to mask the knowledge that subjects may have about the task is that subjects were only allowed to push the reward away from them, which is a particularly difficult action for primates in certain problem solving situations. We presented five orangutans (*Pongo pygmaeus*), two chimpanzees (*Pan troglodytes*), two bonobos (*Pan paniscus*), and one gorilla (*Gorilla gorilla*) with a modified trap tube that allowed subjects to push or rake the reward with the tool. In two additional follow-up tests, we inverted the tube 180° rendering the trap nonfunctional and also presented subjects with the original task in which they were required to push the reward out of the tube. Results showed that all but one of the subjects preferred to rake the reward. Two orangutans and one chimpanzee (all of whom preferred to rake the reward), consistently avoided the trap only when it was functional but failed the original task. These findings suggest that some great apes may have some causal knowledge about the trap-tube task. Their success, however, depended on whether they were allowed to choose certain tool-using actions.

Keywords Causal knowledge · Tool use · Problem solving · Anticipation

Knowing about the relation between causal factors and their effect is a fundamental feature of advanced physical and social cognition. Although humans have the ability to understand such relation it is unclear whether other animals can and if they do, to what extent (Visalberghi and Tomasello 1998; Povinelli 2000). Tool using has been one main avenue to investigate this question in nonhuman animals (Köhler 1925; Natale et al. 1988; Visalberghi and Limongelli 1994; Povinelli 2000; Chappell and Kacelnik 2002; Tebbich and Bshary 2004). One tool-using task that has received considerable research attention is the trap-tube task (Visalberghi and Limongelli 1994; Limongelli et al. 1995). This task involves presenting subjects with a plexiglass tube containing a trap in its center. A reward is placed inside the tube to the left or right of the trap. A tool that fits the tube snugly is provided to the subject and in order to retrieve the reward the subject has to insert the tool into the opening farthest away from the reward and push the reward away from the trap and out of the tube. An individual possessing a causal understanding of the task would be expected to avoid pushing the reward into the trap. Visalberghi and Limongelli (1994) tested four capuchin monkeys with the trap-tube task. After 120 trials only one monkey learnt to insert the tool into the opening farthest away from the reward thereby avoiding pushing the reward into the trap. However, she continued to use this strategy during the control condition in which the reward was once again placed at the side of the trap but now the trap was rendered ineffective by rotating the tube 180°. The authors suggested that she had learnt a simple distant-based procedural rule to solve the task: insert the tool into the opening farthest away from the reward and concluded that capuchins failed to comprehend the causal nature of the trap-tube task.

Limongelli et al. (1995) presented the trap-tube task to five chimpanzees. The test condition was identical to the one in the capuchin experiment, however, the control condition was different. Instead of having the trap inverted it was moved closer to one end of the tube and the reward was placed in the center. This controlled for the distant-based rule because now the reward was equidistant between the two ends of the tube. Two of the chimpanzees were able to solve the test condition across 140 trials. Moreover, they succeeded in avoiding the trap in the control condition in which no distant-based rule was available to solve the task. The authors concluded that, unlike capuchins, the chimpanzees understood the causal nature of the trap-tube task. Unfortunately, there was a second rule that the chimpanzees

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could have been using: always push the reward away from the trap. And by omitting the inverted trap control condition it is unclear whether the chimpanzees were using this procedural rule or whether they understood the causal nature of the task (Tomasello and Call 1997).

Povinelli (2000) addressed this issue by repeating the trap-tube experiment with seven chimpanzees and included the control condition of having the trap inverted. After 120 trials only one subject learnt to avoid the trap during the test condition. However, in the control condition, in which the trap was inverted, she behaved as if the trap was still effective by consistently pushing the reward away from the trap. Povinelli (2000) suggested that this chimpanzee was using the procedural rule of: always push the reward away from the trap. To investigate the strength of this rule, Povinelli (2000) partially inserted the tool into the opening of the tube that was closest to the reward (while the trap was inverted), so that now there was a cost to using the procedural rule. The results showed that the chimpanzee was more likely to take the costly option of removing the tool out of the tube, walking around to the other end of the tube, and pushing the reward away from the trap. Povinelli (2000) concluded that the chimpanzee failed to understand the causal nature of the task, but instead used the procedural rule of always push the reward away from the trap.

Recently, Tebbich and Bshary (2004) tested six woodpecker finches (*Cactospiza pallida*) with a modified version of the trap tube that allowed birds to either rake or push the reward out of the tube. The authors also presented the reward in the center of the tube (with the trap off center) in order to avoid the development of distance-based rules between the reward and the end of the tube. One of the six birds tested mastered the task after 100 trials whereas the others had not reached above chance performance after more than 150 trials. Birds showed a strong tendency to rake the reward out. More importantly, the successful subject also solved the inverted trap test as it ignored the position of the trap when it was nonfunctional. However, this bird solved the problem in a way that suggested that it was not representing the causal relations of the problem but using feedback from her own actions because it inserted the tool on each side of the tube multiple times in successful trials. Tebbich and Bshary (2004) concluded that observing the effect that its actions had on the reward rather than forming the solution in advance was what guided the bird's behavior.

Thus, in each of these studies there was no conclusive evidence of any subject having understood the causal nature of the trap-tube task. The primate studies have failed to provide evidence that subjects understood the function of the trap whereas the study on woodpecker finches suggested that the successful subject solved the problem by closely monitoring (as opposed to anticipating) the effect of its action on the reward. A surprising feature of the results is that the successful subjects learned to avoid the trap after many trials. It is conceivable that a contributing factor to this slow learning curve is that subjects were never given the opportunity to choose the action they preferred to use. Primates were required to push the reward while woodpecker finches could choose between raking or pushing the reward out of the tube (and they chose the former). Since pushing the reward away from the subject is particularly difficult for chimpanzees in detour problems involving tool-use (e.g., Köhler 1925; Guillaume and Meyerson 1930), it is conceivable that having to push the reward out of the tube (and away from the subject) may have hindered their progression in learning how to avoid the trap, and more importantly, it may have masked the expression of their causal knowledge of the problem.

The present study set out to investigate apes' ability in solving the trap-tube task giving the subjects the opportunity to use a more species-specific tool-using action. We tested subjects with a modified trap-tube task analogous to the one used by Tebbich and Bshary (2004) that allowed the subjects to have a choice between raking and pushing the reward out of the tube. Unlike Tebbich and Bshary (2004) however, we did not include an initial phase in which subjects could only retrieve the reward by raking the reward out. Instead, subjects could choose between raking and pushing the reward from the beginning of testing. We expected that when given the choice between raking and pushing, subjects would prefer to rake the reward out of the tube. We also expected that subjects who solved the task by raking the reward away from the trap would learn to solve the task in fewer trials compared to subjects from previous studies that could only solve the task by pushing the reward. In a follow-up test we repeated the original trap-tube task (reward only retrievable by pushing) with those subjects that had successfully retrieved the reward in the modified trap-tube task. We expected that they would have greater difficulties solving this task than they had solving the modified trap-tube task.

We also conducted the inverted trap-tube test (Visalberghi and Limongelli 1994) to find out whether an avoidance of the trap regardless of its possible consequences could explain the performance of successful subjects. Previous primate studies have not been able to rule out this possibility as an explanation for their subjects' successful performance. This means that it is unclear whether subjects were avoiding the trap for the consequences that it had on the reward or simply as a procedural rule without analyzing the causal underpinnings of the task more deeply.

Methods

Subjects

Five orangutans (*Pongo pygmaeus*), two chimpanzees (*Pan troglodytes*), two bonobos (*Pan paniscus*), 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 six females and four males (one juvenile, five adolescents, and four adults). All apes were mother-reared except one of the bonobos. Subjects had participated in a variety of cognitive tests but none had any previous experience with tasks involving traps of any sort. Orangutans and gorillas had preciously partici-

Table 1 Name, gender, age, rearing history, and previous tool-using experience of the subjects that participated in this study

Subjects	Gender	Age (years)	Rearing history	Previous experience of tool-use tasks
Chimpanzees				
Fifi	Female	13	Mother-raised	None
Brent	Male	6	Mother-raised	None
Bonobos				
Joey	Male	23	Nursery-raised	None
Ulindi	Female	23	Mother-raised	None
Orangutans				
Bimbo	Male	24	Nursery-raised	Raking an out-of-reach reward
Walter	Male	15	Mother-raised	Raking an out-of-reach reward
Pini	Female	16	Mother-raised	Raking an out-of-reach reward
Toba	Female	11	Mother-raised	Raking an out-of-reach reward
Dokana	Female	16	Mother-raised	Raking an out-of-reach reward
Gorila				
Viringika	Female	20	Mother-raised	Raking an out-of-reach reward

pated in a tool-use study in which they had to rake a reward placed on a platform (Mulcahy et al. 2005). 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 that included the use of tools. Subjects were individually tested in their indoor cages and were not food or water deprived.

Apparatus

We used two trap-tube sets. The first set consisted of a plexiglass tube (95 cm long and an internal diameter of 10 cm) and a trap 7 cm deep positioned 15 cm to the side of the geometric center of the tube. The tube was positioned inside a booth of the subject's cage (see Fig. 1a). The sidewalls of the booth contained a plexiglass panel (75 cm × 60 cm) containing a hole (6 cm in diameter). Each opening of the trap-tube was mounted over the panel hole using wooden brackets. We use a wooden dowel (120 cm long and 1.5 cm in diameter) as the tool.

The second trap-tube set consisted of a narrower tube with an internal diameter of 3.5 cm and a thicker tool (3 cm in diameter) than those used in the first set. We used this second set to replicate the original relation between the size of the tube and the size of the tool used by Visalberghi and Limongelli (1994). Unlike the first trap-tube set, subjects could only obtain the reward by pushing it away from them. Other than those size modifications, this second trap-tube set was presented in the same manner as the first one.

Procedure

We tested all subjects individually in an observation room (25 m^2 and 3.15 m high) separated from the rest of the group. E used juice to position the subject at the front wall of the booth, in front of the trap-tube's center (see Fig. 1a). E then showed the subject the reward before placing it in the

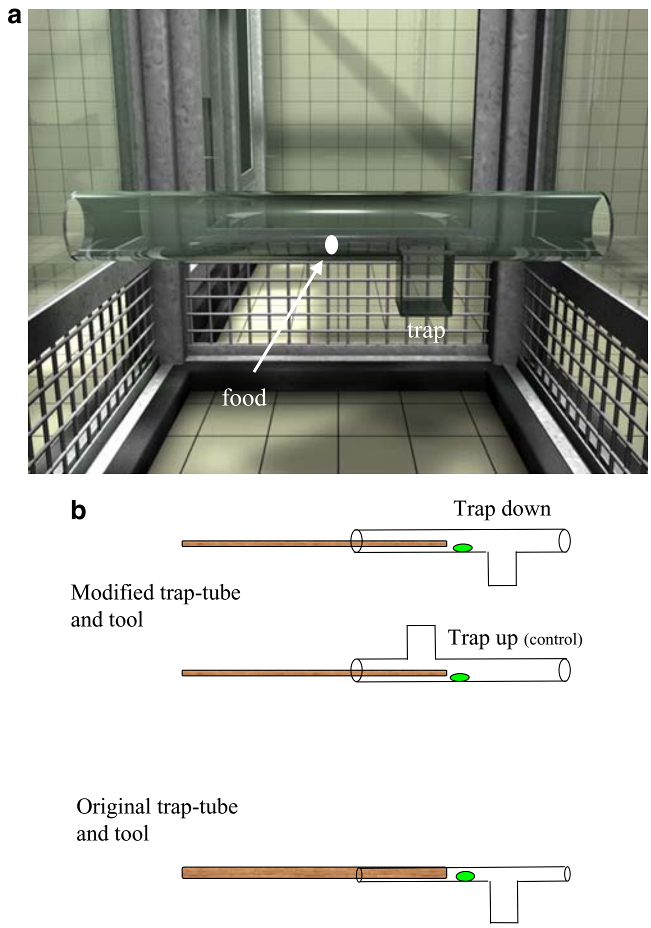

Fig. 1 Experimental setup **a** and experimental conditions **b** the diameter of the tool and tubes is drawn approximately to scale. In video clip S1, orangutan in the initial phase of the study using the tool to rake the reward out. The first part of the videoclip shows a successful trial while the second part shows an unsuccessful trial. Note the attempts of the orangutan to lift the reward over the trap in the second trial

middle of the trap-tube via a small hole (1 cm in diameter) drilled in the middle of the trap tube's sidewall. After 3 s had elapsed, E gave the subject the tool through a mesh hole of the booth's front wall. To retrieve the reward the subject had to take the tool, go to the left or right wall of the booth, insert the tool through the panel hole, and rake or push the reward away from the trap. The trial ended after the subject retrieved the reward, or the reward was displaced into the trap, or after 2 min had elapsed. The position of the trap was counterbalanced across trials so that it appeared the same number of times to the left and to the right of the subject.

Subjects were tested in two phases: initial and follow-up. In the initial phase, the tube was set so that the trap was at the bottom of the tube (see Fig. 1b, see videoclip S1). All subjects received three 12-trial sessions except two subjects (one orangutan and one bonobo) that refused to participate after their second session and another orangutan that was above chance after two sessions and therefore discontinued testing. We administered two and three additional sessions to one orangutan and one chimpanzee, respectively, that showed clear signs of improvement during the initial sessions.

In the follow-up phase, we selected the successful subjects from the previous phase to receive three additional tests (see Fig. 1b). First, we inverted the tube 180° so now the trap was rendered ineffective. Second, we returned the tube to its original position so that the trap was functional again. Third, we replaced the first trap-tube set with the second trap-tube set. We administered two 12-trial sessions in each of these three tests for a total of 72 trials. The general procedure for these follow-up tests was identical to those in the initial phase except for the mentioned changes in tube orientation and trap-tube set.

Data scoring and analysis

We videotaped all trials. For each trial we scored the apes' tool technique to displace the reward (toward or away from the self), whether they succeeded in obtaining the reward, and whether they inserted the tool from one side of the tube only. We calculated the percent of trials in which subjects (1) used each technique, (2) got the reward, and (3) inserted the tool from only one end of the tube. We conducted three main analyses. First, we compared the subjects' performance against chance with a one-sample t-test. Second, we used the binomial test to analyze whether certain individuals differed from chance. Third, we compared the performance of the successful subjects in the current study to the performance of successful subjects in previous studies (one capuchin monkey, three chimpanzees, one woodpecker finch). All statistical tests were two-tailed.

Results

Figure 2 presents the percentage of trials in the first 12 trials in which subjects raked in (as opposed to pushed out) the reward. Subjects significantly preferred to rake

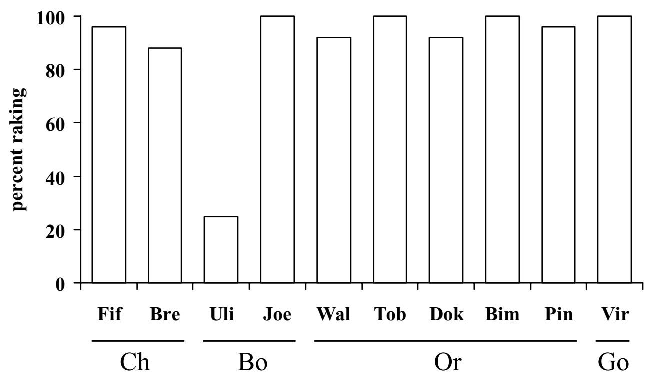

Fig. 2 Percent of trials in which subjects raked the reward toward them as opposed to push it away from them (Ch: chimpanzee; Bo: Bonobo; Or: orangutan; Go: gorilla)

(mean = 88.9%, sem = 7.2) than to push out (mean = 11.1%, sem = 7.2) the reward, $t_9 = 5.39$, $P < 0.001$. There was only one bonobo (Ulindi) that preferred to push the reward out.

Overall subjects were not above chance in the initial testing phase (mean = 56.6%, sem = 4.9, $t_9 = 1.34$, $P = 0.21$). However, three out of 10 subjects solved the problem in the initial phase within 24, 48, and 60 trials, thus raking the reward away from the trap significantly above chance (Binomial test: $p < 0.05$ in all cases, see Fig. 3). Subjects inserted the tool from one side only in most successful trials (Walter: 100%, Toba: 97.1%, Fifi: 80.4%). Even if we eliminated those successful trials in which the chimpanzee Fifi inserted the tool from both sides ($n = 10$), she still succeeded on 82% of the trials, which is significantly above chance (Binomial test: $P < 0.001$).

On average the three successful subjects in the current study reached a consistently above-chance performance after 44 trials compared to the 86 trials required by the five successful subjects from previous studies. This means that the three subjects in the current study solved the problem

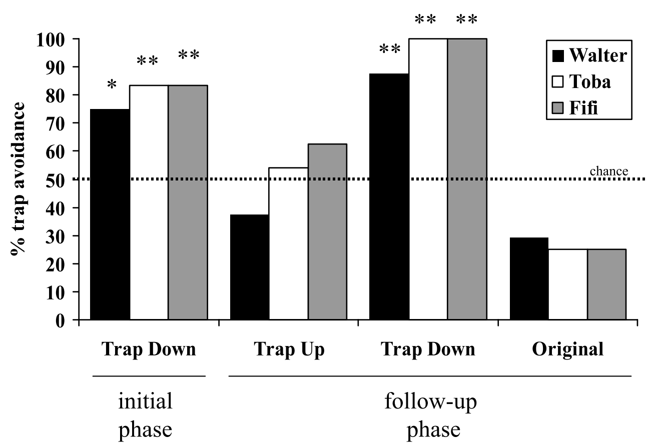

Fig. 3 Percent of trials in which the three successful subjects avoided the trap in the initial phase and the three conditions of the follow-up phase. All conditions are based on 24 trials. For purposes of comparability the results of the initial phase are based on the last 24 trials (in italic below) for each subject (Walter: *18/24*; Toba: 15/24, *20/24*; Fifi: 15/24, 16/24; *20/24*)

faster than the five subjects from previous studies, $t_6 = 3.33$, $P = 0.016$. Even if the capuchin monkey and the woodpecker finch that required 100 trials each to master the task are excluded from the analyses (chimpanzees required 60, 80, and 90 trials, respectively), the performance of the apes in the current study still tended to be better than the three chimpanzees from previous studies, $t_4 = 2.37$, $P = 0.077$.

Figure 3 also presents the percentage of correct trials in the follow-up phase (trap-up, trap-down, and original tests). As soon as the trap was nonfunctional (trap up) subjects ceased to avoid it (Binomial test: $P > 0.30$ in all cases) but once again avoided it after the trap became functional (Binomial test: $P < 0.001$ in all cases). Subjects failed the original trap-tube task and secured the reward on average in only 26% of the trials. This performance is comparable to that reported for the nine chimpanzees tested in previous studies during the first 20 trials, $t_{10} = 1.34$, $P = 0.21$.

Discussion

Subjects overwhelmingly preferred to rake in than to push the reward out of the tube. Although most subjects still failed to avoid the trap, there were two orangutans and one chimpanzee that solved the trap-tube problem within 24, 48, and 60 trials, respectively. More importantly, all three subjects ceased to avoid the trap when it was nonfunctional (trap up) but did so when the trap was functional again (trap down). Additionally, subjects in successful trials typically inserted the tool only once, thus suggesting that they anticipated the solution to the problem without the need of multiple tool insertions. Finally, these three subjects failed the original trap-tube task even after they had become highly proficient in the modified trap-tube task.

Next, we discuss our results in relation to previous studies, first by addressing the primate findings and later by addressing the results on woodpecker finches, particularly focusing on the successful subjects. The performance of our successful subjects differed from previous studies with capuchin monkeys and chimpanzees in two aspects. First, they solved the initial problem faster than the successful subjects in previous studies. For instance, the three apes in the current study solved the problem on average in 44 trials compared to 77 trials for three chimpanzees (Limongelli et al. 1995; Povinelli 2000). Second, and more importantly, they did not avoid the trap when it was nonfunctional. This ruled out the possibility raised by previous studies that subjects may have developed a procedural rule to solve the problem independently of the effect that the trap had on the displaced reward. Instead it suggests that subjects (at least those tested in the current study) understood the relation between the position of the trap and its effect on a displaced reward.

There are various reasons that could explain the differences between the current and previous studies. First, it is possible that our larger sample size may have allowed us to find more successful subjects. However, our sample size ($n = 10$) was not larger compared to the two previous ape studies combined ($n = 9$), and in fact, we found the same number of successful subjects compared to previous studies. Another possibility is that inter-study differences reflect species differences. Note that our two best subjects were orangutans, a species that has great propensity to use tools but that has not been tested until now in this task. Future studies with larger samples of orangutans and chimpanzees are necessary to confirm whether orangutans are more proficient than chimpanzees in this task. Nevertheless, note that the third successful subject in our sample was a chimpanzee. Her speed of acquisition was better than the chimpanzees tested by Limongelli et al. (1995) and equal to the successful subject tested by Povinelli (2000). More importantly, unlike the latter, our chimpanzee did not avoid the trap when it was ineffective.

A third possibility is that our modified method allowed subjects to better display their knowledge regarding the consequences of bringing the reward over the trap. Placing the reward in the center is a feature that may have helped subjects by preventing them from forming a procedural rule based on pushing the reward the shortest distance from the end of the tube. Povinelli (2000) also used this procedure but found no change in performance compared to the original procedure. However, he introduced this modification after subjects had had extensive experience with the original setup in which the trap, not the reward, was in the center. Therefore, it is conceivable that by the time the modification was introduced, subjects had a firmly established set of heuristics that prevented them from solving the problem satisfactorily.

A second, and we argue, key feature of our procedure is that apes could choose between raking or pushing the reward out of the tube. When given the choice between these two alternatives apes overwhelmingly chose the former, which is admittedly an action that they often use to get out-of-reach rewards. Moreover, previous studies had shown that primates find it difficult to push a reward away from themselves to get access to it (Köhler 1925; Guillaume and Meyerson 1930).

Interestingly, even after they had mastered the modified trap-tube task, they were still unable to solve the original trap-tube task (Visalberghi and Limongelli 1994) that required them to push the reward out of the tube. Although one could interpret this failure as evidence of lack of causal knowledge, the fact that they were forced to use a nonpreferred action makes this interpretation problematic. Having to push the reward out may complicate the problem because this action increases the distance between the subject and the reward. This may not only negatively affect the time it takes to master the task, but more importantly, it may lead subjects to engage in the search of procedural rules based on the position of the trap to solve the problem. In other words, seeing the reward go in the wrong direction may lead individuals to recur to procedural rules that may mask their knowledge about the causal structure of the problem. Analogous interference effects have been observed in other studies. For instance, a predisposition to select the largest quantity hinders the ability to engage in reverse contingency tasks (e.g., Boysen and Berntson 1995).

Our results also differed on two main aspects from those on woodpecker finches (Tebbich and Bshary 2004). First, as it was the case with the primate studies, our subjects solved the problem faster than the successful bird, which took 100 trials to master the task. Second, and more importantly, our subjects did not engage in multiple tool insertions in successful trials. Such a direct approach suggested that, unlike birds, apes anticipated the solution to the problem without the need of obtaining information via their own actions in each trial. This is not to say that birds cannot anticipate outcomes or represent certain features of tool-using problems. On the contrary, woodpecker finches and New Caledonian crows can select and fashion tools that are appropriate to get a particular reward (Chappell and Kacelnik 2002, 2004; Tebbich and Bshary 2004). Yet, there was no conclusive evidence that woodpecker finches were able to apply this knowledge to solve the trap-tube problem.

One caveat of our current results is that there were only three out of 10 subjects that mastered the task. One could argue that this outcome casts some doubt regarding the causal knowledge that these species as a whole have on the task. However, it is possible that this result reflects large individual differences in cognitive skill—something that has already been detected in previous studies (e.g., Visalberghi and Limongelli 1994; Tebbich and Bshary 2004). Not only there are large individual differences within a given task, but more importantly, individuals differ substantially across tasks. Tebbich and Bshary (2004) found important individual differences in woodpecker finches in three tool-using tasks. Similarly, some orangutans that performed well in Piagetian conservation tasks (Suda and Call 2004) performed poorly in some spatial tasks (Barth and Call, in press) whereas some chimpanzees that did well in spatial tasks did not do well in conservation tasks. There is no evidence either that experience with a previous raking task (i.e., Mulcahy et al. 2005) affected performance because orangutans with identical experimental backgrounds differed in their ability to solve the current task. Moreover, the successful chimpanzee had not even received a raking problem before, yet she performed successfully while other chimpanzees did not. This implies that observed individual differences cannot solely be attributed to motivational or experiential factors, but they may reflect genuine inter-individual cognitive differences.

Another possibility is that individuals vary on how much they are affected by a particular testing procedure. For instance, it is possible that the strong preference by some of our individuals for moving to one side (even though they were fully habituated to the testing room) may have overridden their tendency to select the correct location. Woodpecker finches and primates also display considerable variability in the way they attempt to solve the problem (Limongelli et al. 1995; Tebbich and Bshary 2004). Finally, it is conceivable that some variables such as sex or age contribute to the expression of the individual differences that we observed. Note that three of the five adolescent apes that we tested were successful while none of the four adults were. Successful apes in previous studies were also adolescent but a comparison across age is not possible because only one adult was included in those studies.

At this point we cannot decide between these alternatives and more research is needed. In addition to a larger sample of subjects, future studies should present different variations of the trap-tube task, for instance with the tool preinserted as it has been done in rooks (Tebbich et al. submitted) or without the need for tools. This latter variation could be achieved by mounting the tube on a seesaw so that the reward can be made to roll to the left or to the right by tilting the tube. Since the current study has shown that procedural modifications can have a significant impact on the abilities that subjects display, this future research would be particularly desirable.

In conclusion, two orangutans and a chimpanzee mastered a modified version of the trap-tube task faster than has been reported in previous studies with primates and birds. In addition, their exclusive avoidance of functional traps and their anticipation of the outcome of their actions indicated by the absence of multiple tool insertions within a trial suggest that they possessed some knowledge about the critical features of this problem. Future studies using different types of traps will be needed to determine how general is their knowledge regarding traps and the effect that they have on rewards that displace over them.

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