What Do Bonobos (*Pan paniscus*) Understand About Physical Contact?

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The present study aimed to test what bonobos (*Pan paniscus*) understand about contact. The task consisted of a clear horizontal tube containing a piece of food and a stick with a disk attached. The bonobos chose which side to push or pull the stick for the disk to contact the food and make it accessible. There were 9 variations in tube design, which differed in the positions of the stick, disk, and food. All 5 bonobos passed at least 1 configuration. A recent study (A. E. Helme, N. S. Clayton, & N. J. Emery, 2006) found that rooks could learn only tube configurations that provided an asymmetrical stick cue, whereas bonobos did not demonstrate an understanding of contact but showed more individual variation, attending to the positions of the food, disk, and stick.

Keywords: physical cognition, bonobo, connectedness, contact, ape

The cognition underlying tool use in bonobos (*Pan paniscus*) has been studied in little detail. In the wild, several cases of tool use have been documented, such as the use of leafy twigs for rain cover or napkins, sticks as flyswatters or scratchers, and other tool-related behaviors such as branch-waving, branch-dragging, bridging, and making seats from vegetation (Hohmann & Fruth, 2003; Ingmanson, 1996; Kano, 1982). However, it has been suggested that bonobos in the wild more often use objects in social situations as a means of manipulating other individuals than as a means of gaining food (Ingmanson, 1996). Therefore, bonobos may have different expectations about the causal effects of tools compared with species that tend to use tools for foraging. In comparison with chimpanzees, tool use appears to be underrepresented in bonobos, although the reasons for this are not clear. One possible reason is that bonobos may not need tools for food extraction because they gain a sufficient amount of food that is more easily accessible. They also may not have access to suitable tool material, for example, sufficiently hard stones with which to crack nuts (Hohmann & Fruth, 2003). The bonobos' lack of tool use can be contrasted with chimpanzees, which use sticks for termite fishing and digging and stones and anvils for cracking nuts (McGrew, 1992). Consequently, bonobos might have a less sophisticated understanding of the physical properties of tools than those species that use tools to a greater extent.

Bonobos also use tools in captivity. For example, objects are waved to attract attention, prod conspecifics, create noise, and scoop water, and materials are used to wipe themselves and absorb water (Jordan, 1982). Other more sophisticated techniques include making ladders (Gold, 2002) and using sticks to dig out raisins (A. E. Helme, personal observation, April–June, 2005). Four bonobos were tested for their ability to extract a food reward from a transparent tube by using a stick to push it out; all performed successfully (Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995). Therefore, bonobos may have the capability to understand the functional properties of tools, but such abilities are rarely required in their natural environment. As some bonobos can use sticks to obtain food, they may appreciate the causal processes underlying tool use; however, they may also simply associate the use of a stick with a food reward.

The current study involved the use of an in situ tool to extract food from a transparent tube. To perform this task efficiently, the bonobos needed to have some understanding of the way that the tool and food needed to contact each other. Previous experiments investigating contact and connectivity have been performed on various species. These experiments fall into two general categories, support-based tasks and raking tasks, yet they all involve the idea of contact between two objects or an object and a reward. Support experiments are based on a paradigm developed by Willatts (1984), which involves pulling a tool, for example, a strip of cloth on which rests a food reward. To solve these tasks, the subject must discriminate between conditions in which the reward is on the cloth compared with next to the cloth. An early study demonstrated that macaques, capuchins, a gorilla, and a chimpanzee were able to perform this task by choosing the cloth with the reward on it (Spinozzi & Potì, 1989, 1993). Non-tool-using tama-

rins were able to successfully learn this distinction, in addition to being able to learn that the functional cloth must be continuous and not broken (Hauser, Kralik, & Botto-Mahan, 1999). Similarly, tool-using chimpanzees could appreciate the need for contact between a food reward and the platform on which it rests, yet not between a peg on the platform and the tool used to gain access to the platform (Povinelli, 2000). In a study that recorded looking time, Cacchione and Krist (2004) found that chimpanzees appreciated the need for a certain amount of contact between objects when one was supporting the other, but not for where that contact had to be, that is, one object should be on top of the other. Some non-tool users learn to retrieve food attached to the end of a piece of string (dogs: Osthaus, Lea, & Slater, 2005; parakeets: Funk, 2002; and ravens: Heinrich & Bugnyar, 2005); however, only the ravens may have responded to the functional connection between the string and the reward.

The second type of experiments requires the use of a tool to rake a food reward toward the subject. Solution of these tasks requires discriminating between tools that would achieve this function and those that would not. Tool-using chimpanzees and capuchins, and non-tool-using macaques, tamarins, marmosets, and a gorilla have all been tested for their understanding of physical contact by using rakes or hook-shaped tools (Cummins-Sebree & Fragaszy, 2005; Fujita, Kuroshima, & Asai, 2003; Hauser, 1997; Natale, 1989; Povinelli, 2000; Spaulding & Hauser, 2005). In no experiment did a species demonstrate an immediate understanding of the problem or the concept of contact, but once subjects had learned to discriminate between functional and nonfunctional tools, some could generalize to novel tools by attending to their functional features, such as shape and material. These previous experiments suggest that being a natural tool user is not necessary for the ability to learn about the functional properties of tools. However, Helme, Clayton, & Emery (2006) found that non-tool-using rooks (*Corvus frugilegus*) did not demonstrate an understanding of contact in a task that required the rooks to pull sticks to extract food from a transparent tube. However, the rooks did demonstrate rapid associative learning and paid attention to the specific visual cue of stick length asymmetry.

The current experiment was designed to allow a direct comparison of the ability of two evolutionarily distinct species to learn how to solve a physical task. Comparative studies on such evolutionarily diverse groups of animals may reveal similarities in the selection pressures driving the evolution of intelligence. It is especially relevant if the animals possess common features thought to be important for the evolution of complex cognition, such as large relative brain size (Lefebvre, Reader, & Sol, 2004; Reader & Laland, 2002), a long developmental period (Iwaniuk & Nelson, 2003), and life in a complex social group (Humphrey, 1976). Although the brain structure of corvids and apes is very different, with the former (nidopallium) having a nuclear structure and the latter (neocortex) a laminar structure, these families appear to possess similar types of intelligence, suggesting a convergent evolution of cognition (Emery & Clayton, 2004). Rooks are suitable subjects for comparison with bonobos as they both fulfill the above criteria (large relative brain size: Emery and Clayton, 2004; MacLeod, 2004; long developmental period: Furuichi, 1989; Iwaniuk & Nelson, 2003; high sociality: de Waal, 1997; Emery, 2004), and on the basis of results of investigations with closely related

species, they are also likely to possess good visual skills (Teller, 1981; Yamamoto, Furuya, & Watanabe, 2001).

One objective of the current study was to investigate whether the bonobos, with their background of relatively limited tool use, would perform better than the non-tool-using rooks on the physical contact task described above (Helme et al., 2006). Emery and Clayton (2004) have suggested that apes and corvids are likely to possess an analogous cognitive toolkit. As such, we predicted that the bonobos would perform similarly to the rooks on this contact task, that is, by learning associatively to discriminate visual cues that signal which way to move a stick to obtain food from a tube. If so, then it would be important to establish whether bonobos respond to the same cues as the rooks. Alternatively, if the bonobos can abstract a generalized rule, which does not rely on simple visual cues but on the way in which objects are positioned relative to each other, and apply this rule to novel situations on transfer tasks, then this would suggest there are differences underlying cognition in these two species.

Experiment 1

The first experiment was designed to show whether the bonobos could solve a contact task, and if so, whether they were using specific cues or a general rule. The task consisted of a transparent tube containing a food reward and an in situ tool (a stick with a disk attached), which could be used to retrieve the food. Two configurations of the apparatus were used, with either the disk or food located centrally in the tube (see Figure 1). If a subject learned a simple relationship, such as to pull the stick on the side to which the food is offset, then this would not allow them to solve the task when the food was located centrally. If, however, they learned a general rule, such as to move the stick in the direction that makes the disk contact the food, then they should transfer immediately (i.e., make a significant number of correct choices in the first block of 20 trials on their second tube) between tube configurations.
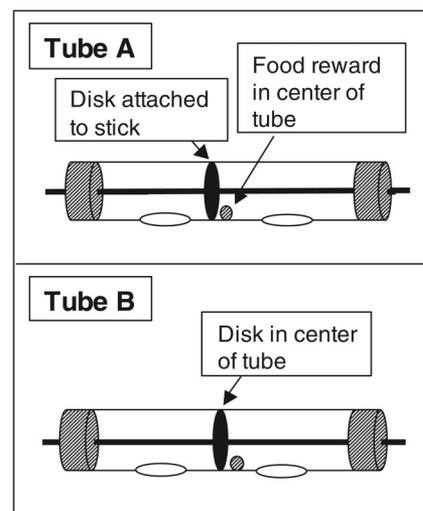

Figure 1. Experiment 1: Tube A configuration with the food central and Tube B configuration with the disk central.

Method

Subjects. Five bonobos (*Pan paniscus*; see Table 1) were tested and housed at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo in Leipzig, Germany. They were tested in individual compartments in their sleeping room. They had access to ad-lib water and had a regular diet containing a mixture of different fruits and vegetables. All 5 bonobos had been previously tested on a wide range of cognitive tasks including visual discrimination, object choice, and tool use experiments.

Apparatus. The test apparatus (tube) was located inside a secure box (70 cm wide × 50 cm high × 60 cm deep) that was attached to a panel on the test compartment holding the subject. A mesh panel was attached inside the box 30 cm from the side that was attached to the test compartment (see Figure 2). A sliding panel controlled by the experimenter provided the apes with access to the inside of the box. A Plexiglas tube (27 cm long × 5 cm diameter) was secured to the mesh panel with Jubilee rings. Both ends were blocked by Perspex disks, which had holes in the center to allow a metal stick to pass through. The stick was 37 cm long and had a Perspex disk located at various positions (see Figures 1 and 3) fixed by using two metal nuts. A hole of 3 cm in diameter was cut in the base of the tube 4 cm from each end. The tube was aligned laterally to the subject, so that the sliding motion of the stick occurred to the left and right of the subject, not towards or away from him or her.

Training procedure. Each subject received 10 training trials in which the stick protruded from one end of the tube, thereby signaling the direction in which to pull. During the first training trial, Limbuko and Kuno chose to push the stick instead of pulling it. Therefore, the training tube was modified for these 2 subjects to allow them to use the behavior that was natural to them (see Figure 3). Throughout the test trials, subjects were allowed to push, pull, or use two hands simultaneously to move the stick and retrieve the food (though it must be emphasized that movement in one direction only was allowed, and the subject was never allowed to move the stick back and forth). Food rewards were pieces of grape and peanuts, depending on the preference of individual subjects. Food was obtained on all training trials, and the orientation of the tube was randomized and counterbalanced so that an equal number of responses were directed to the left and right sides. If a subject responded only to one side over 20 trials during the test phase (i.e., developed a side bias), he or she was given an additional 10 trials with the training tube to make him or her use the stick on both sides of the tube.

Test procedure. The same apparatus was used as in the training procedure. Figure 1 shows that the only difference from training was the position of the stick, which protruded equally from either end of the tube. There were two configurations of the test tube: Tube A, where the food was positioned in the center of the tube with the disk offset, and Tube B, where the disk was located in the center with the food offset. Two bonobos (Ulindi and Limbuko) were tested first with Tube A, and 3 bonobos (Joey, Kuno, Yasa) were tested first with Tube B. A correct movement of the stick
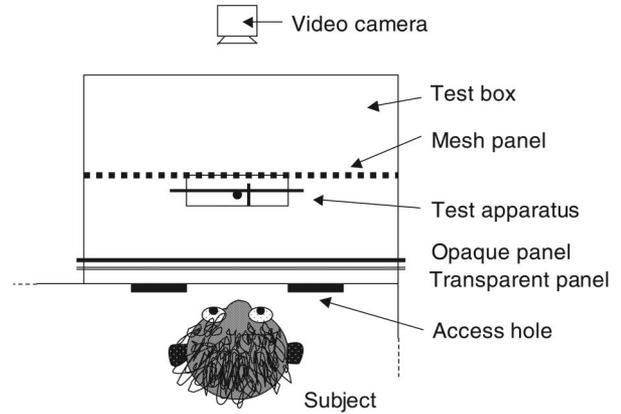
would cause the disk to contact the food and move it towards one of the openings in the base of the tube. An incorrect movement would cause the disk to move away from the food, leaving the piece of food inside the tube. Only one stick movement was allowed per trial, after which the sliding panel was replaced, blocking access to the tube, and so ending the trial. Consequently, the subjects were not rewarded for incorrect responses. The majority of trials consisted of a strong, rapid pull or push of the stick, so incorrect trials were completed (the stick was moved fully towards the end of the tube) before the barrier was replaced, blocking the subject from further manipulations of the apparatus.

Trials were conducted in blocks of 10. Each bonobo usually received 10 trials per day. Testing occurred on consecutive days for all subjects for 3 months, with only minor breaks in this routine. During a block of trials, the position of the disk cue (Tube A) or food cue (Tube B) was offset to the left or right, and this position was randomized and counterbalanced, so that there were five trials with the cue on the right and five with the cue on the left per block. There was an interval of 2 min between each trial. The food reward was placed adjacent to the disk, with a gap of approximately 2 mm separating the disk and food. The apparatus was assembled and baited between each trial behind an opaque screen. The screen was removed, and

Figure 2. Schematic representation of the test apparatus and the subject's position relative to the apparatus.

Table 1
Name, Age, Sex, Rearing History, and Previous Tool-Related Experience of Subjects

Name	Age (in years)	Sex	Rearing history	Tool use tasks[a]
Joey	21	Male	Nursery	1, 2, 3, 4, 5
Ulindi	11	Female	Mother	1, 3, 5
Limbuko	9	Male	Nursery	2, 3, 4, 5
Kuno	7	Male	Nursery	2, 3, 4, 5
Yasa	7	Female	Unknown	3, 4, 5

[a] 1 = trap-tube task (Mulcahy & Call, 2006b); 2 = future planning tool task (Mulcahy & Call, 2006a); 3 = hook task; 4 = physical contact battery; 5 = solidity and gravity task.
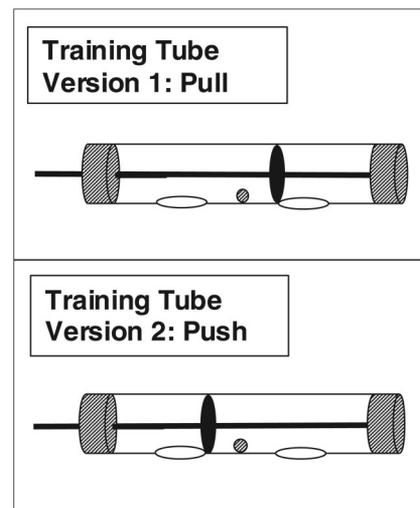

Figure 3. Experiment 1: Training Tube Version 1 for subjects that pull and Training Tube Version 2 for subjects that push.

the partitioning panel lifted to allow the bonobo access to the box. The trial was scored live by the experimenter as successful or unsuccessful on the basis of whether the food was retrieved. If no approach was made within 5 min, the trial was restarted. If still no approach was made, testing was terminated for that subject on that day. A subject was deemed to have learned either Tube A or B if they reached the criterion of significant correct performance across two blocks of 10 trials (assessed by a binomial test, two-tailed, null hypothesis = 50%, α = .05, with significance 15/20 or better). If the bonobos did not reach this level of performance within 200 trials, then tests on that particular tube stopped, with the bonobo deemed to have failed the task. After passing or failing the first tube, the bonobos were presented with the second tube.

Results and Discussion

Figure 4 displays the performance for the 5 subjects on Tubes A and B. Three of 5 bonobos passed Tube A (mean number of trials ± 95% confidence interval [CI] = 80 ± 65.7). Four of 5 bonobos passed Tube B (148 ± 72.3). Yasa, who only learned Tube B, could not subsequently learn Tube A. For the 3 subjects that passed both tubes after learning to solve the first tube, no subject performed above chance in their first block of 20 trials on the second tube (Kuno, Tube A, 9/20; Joey, Tube A, 9/20; Ulindi, Tube B, 12/20; binomial test, one-tailed, $ps > .05$). Therefore, there was no immediate transfer of successful performance between the first and second tube. These results suggest that the bonobos were not able to abstract a general rule that would allow them to transfer between tasks with the same physical problem yet different visual forms. However, some subjects were able to solve the two tasks independently from each other by learning two separate discriminations, such as to which side the food or disk is offset, and then using these cues to decide from which side to push or pull. An analysis of subjects' stick manipulation technique revealed that each subject used an individual combination of pushing and pulling over all trials, but there was no relationship between subjects' manipulation techniques and performance across the tasks.[1]
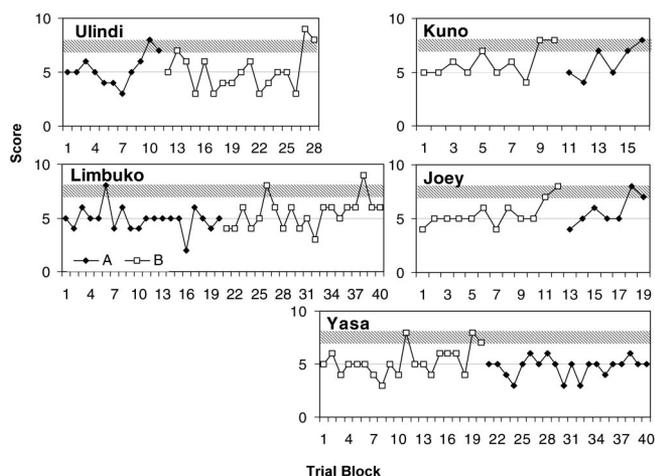

Figure 4. Experiment 1: Number of trials taken to pass Tubes A and B and score per block of 10 trials for individual bonobos. Grey shaded lines indicate regions of significance; 2 consecutive points must fall in or above the line for the subject to have reached the criterion of 15/20.

Experiment 2

To investigate which cues the bonobos had been using to solve Tubes A and B and whether they were able to switch responses between different cues, we presented the bonobos with a retest on the first tube they had passed and a transfer test. The transfer test involved the same type of cue, for example, a piece of food offset from the center of the tube as in Tube B, but with an alteration to the exact position of the food. The cue was exaggerated such that it was offset even further from the center of the tube. If the bonobos were attending to a generalized visual cue, such as asymmetry of food position within the tube, then exaggerating this cue should make the task easier. We expected that the subjects would transfer immediately. If the subjects could not transfer, this would suggest that they had learned a relationship based on exact cue positions only.

Method

Subjects. Of the 5 bonobos, all of them except Limbuko took part in this experiment, as he had not passed either of Tubes A or B in Experiment 1.

Procedure. Experiment 2 directly followed Experiment 1. The apparatus consisted of Tubes A and B from Experiment 1. For the two transfer experiments, the positions of the disk and food were altered relative to their positions in Tubes A and B. For the transfer test of Tube A, the disk was placed further from the center of the tube (4 cm instead of 1 cm; Tube C). Likewise in the transfer for Tube B, the food was placed further from the center of the tube, (Tube D). Hence, in both transfer tube tests the cue of food position or disk position was exaggerated from the form learned in Experiment 1 (see Figure 5).

Initially, each subject was retested on the first tube they had originally passed. They were then presented with the transfer task that involved the same type of cue (e.g., offset food position). If the subject had passed both tubes, they were then retested on the second tube they had passed and given the second transfer task (e.g., offset disk position). Performance on retests was assessed across the first 10 trials (9/10 or better, binomial test, one-tailed, $p < .05$). If the subject did not pass the retest immediately, then they were allowed up to the same number of trials they had taken to pass the tube initially to re-reach significance (i.e., perform significantly correctly over a block of 20 trials, binomial test, two-tailed, null hypothesis = 50%, α = .05, significance is 15/20 or better). Subjects were given 20 trials only on the transfer tubes, to assess their current knowledge and not learning. This is equivalent to the criterion used in the physical contact study with rooks (Helme et al., 2006). The bonobos were determined to have passed the transfer if they achieved 15/20 or better (binomial test, one-tailed, $p < .05$). For example, Kuno was retested on Tube B, then was presented with Tube D as a transfer, then retested on Tube A, and then given Tube C as a transfer.

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[1] The choices of stick manipulation technique (pull, push, or both hands) were analyzed for all subjects passing Tubes A and B in Experiment 1. The 3 subjects that conducted their 10 training trials by pulling (Joey, Ulindi, and Yasa) continued to use this technique for at least the next 50 trials. Yasa and Ulindi pulled the stick on the majority of all trials, but Joey subsequently pushed the stick as well. The 2 subjects that chose to push the stick on their training trials (Kuno and Limbuko) were able to use pushing and pulling techniques in later trials. In the majority of cases, there was no difference in technique between the trials in which the subject had not yet solved the task (all trials except the last 20) and the last 20 trials in which the subject reached significance. There was no regular pattern to the few exceptional cases, which suggests that stick manipulation technique did not affect the ability of the subjects to learn the task.
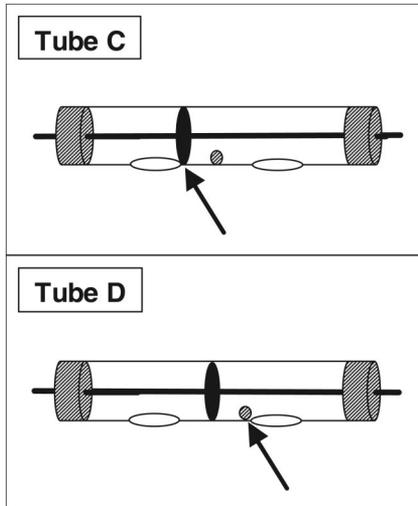
Figure 5. Experiment 2: Tube C configuration with the food central and exaggerated disk offset and Tube D configuration with the disk central and exaggerated food offset. Arrows indicate where Tubes C and D differed from Tubes A and B, respectively.

Results and Discussion

Figure 6 displays the performance of the 4 subjects who were retested on Tubes A and B and given the transfer tests (Tubes C and D). Kuno was the only subject who passed Tube B straight away on retest, as he scored 9/10 in his first 10 trials (binomial test, one-tailed, $p < .05$). Joey and Yasa repassed Tube B in 5 and 6 blocks respectively, which is not as many as it had taken them to learn initially. Kuno was also the only subject to repass Tube A. Despite being given the same number of trials as they had initially required to learn Tube A, Ulindi and Joey did not pass it the second time after having learned or been retested, respectively, on Tube B.
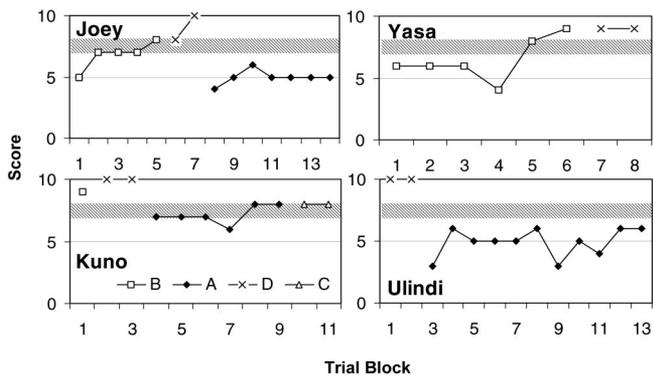

Figure 6. Experiment 2: Score out of 10 per block of trials on Tube A and B retests and on Tubes C and D for individual bonobos. Grey shaded lines indicate regions of significance; 2 consecutive points must fall in or above the line for the subject to have reached the criterion of 15/20. Ulindi was given the Tube D transfer straight away after initially passing Tube B because of the need to undergo surgery and be unavailable for a few weeks, during which time it was possible her learning could be disrupted.

The above results suggest that there may have been some interference between learning two different relationships for two tube configurations. As the bonobos took more trials to learn Tube B than Tube A initially (see Experiment 1), this suggests that they were better able to remember Tube B. All subjects who learned how to solve Tube B were able to transfer within 20 trials to Tube D (Kuno, 20/20; Joey, 18/20; Yasa, 18/20; Ulindi, 20/20; binomial test, one-tailed, all $p < .001$). Kuno, Yasa, and Ulindi were also all correct on their first trial of Tube D. Kuno, who passed the retest on Tube A, transferred within 20 trials to Tube C (16/20, binomial test, one-tailed, $p < .01$). These results demonstrate that some bonobos were able to use cues of food position to solve Tube B, and 1 subject, Kuno, could use cues of food position and disk position to solve both Tubes A and B.

Experiment 3

The purpose of this experiment was to further investigate the abilities of 1 subject. Kuno learned to solve Tubes A and B and remembered them at retest after a delay. Although he demonstrated no initial understanding of the problem, he may have learned something about how the disk caused the food to move. To investigate this, we used a stick with a split disk, where the upper and lower halves of the disk were separated from each other by a gap of 2 cm (Figure 7). If he could pass this test, it would suggest that either he could apply relationships about food and disk posi-
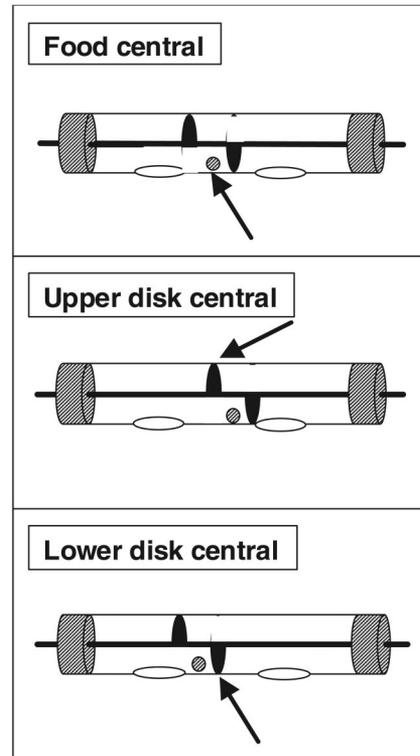

Figure 7. Experiment 3: Split-disk tube with food central, upper disk central, and lower disk central. Arrows indicate the central point of each tube.

tion without interference or that he had abstracted a more general rule about relative food and disk position.

Method

Subject. Kuno was the only subject to demonstrate memory for both Tubes A and B, so he was given the split-disk task to investigate the limits of his understanding.

Procedure. Experiment 3 directly followed Experiment 2. The same apparatus was used as in Experiments 1 and 2; however, three different versions of a split-disk stick were used, so that the food, upper disk, or lower disk were in the center of the tube (see Figure 7). Twenty trials on each tube were given, but these were mixed together to test for transfer of knowledge in an attempt to eliminate opportunities for further learning. Trials were conducted in blocks of six, where one block would contain trials with each version of the split disk twice, oriented so that the reward was obtained equally on the left and right sides, and randomized across all blocks.

Results and Discussion

Kuno appeared to transfer to these tasks immediately, achieving 6/6 in his first session. However, in subsequent sessions his performance declined so that across all sessions his performance was at chance (36/60, binomial test, two-tailed, $p = .16$). He became hesitant in responding, which suggests that the task was perhaps too complex for his level of understanding. He was able to learn by using cues, as demonstrated in Experiments 1 and 2, but did not immediately recognize which ones were relevant in the mixed task.

Experiment 4

Two bonobos were unable to pass Tube A (food–central) in Experiment 1. In the equivalent physical contact study performed with rooks (Helme et al., 2006), all rooks were unable to transfer to the equivalent of Tube A. However, when the rooks were presented with an identical tube but with a stick positioned asymmetrically signaling the correct direction to pull, they were able to solve the task. Therefore, we presented Limbuko and Yasa with an extra asymmetrical cue of stick length to investigate their ability to attend to the way in which this cue signaled the direction the stick must be moved to attain a reward.

Method

Subjects. Limbuko and Yasa, who had failed to respond to the cue of disk position (Tube A) over 200 trials in Experiment 1, were given a stick length cue as an aid to solving the food–central task. This task was not presented to the 3 other subjects because they had demonstrated that they had learned relationships involving attending to both the offset disk and offset food. One of these cues had to be present along with the asymmetrical stick length cue.

Procedure. Experiment 4 followed on directly from Experiment 2 (Yasa) and Experiment 1 (Limbuko). The same apparatus was used as in Experiments 1 and 2, except that, as shown in Figure 8, the positions of the food, disk, and stick were set so that the food was always central and the different lengths of the stick protruding on either side of the tube provided an asymmetrical cue. With Tube E, the short end of the stick signaled the side on which the food was located. Trials on Tube E were completed once the subject reached criterion on the task (i.e., they had performed significantly correctly over two blocks of 10 trials, assessed by a binomial test, null hypothesis = 50%, $\alpha = .05$, with significance 15/20 or better). If the subjects passed Tube E, they were given 20 trials with a reversed cue (Tube
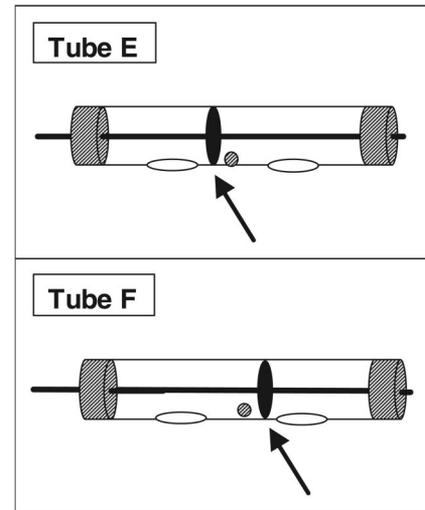

Figure 8. Experiment 4: Tube E configuration with the food central and pulling from short end of stick and Tube F configuration with the food central and pulling from long end of stick. Arrows indicate where Tubes E and F differ from each other. Note that the stick protrudes further from one end of the tubes than the other.

F), with the long end signaling the direction to pull or push the stick to obtain the food. If the bonobos could respond according to an understanding of contact, they should immediately switch to moving the stick towards the long end, whereas if they had learned another individual cue they might continue to move the stick in the direction of the short end. Tube E also contained the visual cue of an offset disk, so the subjects were retested with 20 trials on Tube A to check if they passed Tube E by using the new stick length cue or if they had managed to learn the disk position cue. With Tubes F and A, transfer was determined within 20 trials; subjects passed if they scored 15/20 or better (binomial test, two-tailed, $p < .05$).

Results and Discussion

Figure 9 shows the performance of Limbuko and Yasa on Tubes E, F, and A. They both learned to move the stick in the direction of the short end, taking 120 trials each. The 2 bonobos appeared to have no difficulty in pulling (Yasa and Limbuko) or pushing (Limbuko) from the short end of the stick. During the first block of trials, both subjects had no preference to use the long end of the stick (Yasa, 4/10; Limbuko, 5/10; binomial test, two-tailed, $ps > .05$). Indeed for Limbuko, having to learn the short end as the directional cue is unlikely to have affected his performance because he was using a mixed strategy of pulling and pushing.

When given Tube F, both subjects performed at chance level (Limbuko, 8/20; Yasa, 7/20; binomial test, two-tailed, $ps > .05$). Neither bonobo reversed his or her responses by moving the stick in the direction of the long end, suggesting that they had been using stick length as a cue to solve Tube E and therefore did not possess an appreciation of contact. When given Tube A, both of the bonobos performed as predicted and responded at a chance level, which suggests they had solved Tube E by attending to stick length and not disk position. Limbuko, therefore, was motivated enough to learn something during this series of experiments but only attended to stick cues. Yasa was capable of attending to food and stick cues but not the position of the disk.
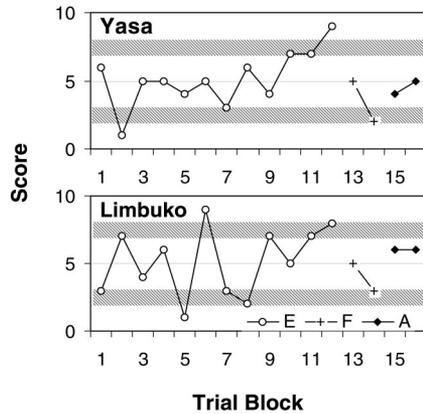
Figure 9. Experiment 4: Score out of 10 per block of trials on Tubes E and F and retests on Tube A for Yasa and Limbuko. Grey shaded lines indicate regions of significance; 2 consecutive points must fall in or above the line for the subject to have reached the criterion of 15/20.

General Discussion

The bonobos did not demonstrate any immediate understanding of the problem of contact, that is, how the disk has to make contact with the food to move it out of the tube. To solve the tasks in Experiment 1, 4 bonobos were able to use a food position cue and 3 of them could also use an asymmetrical disk cue. It is interesting that there was no immediate transfer between the two tasks, which suggests that the subjects learned each task independently and did not abstract a more general rule based on the relative positions of the disk and food. Only 1 bonobo, Kuno, was able to transfer back to food–central (Tube A) after he had been retested on disk–central (Tube B). The two other bonobos may have failed to transfer back to Tube A because of interference in trying to recall two relationships they had learned sequentially. The food position cue may have been more salient than the disk position cue and thus replaced the ability to remember to pay attention to the position of the tool that had been learned earlier.

Kuno was able to remember both cues, but he subsequently could not apply his knowledge of the predictive relationship between the disk and the food in a transfer in which there was a mixed sequence of split-disk cues. His failure suggests that he had not abstracted any general understanding of the problem with respect to physical contact. A general understanding is not necessary for Experiments 1 and 2, which can be solved using simple relationships, but a general rule may be advantageous in the mixed transfer when the part of the apparatus that must be attended to (food, upper disk, or lower disk position) changes from trial to trial.

The 2 bonobos that were tested on Tube E with the asymmetrical stick cue showed that they were capable of using this cue and attending to stick length. As they failed Tube F, this demonstrates that they did not solve Tube E using a rule based on an understanding of contact.

All individual bonobos and rooks that participated in this series of contact experiments were able to solve some form of the task after repeated trials (Helme et al., 2006). It appears that all subjects were using positional cue-based relationships. Two of 2 bonobos and 4 of 4 rooks were shown to have solved Tube E using the cue

of stick length, yet none of these subjects could solve Tube F, so they did not demonstrate an understanding of contact. Unfortunately, as only 2 bonobos performed the stick-asymmetry task (Tube E), the sample size is too small to be compared with the rooks for speed of learning. Surprisingly, the rooks did not attend to the position of the food. When comparing those subjects that were presented with Tube B first, 3 of 3 bonobos learned to solve this tube, whereas 4 of 4 rooks did not learn it within 150 trials. Therefore, the bonobos used more cues and showed more individual variation than the rooks. Some of the bonobos attended to cues they did not directly manipulate, such as food position and disk position, and 4 of 5 bonobos displayed an ability to use two different cues, although only sequentially.

Previous experience may have affected the subjects' performances in these experiments. The bonobos had been previously tested on a wide range of cognitive tasks. These included experiments investigating tool use (Mulcahy & Call, 2006b) and a study that tested for knowledge of physical contact (J. Call, personal communication, July 2, 2005). In the previous study on physical contact, the bonobos pulled objects toward themselves instead of sliding tools laterally, so they did not have direct experience of the apparatus and problem as presented to them in these experiments. However, they had experience with tools and may have learned the importance of attending to the relative positions of objects, which may explain why some subjects attended to the position of the disk in Tubes A and C. In many studies, it has been necessary for the bonobos to pay close attention to the movements or location of a piece of food, and indeed they can remember the position of hidden food even with a 30-s delay (Barth & Call, 2006). This experience in attending to food could explain why the bonobos were successful at solving Tubes B and D that had a food position cue. By contrast, the rooks may have found it harder to learn the relationship between the disk and the food in this contact task because in a previous test of physical cognition—the two-trap tube—the food was trapped between two disks and thus always moved in the same direction as the stick was pulled (Seed, Tebbich, Emery, & Clayton, 2006). The bonobos had not performed this two-trap task and therefore did not have this added potential interference. In addition, although the Seed et al. (2006) task used a food reward, it was not necessary to pay attention to the location of the food to solve this task.

The salience of different parts of the apparatus may have also affected the animals' performance. It appears that food might have been a stronger cue for the bonobos than for the rooks. This is unlikely to be due to poorer visual skills in the rooks, as most birds, pigeons in particular, are well known for excellent visual discrimination abilities and jungle crows, another member of the corvid family, have been shown to perform better than pigeons on a visual acuity task (Yamamoto et al., 2001). It is possible therefore that the bonobos may have been more motivated by food than the rooks. Captive bonobos use tools as an aid in obtaining food, unlike rooks. Therefore, the bonobos may have been more likely to look at where the tool was located and hence could make use of disk cues as well as stick cues. Sticks would probably be salient cues for rooks, as they construct their intricate nests with them. In the wild, rooks demonstrate preferences for types of stick on the basis of properties such as length and shape (Rutnagar, 1990).

In line with the theory put forward by Emery and Clayton (2004), the bonobos and rooks appeared to solve this physical

contact task using the same method, suggesting convergent mental evolution. However, when comparing the abilities of the two species on the first experiment only in these two studies, it is notable that all 8 rooks were only able to solve one version of the tube (Helme et al., 2006), whereas 3 of 5 bonobos were able to learn to pass both versions of the tube. In the current experiments, the ability to demonstrate different behaviors is dependent on attending to the appropriate stimuli. It is not known how important this attentional difference might be for the overall cognitive abilities of the two species.

In addition, a recent article has suggested that tool-using species have an advantage over non-tool-using species when it comes to success at physical tasks (Cummins-Sebree & Fragaszy, 2005). Although non-tool-using tamarins can learn to solve connectivity tasks and generalize the functional properties of tools (Hauser, 1997), tool-using capuchins are better at manipulating the tools to obtain food even on incorrect trials. Cummins-Sebree and Fragaszy (2005) suggest that experience gained through species-typical object manipulation constrains what an animal is able to learn about the physical properties of their environment. However, although rooks are not tool users, the fact that they are opportunistic generalists (Cramp & Perrins, 1994) means that they should also have experience with manipulating objects, and so their lack of tool use may not explain the results found in the previous rook study (Helme et al., 2006). Further experiments are required to determine whether the differences observed between the results of rooks and bonobos on this physical contact task are specific to this paradigm or reflect genuine variance in cognitive ability between these species. Such tasks could involve presenting the problem of physical contact in a different visual form to alter subjects' attention. It would also be useful to present a task that tests current knowledge, without requiring subjects to learn a relationship that allows them to solve the task by means other than understanding the concept of contact.

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