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Chimpanzees Solve the Trap Problem When the Confound of Tool-Use is Removed

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The trap-tube problem is difficult for chimpanzees to solve; in several studies only 1 to 2 subjects learn the solution. The authors tested eight chimpanzees on a non-tool-using version of the problem to investigate whether the inclusion of a tool in previous tests of the trap problem may have masked the ability of chimpanzees to solve it. All eight learned to avoid the trap, in 40 to 100 trials. One transferred to two tasks that had no visual cue in common. The authors examined the performance of 15 chimpanzees on a new task in a 2 × 2 design: seven had experience on the two-trap box, eight had not; half of each group was tested with a tool, half without one. An ANOVA revealed a significant effect of tool-inclusion and experience ($p < .05$). Our results show that including a tool in the trap problem profoundly affects the ability of chimpanzees to solve it. With regard to what the chimpanzees had learned, the results support the notion that rather than using the available stimuli as arbitrary cues, the subjects had encoded information about functional properties.

Keywords: chimpanzees, cognition, casuality, tool

The physical world is rich in information, with many environments bombarding the senses with a wealth of stimuli. Animals must somehow decipher this information to use it to guide their behavior (most obviously that concerned with locating and processing food). Evolution has provided most animals with a powerful tool that allows them to respond to changing environments: learning. The ability to associate particular stimuli and responses with a given outcome means that animals are able to tolerate changes in their environment and exploit variable sources of information that a hard-wired mechanism would struggle to process. However, many of the changing events in the physical world are underpinned by common and predictable causal structures. For example, objects always fall under gravity and will move together with others with which they are interlinked. The ability of humans to perceive and conceptualize such regularities frees their behavior from the reinforcement history of the stimuli immediately available to perception, allowing them to transfer what has been learned in one situation to a completely new one based on the same principles. Can other animals also form flexible solutions to the problems in their environment by using complex cognitive strategies like those of humans?

The majority of studies of physical cognition have been conducted on tool-using primates such as chimpanzees and capuchin monkeys (reviewed in Fujita, Kuroshima, & Asai, 2003; Povinelli, 2000; Tomasello & Call, 1997). Although many studies reveal that tool-users are capable of solving physical 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 contention (Call, 2000). Visalberghi and Limongelli (1994) examined whether or not tool-users understand causal relations, in a task that has since been widely employed: the trap-tube task. In this task, an animal must use a tool to extract a food reward from a horizontal tube, which has a trap along its length into which the food will drop if pulled or pushed over it. Only one out of the four capuchin monkeys originally tested was able to learn the solution to this task, after 100 trials. To find out whether the monkey had formed a "causal understanding" of the task's properties, or simply learned a rule of action based on an arbitrary cue, she was given a control task. In this task, the original tube is simply rotated through 180° so that the trap is no longer functional.

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The capuchin monkey persisted in her strategy of pushing the food away from the trap in the control condition, suggesting that she solved the task using a simple distance rule (Visalberghi & Limongelli, 1994). In a study by Povinelli and Reaux (2000), the one successful chimpanzee also continued to avoid the inverted trap. These findings for chimpanzees are in contrast to those of Limongelli, Visalberghi, and Boysen (1995), where the two successful chimpanzees passed a transfer task in which the trap was offset rather than being at the center, thus preventing the chimpanzees from succeeding if they were using the rule 'push from the side furthest from the food.' However, it should be noted that other rules such as 'push the food away from the trap' were not discounted (Call, 2000). A species of tool-using bird has also been tested on the trap tube problem, the wood-pecker finch (Tebbich & Bshary, 2004). One subject succeeded on the initial problem, and furthermore, she reverted to random responding on the inverted control task. However, the authors did not claim that she had formed a causal understanding; they noted the control only examined one of the rules she could have used. Furthermore, they pointed out that like the capuchin monkey (Visalberghi & Limongelli, 1994), and unlike the chimpanzees (Limongelli et al., 1995), she made multiple insertions and made careful observation of the effect of her action upon the reward. They argued that she was thus unlikely to have formed a mental representation of the task.

The results of these experiments have led some theorists to argue that nonhuman animals are incapable of reasoning about unoberservable causal forces (Povinelli, 2000; Tomasello & Call, 1997). However, we propose that two factors may have precluded investigation of the cognitive mechanisms underpinning the solution to the trap problem in nonhuman primates: the tool-using requirements of the paradigm; and the use of a problematic control task.

Tasks That Require the Use of a Tool May Have Obscured the Investigation of Physical Cognition

The performance of chimpanzees on the trap problem varies considerably when changes are made to the tool-using component of the task. Povinelli (2000) ran a trap-table study in which, rather than inserting a tool, the chimpanzees were simply required to choose one of two tools with which to pull in a food reward across a table. One side of the table contained a trap, whereas the other was a smooth continuous surface. The performance of Povinelli's seven chimpanzees on the trap-tube test was surprisingly poor: only one chimpanzee was able to learn the solution (she reached criterion after 50 trials), and four chimps never learned, despite having received 200 trials and around 70 shaping trials. In contrast, in the trap-table study, six of the seven apes were able to learn the solution within 120 trials (20 given initially, the remainder 1 year later), with one of the chimpanzees reaching the criterion in the first 20 trials. In a recent study, Girndt, Meier, & Call (in press) demonstrated further the importance of the manner of task presentation. They tested 20 chimpanzees on the trap-table problem, and reported that apes performed significantly better when they were given one tool to use, rather than a choice between two prepositioned tools. When tested using Povinelli's original set-up, the chimpanzees performed at chance, but when they were tested with just one tool, 80% of subjects raked from the correct side in their first trial.

Mulcahy and Call (2006) highlighted the fact that pushing food away from oneself (as subjects in the previous trap studies were required to) is an action rarely performed by primates in their natural habitat. In their study, Mulcahy and Call (2006) made a very simple modification to the trap-tube problem in which the tube was made wide enough for the chimpanzees to push or pull the reward with the tool. Nine out of 10 apes preferred to pull. Not only was the three successful subjects' (two orangutans and one chimpanzee) speed of learning better in this study than in previous ones (they took an average of 44 trials to reach criterion), but all of these subjects passed the inverted control task. This result raises a very important point: changing the manner of task presentation may not only allow more subjects to learn the solution, it may also impact the investigation of how they solve it.

There Are Limitations to the Inverted Control Task

This task has been described as conceptually flawed (Silva, Page, & Silva, 2005). Negative results, when subjects' continue to avoid the trap, are inconclusive because there is no cost to continuing to use this strategy. Positive results, when subjects revert to random responding (such as the woodpecker finch in Tebbich & Bshary, 2004) are also hard to interpret, as explained above. Furthermore, there are two facets to problem-solving that are worth investigating, namely, *what*, and *how*, an animal has learned (Heyes, 1993, 1998). The first is concerned with the information that predicts the outcome. Reinterpreting stimuli in terms of their functional properties can allow an animal to transfer solutions across a change in the absolute appearance of a problem. The second concerns the mechanism by which this information is processed, and feeds in to behavior (e.g., associative learning, or causal reasoning). As Heyes (1993, 1998) has pointed out in articles related to the psychology underpinning perspective-taking, these two facets are often confounded. When an animal fails a control such as the inverted trap-tube the assumption is that the animal has used arbitrary cues to form a solution based on an associative learning mechanism. However, in reality, it is unclear whether the animal's failure can be ascribed to a failure to abstract functional information from the stimuli (i.e., viewing the trap as an arbitrary cue, akin to a stop light, rather than as an impassable barrier) or from an inability to perceive the causal relationship between the trap and the loss of food.

Seed, Tebbich, Emery, & Clayton (2006) aimed to assess *what* rooks could learn about the trap problem, and tested the null hypothesis: 'a successful animal will use an arbitrary cue to solve the task.' Eight birds were tested on a version of the trap problem that featured two "traps" along a horizontal tube. A food reward was placed in between the two traps, and a stick was prepositioned inside the tube with two disks attached to it, such that pulling the stick would move the food. One of the traps, a vertical tube sealed with a black disk at the bottom, was functional and would trap the reward if the rooks pulled the food over it. The other was nonfunctional; in one design (Tube A) it was a vertical tube with a black disk at the top, which the food could pass across; in another (Tube B) it was a vertical tube with no black disk, through which the food could fall. Seven of the eight birds learned to avoid the functional trap, in between 30 and 140 trials.

All seven rooks transferred from one design to the other (once they had learned to solve Task A they immediately solved Task B and vice versa). However, both of these tasks could have been solved by learning to avoid the trap with the black disk at the bottom, without anything about the properties of the task being encoded. Therefore, the seven birds were given two transfer tasks, both featuring the two previously nonfunctional traps (pass-across or fall-through). In one design (Tube C) both ends of the tube were blocked with bungs, so the food could not be recovered from the end of the tube, and the birds needed to pull away from the trap with the black disk at the top; in another (Tube D) the tube was lowered to the surface of the testing shelf, so that the food could not be recovered from beneath, and the rooks needed to pull toward the trap with the black disk at the top to be successful. Crucially, therefore, both tasks featured the same familiar cue, but each required the opposite response to it (pull away from the black disk in Task C, pull toward it in Task D). The birds were given 20 trials on both of these transfer tasks. Six of the subjects performed at chance on both tasks, but one bird was able to solve these transfers, suggesting that she did not solve the two-trap task simply by using the appearance of the functional trap as an arbitrary cue (Seed et al., 2006).

This approach works on the premise that if the subjects simply used the visual stimuli as arbitrary cues, rather than abstracting something about functional properties, they will be intolerant to changes in the task's appearance, even if the conceptual nature of the task remains unchanged. Therefore, it is concerned with the level of abstraction with which the subjects view the stimuli (i.e., as arbitrary cues or as functionally relevant features), rather then the mechanism by which they use the information to solve the task (in other words what, not how, they learned). In this study, we will adopt a similar approach, and investigate the effect of removing both the tool-using requirements of the paradigm, and the use of a problematic control task, on the performance of chimpanzees on the trap problem.

Experiment 1: The Two-Trap Box

The aim of this experiment was to test chimpanzees on the two-trap problem without a tool, and to test any successful subjects on the transfer tasks used by Seed et al. (2006) to ascertain what they had learned. It is possible to form predictions for the results of this study with regard to each of the two major changes to the design of the trap-problem discussed above.

Removal of the Tool-Using Component

If tool-use places a cognitive load on subjects, then the chimpanzees in this experiment should perform better than the chimpanzees tested by Limongelli et al. (1995) and Povinelli (2000); more subjects should learn to solve the task, and in fewer trials.

Introduction of Transfer Tasks

If successful solutions were simply the result of using the predictive stimuli as arbitrary cues, then subjects should not solve both of the critical transfers C and D, because both feature the same familiar arbitrary cue, but each requires the opposite response.

Methods

Subjects and housing. The chimpanzees that participated in the study were housed at the Wolfgang Kohler Primate Research Centre at the Leipzig Zoo in Germany. Chimpanzees at the zoo spend the day in a 4,000 m^2 outdoor area, and a 400 m^2 indoor area, both of which have natural vegetation, climbing structures, trees, streams and other natural features, as well as enrichment facilities such as spinning treat logs and artificial termite mounds. At night they stay in a series of sleeping rooms (about 47 m^2). The chimpanzees are fed a variety of fruits, vegetables and cereals several times per day. The subjects are never food deprived and water is available ad libitum. Subjects were drawn from two groups, A and B. Group A was a stable group of 18 individuals (one adult male, six adult females, four adolescents of 7–11 years, and four youngsters of 6 months to 4 years), which have been housed together for over 12 years. Group B consisted of seven chimpanzees: three hand-raised nursery-reared juveniles (two females and one male), three adolescent females that were moved from the A group into this group in 2005, and one juvenile male that was transferred to the Leipzig zoo in 2005. Their housing conditions were similar to, although separate from, the A Group. Four subjects from the B group (Alex, Annette, Trudi, and Fifi) were tested between June and July 2005, and four from the A group were tested between April and May, 2006 (Lome, Fraukje, Patrick, and Sandra). Chimpanzees were tested in their sleeping rooms, in the morning between 8 a.m. and 12 p.m. Subjects could choose to stop participating at any time. Their ages at the time of the study and their rearing histories are shown in Table 1.

Experimental procedure and apparatus. The two-trap box (80 cm wide × 60 cm high × 10 cm deep) was mounted on the wall, inside the sleeping room (see Figure 1). The box has a transparent Perspex front. Behind it there is a 60 cm long shelf onto which the food is placed, 10 cm below the top of the box. There are vertical channels either side of the shelf, 10 cm wide. A series of rectangular openings (5 cm long, 1 cm apart) in the Perspex panel run for 60 cm in line with the shelf, which are large enough for the chimpanzees' fingers but too small for the food to pass through. Subjects can insert their fingers and move the food reward along the shelf's length to the left or the right. The configuration of the box can be changed from outside of the sleeping room by the

Table 1
Details of the Chimpanzees Tested in the Experiments Reported in This Paper

Name	Group	Age	Sex	Rearing	Experiment
Robert	A	29	M	Nursery	2
Riet	A	27	F	Nursery	2
Dorien	A	24	F	Nursery	2
Fraukje	A	29	F	Nursery	1, 2
Ulla	A	28	F	Nursery	2
Sandra	A	12	F	Mother	1, 2
Frodo	A	11	M	Mother	2
Patrick	A	8	M	Mother	1, 2
Swela	A	9	F	Mother	2
Pia	A	5	F	Mother	2
Lome	A	3	M	Mother	1, 2
Tai	A	3	F	Mother	2
Fifi	B	10	F	Mother	1, 2
Gertrude	B	10	F	Mother	1
Alexandra	B	5	F	Nursery	2
Annette	B	5	F	Nursery	1, 2
Alex	B	4	M	Nursery	1

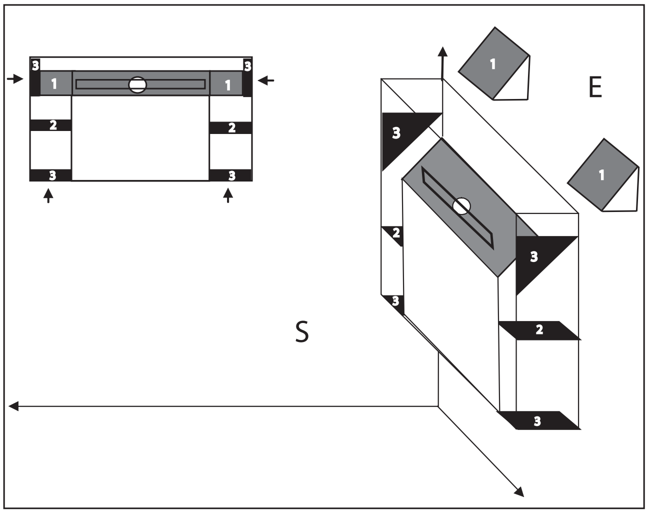

Figure 1. Apparatus used in Experiment 1. The experimental set-up is seen in isometric view, the insert shows the front view. From outside of the cage, the experimenter (E) can change the configuration of the two-trap box using pieces 1 through 3 (see text for description): (1) The gray shelf pieces; (2) the blue trap pieces; (3) the blue blocker pieces. The subject (S) can work on the food with their fingers through a series of holes in the front, shown as a continuous rectangle in the figure. In the insert the apparatus is shown with all of the removable pieces inserted, to show their potential locations, the arrows show the four exits. The isometric view shows all of the pieces inserted except for the shelf pieces, which are depicted behind the box.

experimenter through the use of removable pieces (the shelf pieces, the trap pieces and the blocker pieces), which can be inserted from the back of the box (see Figure 1). All of the pieces can be clearly seen by the chimpanzee. There are four exit holes through which the food can pass (7 cm × 7 cm). Each of these exits can be blocked with a rectangular piece of blue Perspex (the blocker pieces, 10 cm × 10 cm × 1 cm). There are two exits either side of the shelf, through which the food can be pushed out if the block that extends the length of the shelf (the shelf piece) is inserted. Additionally, there are two exits at the bottom of the box below the vertical channels either side of the shelf, through which the food will fall out if pushed off the shelf when neither the shelf pieces nor the trap pieces are inserted. The trap piece, a blue rectangular piece of Perspex 10 cm × 10 cm × 1 cm, can be inserted halfway down the vertical channels. If the food is pushed off the shelf when the trap piece is inserted, its passage down the vertical channels will be blocked. A hole in the back of the box at the height of the trap piece allows the experimenter to remove trapped food.

There were four trap box designs corresponding to Tubes A-D in Seed et al. (2006) (depicted in Figure 2). Box A features the shelf piece and the trap piece, and to retrieve the food the chimpanzees have to push the food away from the trap piece and along the shelf piece to the side exit. B features just the trap piece, and to retrieve the food the chimpanzees have to push the food away from the trap piece so that the food will fall down the unblocked channel to the bottom exit. C features the shelf piece and the side blocker pieces, and the chimpanzees need to push the food away from the shelf piece so that the food can fall down the vertical channel to the bottom exit. D features the shelf piece and the bottom blockers, and the chimpanzees need to push the food reward along the shelf piece to the side exit. The remedial training box, which was used if a subject pushed the food only in one direction for 30 consecutive trials, featured two shelf pieces and one side blocker, and gave the chimpanzees experience of retrieving the food from both sides of the box.

In each trial, the experimenter placed the blocks into the apparatus from left to right in view of the subject. The food reward was placed in the center of the shelf at the start of each trial through a hole at the back of the box. The experimenter then stood back and looked straight ahead as the chimpanzee worked on the food. The trials were recorded on miniDV video tape. In every condition, moving the food in one direction resulted in the food being trapped, and the other resulted in success. The trial was scored as correct if the subject successfully retrieved the food reward, and as incorrect if food was trapped. The direction that the subjects first pushed the food in was also coded. If subjects were incorrect then the reward was removed from the back of the box and thrown into the food bucket by the experimenter. Subjects were tested in two phases, testing and transfer.

Subjects were tested in blocks of 10 trials, and received no more than one block per day. In Phase I, four chimpanzees were presented with Box A, (Alex, Trudi, Fraukje, and Patrick) and four with Box B (Annette, Fifi, Lome, and Sandra). In both cases, the trap appeared five times on the left and five on the right in a random sequence (with the constraint that the trap was presented in the same orientation no more than twice in a row). The criterion was the same as for the rooks in Seed et al. (2006), the chimpanzees were deemed to have solved the problem if they made 15 or more correct responses over two consecutive blocks of 10 trials (which is significant according to a Binomial test with alpha set at 0.05). A criterion was used rather than testing the chimpanzees over a set number of trials to avoid habit formation, but because the probability of reaching the criterion by chance increases with the progressive number of blocks of testing, we used post hoc Monte Carlo simulations to investigate this possibility. If after 30 trials the chimpanzee had a persistent side bias (100% responses to one side), they were given 10 trials with the remedial training box (see Figure 2). If after 100 trials they had not reached the threshold, then testing ended. Subjects that successfully solved Task A were then given Task B, and vice versa, to give the chimpanzees experience of both types of nonfunctional trap. Again, the subjects were deemed to have solved the problem if they made 15 or more correct responses over two consecutive blocks of 10 trials. If after 100 trials the ape had not reached the threshold, then testing ended. If they were successful, they were given 20 trials on their original task, and proceeded to Phase II.

In Phase II subjects were presented with Tasks C and D (see Figure 2), half first on C and half first on D, and tested as in Phase I. As in Seed et al. (2006), the cue common to the boxes in Phase I, in this case the blue trap piece, was absent. Both C and D contained one familiar cue from Phase I, the shelf piece, and the unfamiliar blocker pieces that either blocked the holes at the side (C), or the holes at the bottom (D). Critically, the visual stimulus that could have been used as an arbitrary cue to solve these tasks, namely, the position of the shelf piece, was the same in both tasks, but each task required the opposite response (push away from the shelf piece in Box C, push toward it in Box D). Subjects could not,

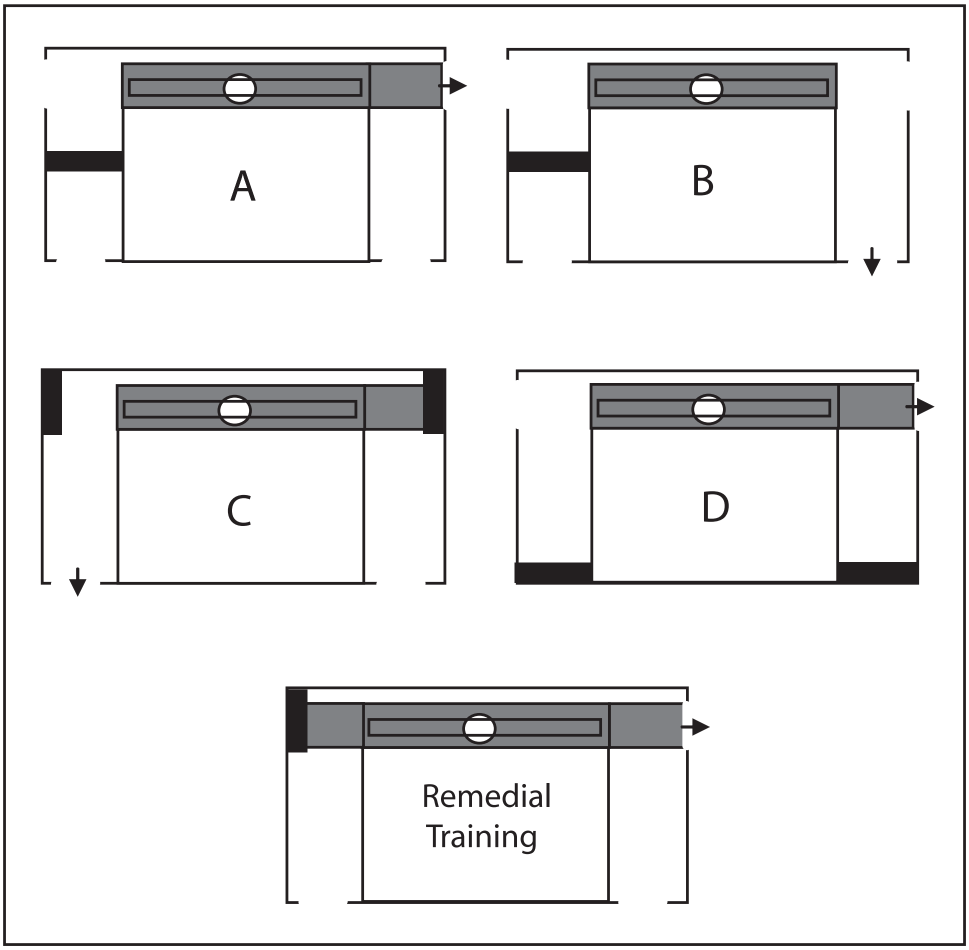

Figure 2. The two-trap box designs. The arrow shows the exit location of the food on a successful trial. Each box is shown in one of the two possible configurations, and can be set up so that the food should be pushed in the other direction. The identity of each box is given in its center. The "remedial training" box was used to correct persistent side biases after 30 consecutive responses to the same side (see Table 2).

therefore, solve both tasks through the use of a single procedural rule based on the configuration of the familiar cue. We gave the chimpanzees two blocks of 10 trials in which to achieve significance according to a binomial test (9 or 10 correct out of 10, or 15 or more correct out of 20).

Results

Phase I: Testing (Boxes A and B). All eight chimpanzees were able to solve their initial problem, although with the exception of Patrick and Fifi, all of the chimpanzees had a side bias initially, and moved the food reward in one direction only for 30 trials. These six subjects were given 10 trials on the remedial training box, to teach them that food could be recovered from both sides of the apparatus (see Table 2). After this correction, all six went on the solve the problem. Six of the chimpanzees were able to solve their second problem, but Trudi and Fraukje, who were both in the group that received Task B as their second task, did not do so in 100 trials. Their individual block-by-block performances are presented in Figure 3. Post hoc Monte Carlo simulations revealed that the performance of four of the apes on their first box was significantly different from chance. Three of the apes reached borderline significance on their first box (Annette, Alex, and Fifi, $p = .05$), and Patrick's performance tended toward significance ($p = .08$). Importantly, all of the apes passed a retest on this box after reaching the criterion on their second, within two blocks of testing, which is significant when compared to a Monte Carlo simulation. A Monte Carlo simulation gave a p value of 0.08 for Alex's performance on his second box. The performances of the other five apes that reached the criterion on their second box were significantly better than chance (Monte Carlo simulations, $p < .05$).

There was no significant difference between the mean number blocks taken to reach criterion on the second box each subject received, as compared to the first one (Wilcoxon signed-ranks test $t = 13.5$, $p > .05$, $n = 8$). However, regardless of the order of presentation, the subjects took fewer trials to reach criterion on Box A then Box B (Wilcoxon signed-ranks test $t = 0$, $p < .01$, $n = 8$). A summary of the performance of each subject in terms of the number of blocks taken to reach criterion, and whether or not remedial training after 30 trials was required, is presented in Table 2.

Table 2
Individual Performance in Experiment 1. 'T' Denotes That 10 Training Trials Were Given After 30 Side Biased Responses in This Task

		Phase I: Blocks to criterion		Phase II: Prop. of correct trials	
Subject	Order	A	B	C	D
Alex	ABCD	5 T	6	0.55	0.8
Patrick	ABDC	6	10	0.55	0.55
Fraukje	AB	5 T	—	—	—
Trudi	AB	5 T	—	—	—
Annette	BACD	4	5 T	0.9	1
Lome	BACD	4	10 T	0.45	1
Fifi	BADC	2	10	0.75	1
Sandra	BADC	4	7 T	0.65	1
Means	—	4.4	8.6	0.64	0.89

Phase II: Transfer (Boxes C and D). All six chimpanzees tested in this phase with the exception of Patrick were able to transfer to Box D within 20 trials. However, only two chimpanzees, Annette and Fifi, were able to solve Box C, Annette scored 9 out of 10 correct; Fifi scored 15 out of 20. Table 2 shows the individual results beside their performance on Tasks A and B, Figure 4 shows their block-by-block performance.

There was no significant difference between the mean number of trials correct out of 10 on the second box each subject received, as compared to the first one ($t = 6.5$, $p > .05$, $n = 6$). However, regardless of the order of presentation, the subjects scored significantly more trials correct on Box D then Box C (Wilcoxon signed-ranks test $t = 0$, $p < .05$, $n = 6$, Table 2).

Discussion

It is clear from the results of this experiment that changing the way in which the trap problem is presented has a profound impact on the ability of chimpanzees to solve it. In stark contrast to previous studies, 100% of the eight subjects tested in this experiment were able to learn to avoid moving a food reward into a trap, and all eight subjects learned to do so in 100 trials or less (although after 30 trials six subjects needed 10 trials with the remedial training box to correct their side bias). The success rate and speed of learning from this experiment is therefore comparable to that shown by the rooks on the two-trap tube task (Seed et al., 2006). A more detailed analysis of the performance of the chimpanzees, with comparisons drawn to the performance of the rooks may shed some light on similarities and differences between their strategies. The testing and transfer phases will be examined in turn.

Phase I: Testing (Boxes A and B). Only one of the chimpanzees was able to transfer immediately from the first task to the second (Fifi). In contrast, the rooks that learned to solve Task A were able to transfer immediately to Task B, and vice versa. It is clear that the chimpanzees did not base their solution on the presence of the blue trap piece in Boxes A and B as the sole cue when solving their initial tasks, because had they done so, they would have been able to transfer from A to B and vice versa (as this cue was common to them both). In contrast, it seems that all of the rooks with the exception of Guillem used the appearance of the functional trap to solve Tasks A and B.

The chimpanzees took significantly more blocks to solve Box B than Box A, regardless of the order of presentation (no such difference was shown by the rooks). There are three possible reasons for the fact that the chimpanzees performed better on Box A than on Box B. The first is the difference in the amount of available *tactile information.* Although the only discriminatory stimulus in Box B that can be used to solve it is the blue trap, Box A also contains the piece of shelf across which the food can pass to the opening. This is a tangible cue that can be touched. All of the chimpanzees had to touch the piece of shelf in Box A when recovering the food reward from the side opening. The second difference between boxes A and B involves c*ontiguity.* The piece of shelf may have been a more salient discriminatory cue because its proximity to the hole from which the chimpanzees retrieved the food put it in closer spatial and temporal contiguity with the rewarding outcome. The importance of close contiguity between stimulus and outcome for effective learning has been well documented (Dickinson, 1980). Third, the fact that the training box also featured the continuous piece of shelf might have meant that it facilitated acquisition of Task A but not B.

Phase II: Transfer (Boxes C and D). Four of the six chimpanzees tested in the transfer phase were not able to solve both Box C and Box D, similarly to six of the seven rooks. Therefore, it seems that, like the rooks, the majority of the chimpanzees did not form a robust understanding of the physical properties of the task during the testing phase. However, all of the six chimpanzees tested on the transfer tasks were able to solve Box D except Patrick, whereas with the exception of Guillem, all of the rooks performed at chance level on both Tube C and Tube D. Although six of the seven rooks seem to have used a rule that relied on the appearance of the functional trap, the chimpanzees seem to have attended to the side of the box from which they obtained the reward, using rules such as push toward the shelf piece or toward the clear channel. Indeed, with the exception of Annette, all the chimpanzee subjects tested in the transfer phase pushed the reward along the shelf piece for the first five trials in Task C, which supports the notion that they had continued to use a procedural rule of the form 'push toward the shelf piece'. Only Fifi pushed the food reward in the correct direction in the remaining 15 trials, making her performance on this task statistically significant. Therefore, she passed both Task C and Task D. However, the fact that in Task C she always started the trial by pushing the food in the incorrect direction (changing direction before the food fell into the trap) makes her performance less convincing. Annette was the only chimpanzee to solve both tasks in the first 10 trials like the successful rook, Guillem, who scored 9 out of 10 on Task C, and 10 out of 10 on D. Note that she always pushed the food in one direction only. What can we conclude from this experiment with regard to our initial predictions?

Removal of the tool-using component. The chimpanzees in this experiment did perform better than the chimpanzees tested by Limongelli et al. (1995) and Povinelli (2000); more subjects learned to solve the task, and in fewer trials. It therefore seems that using a tool does place a cognitive load on subjects independent of the processing requirements of the task at hand. However, there are several differences between the two-trap box and the traditional trap tube aside from the tool-using component, and so this hypothesis will be tested further in the next experiment.

Introduction of transfer tasks. The results of just one or two subjects must be interpreted with caution, however, we argue

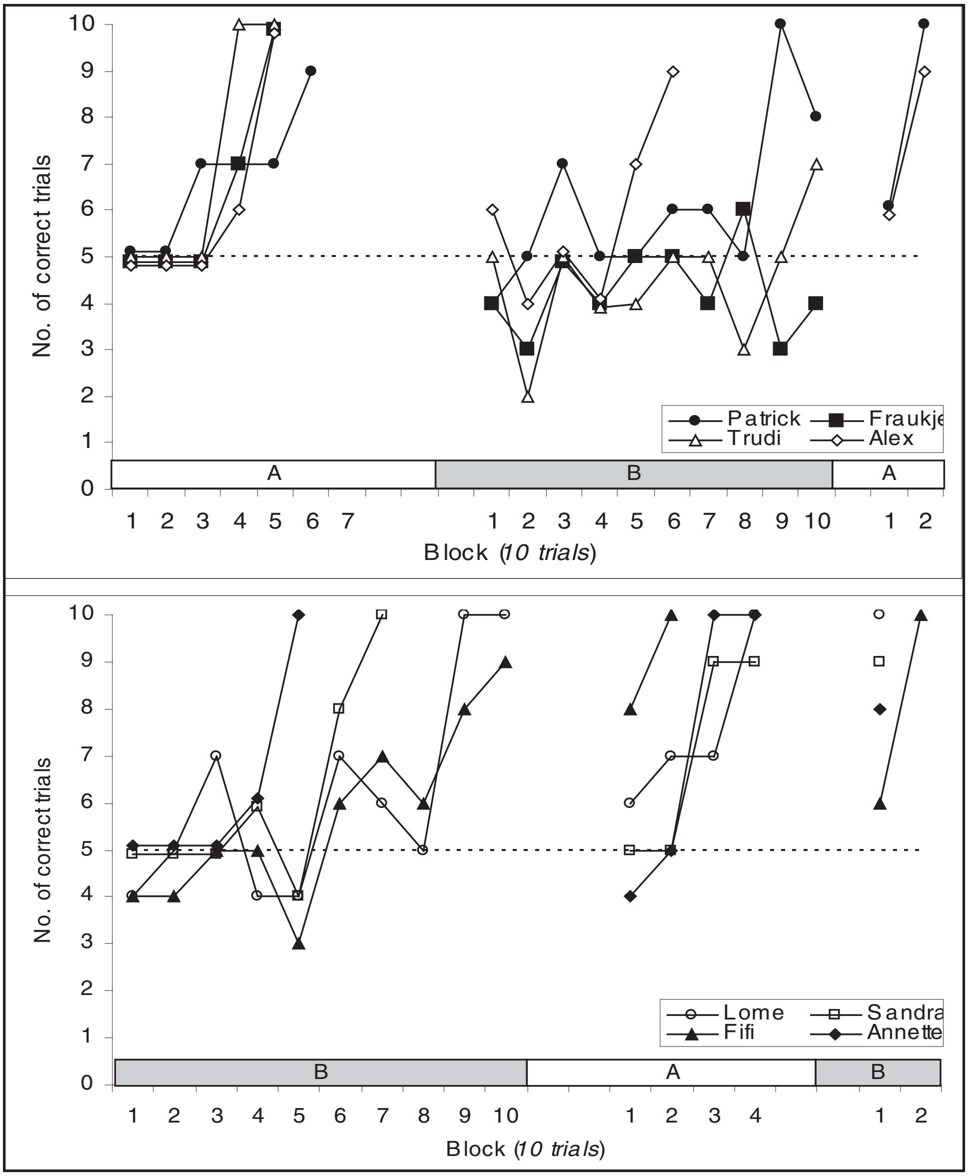

Figure 3. Individual Results from Experiment 1, Phase I (Boxes A & B). The top graph shows those chimpanzees that received A then B, the bottom graph shows those that received B then A. The horizontal dotted lines show chance performance (5 out of 10 correct).

that relationships between arbitrary stimuli (such as the blue line, or the gray block) and responses (push the food to the left or the right) could not account for the ability of Annette to respond correctly when the familiar stimuli required two different responses depending on the presence of novel obstacles (the blocker pieces). Instead, we hypothesize that she had encoded functional information, concerning features such as the solid and continuous shelf and the inability of objects to pass through barriers such as the blockers. However, only the minority of subjects behaved in a way that is consistent with this hypothesis, and the differences between the different boxes were small (the position of familiar cues such as the blue blocks), and so further work will be needed to test this hypothesis. This question will therefore also be addressed in the next experiment. It should also be noted this hypothesis is concerned with the way in which animals parse the stimuli in the environment, rather than the psychological processes by which they use these stimuli to direct their behavior (e.g., associative learning vs. reasoning). More experiments are needed to address the psychological mechanisms underpinning the flexibility displayed by the successful chimpanzees, as well as the successful rook.

Experiment 2: Reintroducing a Tool

The fact that the chimpanzees in the previous experiment were able to act on the food reward directly, rather than using a tool, was

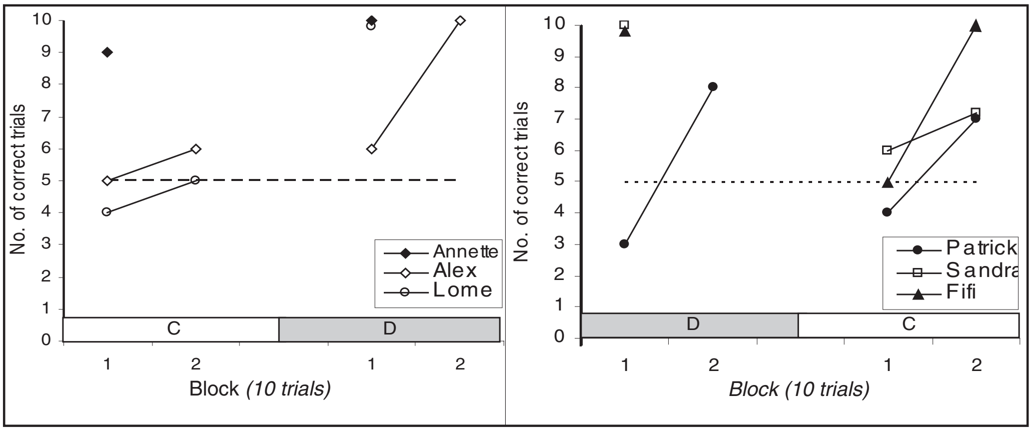

Figure 4. Individual Results from Experiment 1, Phase II (Boxes C & D). The left graph shows data from chimpanzees that received C and then D, the right graph shows those that received D first. Subjects are shown by the same symbols as used in Figure 3.

arguably the most conspicuous difference between the two-trap box and the other trap problems used to test chimpanzees. However, it would be premature to ascribe the difference in performance to the removal of the tool-using component of the task, because other features of the apparatus differed from that used in previous studies, for example, the use of opaque rather than transparent materials for the substrate on which the food rested, or the ease with which the chimpanzees could make a tactile exploration of some the functional parts of the task. Alternatively, perhaps the eight subjects tested would have been capable of solving the problem no matter what the mode of presentation. In this experiment, we directly tested the hypothesis that including a tool in a cognitive task makes it harder to solve, by comparing the performance of chimpanzees with and without a tool on the same task.

We compared the performance of the subjects that solved the two-trap box task and inexperienced subjects on a novel test of the trap problem, one conceptually identical to the two-trap box. Half of each group was required to use a tool, and half was not. This 2 × 2 design allowed for an investigation of the interaction between two variables: tool-use and experience, resulting in four groups: Experienced + No Tool (E + NT); Experienced + Tool (E + T); Inexperienced + No Tool (I + NT) Inexperienced + Tool (I + T). Why compare naïve and experienced subjects? There was the intriguing possibility that one chimpanzee, Megan, in Povinelli's (2000) experiment had learned something in the first test that transferred to the second one, despite the lack of visual constants, as she was the only successful chimpanzee from the initial trap-tube test, and she was the only subject to solve the trap-table problem in the first 20 trials. By comparing naïve and experienced subjects on the same task, we can investigate whether or not the chimpanzees from the previous experiment had learned something about the task's physical properties, such as the solidity of barriers and the continuity of surfaces, which would allow them to transfer to a perceptually distinct task. Furthermore, a 2 × 2 design allows an assessment of the impact of introducing tool-use to any such transfer. The different models for explaining the performance of chimpanzees on traditional tool-using tasks yield different predictions for the results of this experiment.

Abstracting Information About Functional Object Properties: E > I

The results of the transfer tests in the previous experiment led us to reject the idea that the chimpanzees had simply used the predictive stimuli as arbitrary cues when forming their solution. If this was the case, then experienced subjects should perform better on this new task than the inexperienced subjects, that is, more should be able to solve the task, and in fewer trials.

Using the Stimuli as Arbitrary Cues: E = I

If, on the other hand, the chimpanzees had based their solution to the previous task on associations between arbitrary cues and responses, then a new set of stimuli should result in the task being solved equally well by experienced and inexperienced animals alike.

Tool-Use Imposes a Cognitive Load: NT > T

If tool-use places a cognitive load on subjects, then it should impair performance on a task that requires cognitive processing. If it does not, then there should be no significant difference between performance with and without a tool. How such an effect would interact with experience is an open question, though it seems logical that an additional load on subjects' cognitive systems would interfere both with the acquisition and transfer of information.

Methods

Subjects and housing. Seven subjects were "Experienced" with respect to the two-trap problem from previous experiments (including Experiment 1); three of these were tested without a tool (E + NT: Fifi, Alexandra, Annette) and four with one (E + T: Sandra, Patrick, Lome, and Fraukje). Alex, the eighth subject, was involved in serious bouts of aggression from the other male in his group and was excluded from the study. All of the experienced subjects had solved the two-trap box in one configuration, and all but Fraukje had solved both Tasks A and B. The average number of trials to reach criterion on the tasks was 5.8 for E + NT, and 6.3

for E + T. A further eight subjects from the A group were tested (see Table 1). These made up the "Inexperienced group" and were divided into two groups, four tested without a tool (I + NT: Pia, Robert, Dorien, and Riet), and four with a tool (I + T: Frodo, Swela, Ulla, and Tai).

Experimental procedure and apparatus. The apparatus was a flat version of the two trap tube that incorporated some of the design features of the two trap box, allowing it to be mounted on the inside of the cage (see Figure 5). It was made of transparent Perspex, with the solid bottom surface shaded in black. The "tube" was square so that it lay flush with the panel, to prevent the chimpanzees from snapping the traps from the apparatus. The working part was 0.5 cm deep, but the apparatus had to be mounted on a 10 cm projection for it to be of sufficient distance from the edges of the panel for the chimpanzees to insert a tool into the sides of the tube. This projection contained channels that allowed the experimenter to add and remove the food from the tube. The tool itself was a thin piece of dowel, around 15 cm long. There were small holes at the top that the tool could be inserted into. These were added to the design because one of the subjects, Tai, was unwilling to use the tool from the sides of the tube. She would use a small tool to work on the food from the top of the tube, and was the only subject to use these small holes.

The configuration of the apparatus could be changed from the back of the panel by the experimenter without having to send the chimpanzee away. As in Experiment 1, removable pieces were used to form the different configurations. Black pieces of Perspex, 4 cm wide × 2 cm deep × 0.5 cm high could be inserted either at the top or the bottom of the traps. They were mounted on 10 cm clear Perspex handles to allow the experimenter to reach the tube through the projection to insert the pieces. The pieces were inserted at the bottom of the traps to form the functional trap in designs A and B, and at the top to form the nonfunctional trap in design A. In design B, the nonfunctional trap had no piece inserted, so the food could fall through it. In each trial, the experimenter placed the pieces into the apparatus from left to right in view of the subject. The food reward was placed in the center of the tube at the start of each trial. The experimenter then stood back and looked straight ahead as the chimpanzee worked on the food. The trials were recorded on miniDV video tape. In every condition, moving the food in one direction resulted in the food being trapped, and the other resulted in success. The trial was scored as correct if the subject successfully retrieved the food reward, and as incorrect if the food was trapped. The direction that the subjects first pushed the food in was also coded. If subjects were incorrect then the reward was removed and thrown into the food bucket by the experimenter. The subjects were given 10 trials a day, almost daily. Subjects in E + T and I + T were tested between May and June 2006, subjects in E + NT were tested between June and July 2006, and subjects in I + NT were given two blocks of trials in July 2006, before an unavoidable interruption halted testing. Testing continued in January 2007.

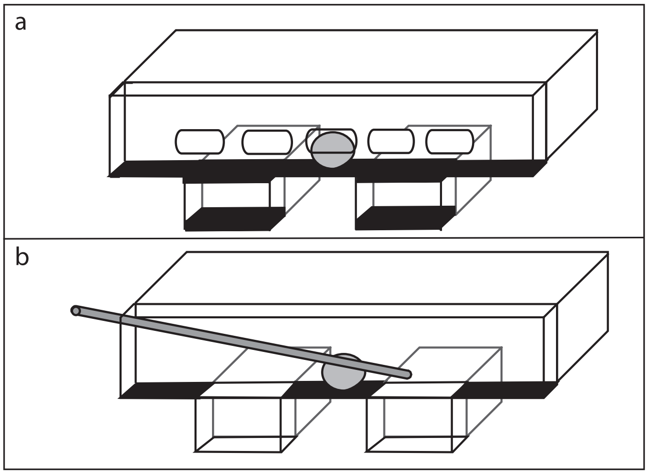

Figure 5. Apparatus used in Experiment 2. Panel a shows the 'No-Tool' set-up, with all of the removable pieces inserted, to show all of their possible locations (see text for description). Panel b shows the "Tool" set-up, with none of the removable pieces inserted.

Results

Seven of the eight inexperienced chimpanzees did not learn to solve the task in 150 trials, either with a tool or without one. Pia, in the I + NT group, did learn to solve the task according to our criteria, in six blocks of trials, but the post hoc Monte Carlo simulation revealed her performance to be a trend ($p = .08$). Strikingly, the experienced chimpanzees that did not have to use a tool (E + NT group) all solved the task within four blocks. In all cases their performances differed significantly from chance (Monte Carlo, $p < .05$). In contrast, in the group of experienced chimpanzees using a tool (E + T group), only two subjects were successful, after 110 and 120 trials using our criteria, and their performances were not statistically different from chance when compared to the Monte Carlo simulation ($p = .29$ and 0.35, respectively). Both of these subjects were tested with Task B. Figure 6 shows the pattern of individual responding.

We used a two-way ANOVA to examine the effect of the two variables (tool and experience) on performance, as measured by the number of blocks taken to reach criterion (with those subjects that did not learn being ascribed a value of 17, the minimum number of blocks in which they could have reached criterion). There was a significant effect of experience ($F_{(1,12)} = 14.78$, $p < .05$); of including a tool ($F_{(1,12)} = 14.78$, $p < .05$), as well as a significant interaction ($F_{(1,1)} = 5.1$, $p < .05$). Table 3 shows the pattern of results.

Discussion

It is clear that this task was a difficult one to learn: only one of the inexperienced subjects was able to do so in 150 trials. This makes the difference between the experienced and inexperienced subjects a striking one, as despite this evidence of task difficulty, the experienced subjects that were not using a tool (E + NT) were able to solve this test remarkably quickly, making just 5.7 errors on average before reaching criterion. The effect of experience on performance on this task is clear. There was also a significant effect of the inclusion of a tool. Unlike the E + NT group, only two of the subjects in the E + T group were able to solve this new task, and furthermore, these two took more trials to do so. Similarly, the one inexperienced subject that was able to learn to solve the task (Pia) was in the group that did not have to use a tool. Monte Carlo simulations revealed that the performances of subjects in the E + T group may be explicable by chance.

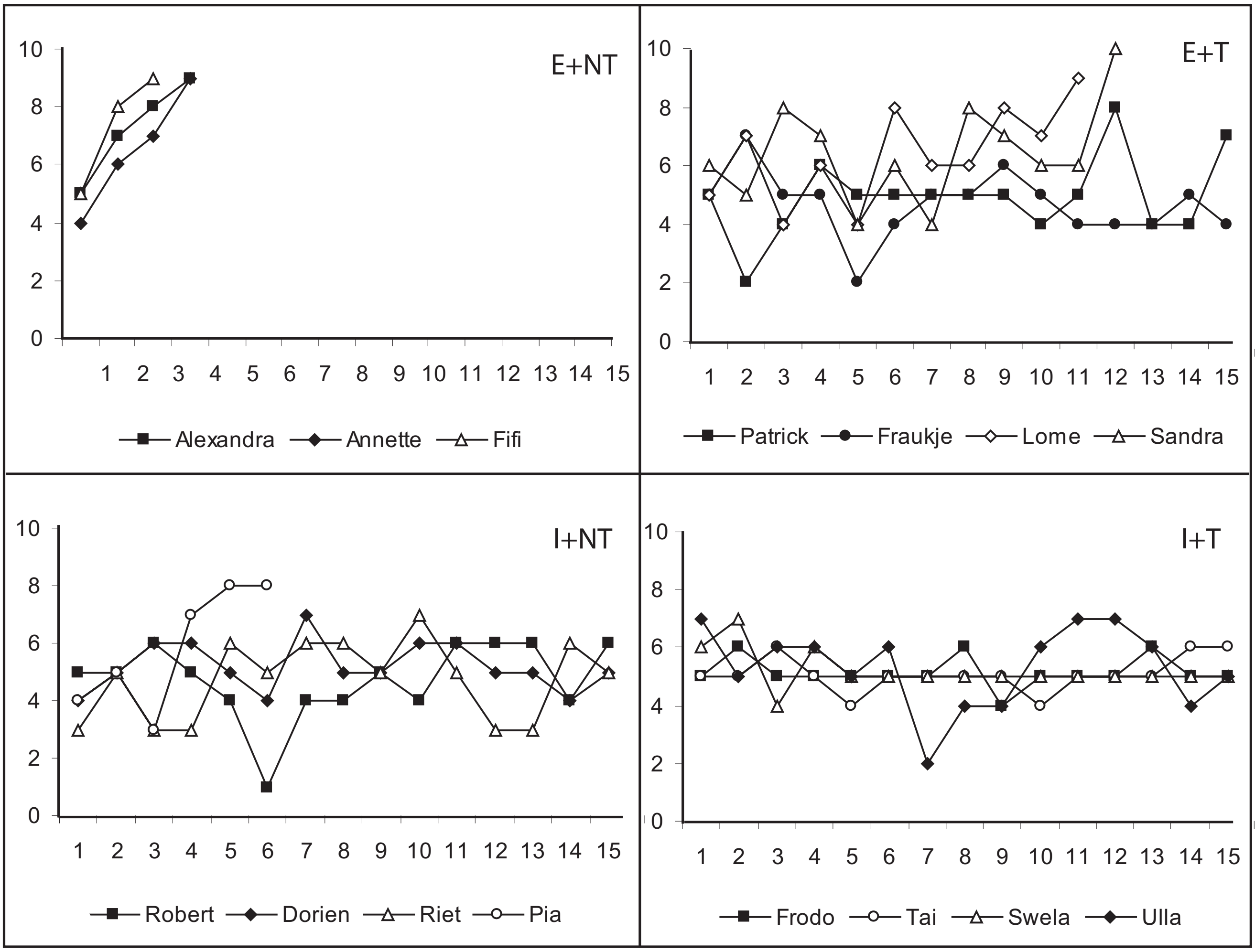

Figure 6. Individual results from Experiment 2. The four graphs show data from the four groups, the identities of which are given in the top right hand corner. Results from Tube A are shown in solid points and results from Tube B are shown in open points.

Importantly, whether these subjects are regarded to have passed or failed, the results of the ANOVA are unaffected. The implications of these two findings are discussed below.

Experience. There has been much suggestion that the physical cognition of primates, in particular chimpanzees, features mental representation, which is usually operationally defined as the ability to solve a novel problem without extensive trial and error. Tomasello and Call (1997) identify evidence from observational studies of chimpanzee tool use to support this. There are several accounts of the apes deploying a tool-using technique in a situation that field workers can be almost sure is novel. In one such example, Goodall (1986) reported that chimpanzees at Gombe used sticks to open human-made boxes, which was a novel task to them. However, the authors note that it is hard to be confident in the conclusions drawn from such studies in the absence of experimentally controlled settings. Similarly, Povinelli, while concluding that there was no evidence that chimpanzees use information about unobservable phenomena to guide their behavior, suggests that "... chimpanzees form principles of folk physics that are grounded to the world of visual images" (Povinelli, 2000, p. 309).

The chimpanzees in Povinelli's studies never passed all of the transfer tests that they were given, and so did not demonstrate a robust, human-like understanding of the unobservable causal forces involved in the tasks. However, on many occasions, one or two of the chimpanzees did immediately solve some novel configurations of the problems. The difficulty in interpreting these findings is that it was often unclear that the subjects were exhibiting anything other than an idiosyncratic perceptual preference for one of the two options pre-

Table 3
Results of Experiment 2

		No. of successful subjects	No. of blocks to criterion (mean ± *SE*)
Experienced	No tool	3/3	3.7 ± 0.33
	Tool	2/4	14.25 ± 1.6
Inexperienced	No tool	1/4	14.25 ± 2.75
	Tool	0/4	17 ± 0

sented, or that they were continuing to employ a procedural rule based on some perceptual constant between the task being faced, and one of those faced previously.

The current experiment, however, directly compared the performance of subjects that had been given the opportunity to learn about relevant functional properties (such as the discontinuity of the surface on which a reward was resting, and the solidity of a trapping structure) on a novel task, with those that had not had such an opportunity. The greatest advantage of such an approach is that it does not depend on immediate success, or significant performance over a very small number of trials, such as the 8 trials usually employed by Povinelli, for the demonstration that the subjects have learned something more abstract about the properties of the stimuli than simply using them as arbitrary cues to solve the problem. Subjects may fall short of such a steep criterion for reasons unrelated to the cognitive ability under question, and given the number of "mistakes" that adult humans make on similar tasks (Silva et al., 2005; Silva & Silva, 2006), these errors might not reflect an inability to represent functional properties. The between-subjects comparison gives a baseline indication of how quickly a new task can be acquired in the absence of experience, and how likely it is that a good performance can result from an idiosyncratic preference for one of the two stimuli.

The results of this experiment reveal that chimpanzees with experience of solving the two-trap problem are capable of rapidly solving it in a visually distinct form. The results of the inexperienced subjects strongly indicate that reasons unrelated to experience, such as perceptual preferences or rapid trial-and-error learning based on the new arbitrary cues could not explain the results of the experienced subjects. Their transfer to this new task suggests that they had not solved the two-trap box task simply by treating the predictive stimuli as arbitrary cues (e.g., a blue line). Instead, it supports the notion that they had used some form of mental representation: a reinterpretation of the stimuli that could be transferred to the new task. However, the results of this experiment do not reveal the content of such a representation. While one possibility (and our hypothesis) is that they had abstracted functional information, another is that they had generalized along some other, arbitrary parameter (such as equating blue lines to black lines and responding differentially to them). Further work, comparing the performance of experienced subjects on novel tasks that are either functionally, or conceptually identical (such as this one), and tasks that feature arbitrary similarities, such as patterns of horizontal and vertical lines either side of a food reward, may shed some light on this issue.

It is possible that other aspects of experience with the task might have facilitated better performance besides abstraction of functional information. The experienced animals might have learned to inhibit certain kinds of detrimental responses, or they may have learned to examine the task more carefully. We think that such general effects of testing are unlikely to explain the large difference in performance between the experienced and inexperienced subjects, because all of the chimpanzees in Leipzig have been extensively tested on a large number of social and physical tests, and any such "learning to learn" effects should be seen across subjects, or perhaps vary with age, or number of tests participated in. Ideally, however, we would need to test a further group on the two-trap tube, with experience on a perceptually similar but conceptually different test, to reinforce our conclusions. Unfortunately, this was not possible with our sample size.

Tools. The "floor effect" demonstrated by the results of the inexperienced chimpanzees on this problem, while giving a very clear indication that neither perceptual preferences nor rapid learning based on the new arbitrary cues could explain the results of the experienced subjects, precludes investigation of the effect of including a tool during the acquisition phase of a new problem. The one subject that was able to learn was in the "No Tool" group, but it is difficult to interpret this finding, given that none of the other three subjects in the I + NT group were able to learn. It is impossible to know the reasons for the difference between the difficulty of this task and the two-trap box. One possibility is that the 10 cm projection that put the task far enough into the cage for the chimpanzees to use a tool was distracting. Another is the increased use of transparent materials, which do not exist in the natural world of chimpanzees.

The use of a tool did have a significant effect on the performance of the experienced subjects. This result is unlikely to be because of the increased motor difficulty of the action per se, because the chimpanzees were highly dexterous and skilled when using the tool, and were able to move the food both by raking and pushing from each side of the apparatus. We suggest that the results support the idea that tool-use places a cognitive load on chimpanzees, independent of the cognitive challenge of solving a task involving tertiary relations between external objects. The exact nature of this challenge will be an interesting question for future research.

General Discussion

The results of this study support the notion that the inclusion of a tool in the trap problem confounds the examination of both its solution and the cognition underpinning its solution. By testing chimpanzees without a tool, we have found that they are capable of solving trap problems with far greater ease than has been previously thought. Furthermore, we have provided evidence to support our hypothesis that the successful subjects did not treat the predictive stimuli as arbitrary cues but instead formed mental representations of their functional properties. We suggest that tool use is an activity that imposes cognitive demands of its own. Byrne (2004) has identified a number of features of the complex manual skills of great apes (including tool-use) that are likely candidates for requiring cognitive governance, such as precision handling, bimanual role differentiation and hierarchical organization involving subroutines. Three factors that might contribute to a cognitive load imposed by tool-use are proposed below: (1) a load on the attentional system; (2) cross modal matching; and (3) increased response variability.

First, even a simple tool-using task is likely to place a load on the attentional system, because unlike the automatic movements of the hands, manipulating a tool to bring about an effective action will require increased attention. The amount needed is likely to depend on the complexity of the task, and the degree of familiarity with the tool-using action required. Moreover, the need to split attentional focus between the end of the tool that is held by the chimpanzee, the end that contacts the food, and any relevant features of the substrate on or in which the food rests (such as a trap) may be a further challenge. This factor is likely to be of particular importance when learning a new technique, when specific discriminatory stimuli must be attended to for a solution to be found.

Second, the ability to infer functional properties through the visual modality may involve some cognitive skill. Chimpanzees are capable of cross-modal matching, in other words, recognizing that an object detected through one sensory modality (such as touch) is equivalent to the same object detected through another (such as sight) (Davenport, 1976). However, inferring information about an object's functional properties from its visual appearance may be a steeper cognitive challenge. After all, one can only be sure that an apparently solid object constitutes a functional barrier through experience; plastic and tissue paper may appear similar when detected visually, but they are very different to touch, and therein lies the functional difference. If an animal is required to use a tool to act on a task, it usually means that it cannot touch some aspects of the task. If it is to use functional information, it must infer this information through visual perception. In some tool-using tasks, such as ant dipping or termite fishing by chimpanzees, even this information is not available. This factor is likely to be most important when a novel task is encountered that has not been explored through another sensory modality.

Third, there may be considerable variation between individuals in the way in which a tool is employed to achieve a given end. For example, in the case of a trap task, both pushing the reward from one side, and raking it from the other could move it away from a trap. The tool could be held in the left or the right hand; it could be held at a variety of different angles. Scope for variety is present in any manual task, but is almost certainly increased when a tool is introduced. As a consequence, the executive brain will be faced with a greater number of decisions. Furthermore, during learning, a wide range of different actions might be equally rewarded, meaning that the learning animal must sort the relevant differences (e.g., in the trap problem moving the food left or right) from the irrelevant ones (manipulating the tool at an acute or an oblique angle).

Examining these three hypotheses systematically is likely to shed light on the types of minds that are capable of different tool-using tasks. For example, varying the length of the tool may shed light on the impact of splitting attention; varying the degree of tactile exploration possible could reveal if cross-modal matching plays a role; and tool-using tasks can be compared with manual tasks of varying degrees of complexity to investigate the impact of response variety. Isolating the importance of the different specific demands of tool-use will give us insights into the limitations of this ability in nonhuman animals. Furthermore, such an investigation would reveal which facets of tool using in early hominids would likely have necessitated a change in cognition, and the likely nature of that change (e.g., increased executive control, broader attentional focus). Meanwhile, using tasks that isolate the cognitive challenges of representing the properties of objects and the interactions between them, from the challenges of tool use, will give us a better understanding of the ability of nonhuman animals to do so. An important advantage of this development is the fact that it will also allow for more meaningful comparisons with non-tool-using species (such as non-tool-using primates, and corvids such as rooks), which is another avenue for future research.

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