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Great Apes' (*Pan troglodytes, Pan paniscus, Gorilla gorilla, Pongo pygmaeus*) Understanding of Tool Functional Properties After Limited Experience

Esther Herrmann
Max Planck Institute for Evolutionary Anthropology

Victoria Wobber
Max Planck Institute for Evolutionary Anthropology and Harvard University

Josep Call
Max Planck Institute for Evolutionary Anthropology

Primates' understanding of tool functionality has been investigated extensively using a paradigm in which subjects are presented with a tool that they must use to obtain an out-of-reach reward. After being given experience on an initial problem, monkeys can transfer their skill to tools of different shapes while ignoring irrelevant tool changes (e.g., color). In contrast, monkeys without initial training perform poorly on the same tasks. Compared to most monkeys, great apes show a clear propensity for tool using and may not require as much experience to succeed on tool functionality tasks. We investigated this question by presenting 171 apes (*Pan troglodytes, Pan paniscus, Gorilla gorilla,* and *Pongo pygmaeus*) with several tool-use problems without giving them initial training or familiarizing them with the test materials. Apes succeeded without experience, but only on problems based on basic properties such as the reward being supported by an object. However, only minimal experience was sufficient to allow them to quickly improve their performance on more complex problems in which the reward was not in contact with the tool.

Keywords: tool use, tool properties, object choice task, problem solving, causal knowledge

Tool use, once thought to be something unique to humans, has now been demonstrated in a number of other primate and nonprimate species (Anderson, 2002; Beck, 1980; Tomasello & Call, 1997). From ant dipping in chimpanzees to hook making in New Caledonian crows, a number of species are able to manufacture and use quite sophisticated tools (Hunt, 1996; Whiten et al., 1999). However, it is still unclear to what degree such tool-using animals understand the functional properties of the tools that they use. To investigate this issue, past research has presented animals with experimental paradigms that require subjects to understand certain principles of functionality to succeed on a given tool-using task (most often, this task is using the tool to obtain out-of-reach food).

In nonhuman primates, experiments testing an understanding of tool functionality have been carried out with numerous naturally tool-using and non–tool-using species. These experiments have explored a number of dimensions, such as the properties of the tools, the relation between the tool and the reward, and the effect of introducing obstacles such as barriers or traps in problem-solving situations. Although several studies have suggested that various species have some knowledge about the relation between the reward and the tool (Natale, 1989), the reward and obstacles (Mulcahy & Call, 2006), the properties of the tool (Hauser, 1997; Mulcahy, Call, & Dunbar, 2005), or the relation between the tool and the obstacles (e.g., Visalberghi, Fragaszy, & Savage-Rumbaugh, 1995), other studies have produced more mixed results in each of these areas (Natale, 1989; Povinelli, 2000; Santos, Rosati, Sproul, Spaulding, & Hauser, 2006; Visalberghi & Limongelli, 1994). These mixed results suggest that other factors may be affecting success besides the nature of the task, the response required to solve the task, or the species' propensity to use tools.

Esther Herrmann and Josep Call, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany; Victoria Wobber, Max Planck Institute for Evolutionary Anthropology and Department of Anthropology, Harvard University.

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Correspondence concerning this article should be addressed to Esther Herrmann, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, D-04103, Leipzig, Germany. E-mail: eherrman@eva.mpg.de

One of the most surprising findings is that success or failure does not necessarily correspond with whether a species uses tools in the wild. For example, vervet monkeys and tamarins both succeeded at tasks which chimpanzees failed (e.g., trap table; Povinelli, 2000; Santos, Pearson, Spaepen, Tsao, & Hauser, 2006). Furthermore, within a given species performance is inconsistent across studies, as chimpanzees in one study succeeded on a certain task and chimpanzees in another study failed on that same task (trap tube; Martin-Ordas, Call, & Colmenares, in press; Povinelli, 2000).

One factor that varies between studies that might explain these discrepancies is the degree of training and past experience subjects have with the test objects or similar materials. Past tool-use experiments with nonhuman primates have used a range of training levels, training subjects with the exact test objects, using objects that subjects are familiar with from their daily lives, providing a general familiarization session with the test objects without explicit training, or training subjects with objects that are similar to (but not exactly the same as) those used in the test. Subjects are largely successful with any of these types of training, although even a great deal of experience does not guarantee success (e.g., capuchins, Visalberghi et al., 1995; flimsy tool, trap tube, and trap table, Povinelli, 2000). Most studies that have reported some understanding of tool functionality in nonhuman primates have invariably required some sort of training (e.g., Cummins-Sebree & Fragaszy, 2005; Evans & Westergaard, 2004; Fujita, Kuroshima, & Asai, 2003; Hauser, 1997; Hauser, Kralik, & Botto-Mahan, 1999; Hauser, Pearson, & Seelig, 2002; Limongelli, Boysen, & Visalberghi, 1995; Povinelli, 2000; Santos, Mahajan, & Barnes, 2005; Santos et al., 2006; Santos, Rosati, et al., 2005; Visalberghi et al., 1995).

Without such training or experience, however, it seems that performance on the functionality test is markedly decreased. Only one experiment has systematically varied this factor, using cotton-top tamarins and common marmosets in a test paradigm in which trained cotton-top tamarins had been successful in prior work. In this experiment, Spaulding and Hauser (2005) tested whether these two non–tool-using species would be able to understand functional distinctions in potential tools with no training whatsoever. Despite their ability to understand a wide variety of functional properties with training (Hauser, 1997; Hauser et al., 1999, 2002; Santos et al., 2006), cotton-top tamarins in this experiment were not able to make such distinctions in the absence of training. They were successful in the control trials, in which the location or presence of food created the choice, but they were only able to choose a functional tool over a nonfunctional tool after more than 70 trials—suggesting some effect of experience beginning to play into their performance. Marmosets, on the other hand, were able to preferentially choose the functional tool; however, it seems that experience may also have enhanced their performance as subjects performed significantly better on the fourth 10-trial session than on the first 10-trial session, in which their performance was not significantly above chance (Spaulding & Hauser, 2005). Thus, it appears that without training, subjects have more difficulty in tool functionality tests, although there is some possibility for success in naïve individuals.

In this study, we investigated whether the great apes, which together with capuchin monkeys are the primates that use tools regularly either in the wild or in the laboratory (see Tomasello & Call, 1997, for a review), would succeed in the functionality test without any prior training or familiarity with test materials. These data are important for two reasons. First, they can inform us about whether tool-using species show certain functional predispositions in the absence of training. Although presenting these tests without prior practice with the tool materials may be unproductive, we think that this is a necessary step to establish what knowledge individuals gain from experience. Additionally, we also assessed the effect of experience with the materials and tasks by comparing the results of two experiments that presented the same tasks but before and after experience with the materials.

Second, including the four great apes allowed us to assess the possible interspecies differences using the exact same methods, something that is rather uncommon when comparing across studies. Although all species use tools, it appears that chimpanzees and orangutans might show a greater propensity than bonobos and gorillas, at least in the wild. It is unclear whether this difference will translate into a deeper understanding in some species compared to others. Moreover, including non-chimpanzees in the study will help remedy to some extent the “chimpocentric” bias that exists in the ape literature.

We used the functionality choice paradigm, which has been successfully used in numerous species (Fujita et al., 2003; Hauser, 1997; Natale, 1989; Povinelli, 2000; Santos, Mahajan, & Barnes, 2005), in which subjects are forced to choose between a functional and a nonfunctional tool when attempting to obtain food. In four experiments, we set up a 2×2 design to discriminate between two potential factors affecting subjects’ performance on tool-using tasks: the amount of familiarity with the test material and the complexity of the functional property being tested. The complexity of functional properties was inferred from the results of past experiments using these paradigms by examining which conditions led to the most success across species and which were more variant.

Experiments 1 and 2 served as baselines to establish, first, subjects’ abilities to discriminate straightforward functional principles with a familiar material and, second, subjects’ skills when presented with more complex functional distinctions with an unfamiliar material. Then, in Experiments 3 and 4 we further elucidated the relative importance of the two factors by manipulating each independently. Experiment 3 manipulated familiarity, providing subjects with simple properties of unfamiliar materials. Experiment 4 did just the opposite, giving subjects familiar materials but with complex properties. By juxtaposing the results of these two experiments with the first two experiments, we assessed whether property complexity or merely familiarity affected success more strongly.

Experiment 1: Familiar Material, Simple Properties

In this experiment, we obtained a baseline of apes’ performance in tool-use tasks with a familiar material, manipulating functional properties that animals such as tamarins and marmosets have been shown to understand even without training (Hauser et al., 1999; Spaulding & Hauser, 2005). Such properties consist of food being supported by a cloth (vs. not being on the cloth) and that cloth being a connected versus disconnected piece (see Hauser et al., 1999, Figures 2 and 3, and Spaulding & Hauser, 2005, Figure 2, for examples of similar conditions used in cotton-top tamarins and common marmosets). If subjects succeeded at these conditions, this would demonstrate that all four great ape species are able to infer functionality simply on the basis of general material familiarity, as has been demonstrated in chimpanzees (Povinelli, 2000), and that our particular population of apes understood the nature of the object choice functionality paradigm. If subjects failed in this experiment, this would imply that apes have difficulty understanding even simple functionality distinctions without training, perhaps with a distinction between chimpanzees and non-chimpanzees given chimpanzees' past success in most instances in which they have had no explicit training (although not in all instances; see Povinelli, 2000).

Method

Subjects

Eighteen chimpanzees (*Pan troglodytes*), 5 orangutans (*Pongo pygmaeus*), 5 gorillas (*Gorilla gorilla*), and 5 bonobos (*Pan paniscus*) participated in this study. There were 23 females and 10 males ranging from 3 to 31 years of age. Not all subjects participated in all experiments, so Table 1 shows each subject's experimental participation along with its species, sex, age, and rearing history. All apes lived in social groups at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo, Leipzig, Germany. Subjects were tested individually in a familiar indoor testing room. Water was available ad libitum, and subjects were not food deprived for testing. Their normal diet consisted of different fruits and vegetables given five times a day.

Materials

The table on which these tests were performed was a gray plastic platform (80 cm × 39 cm) with a sliding plastic board on top of it (78 cm × 35 cm) and a sliding Plexiglas panel (65 cm × 10 cm) along the front. The platform was attached to a metal L-frame in front of a Plexiglas testing window (69 cm × 48 cm). There were three hand holes (6 cm in diameter) in the testing window through which subjects could reach their fingers to move the sliding Plexiglas and pull the tools. The sliding Plexiglas panel could be moved to the right or left and was of the length that when pushed to one side it blocked two of the three holes. It thus prohibited subjects from being able to reach both choices at once, making their choice unambiguous. Each condition consisted of two different tools placed on the sliding platform 58 cm apart. This same general apparatus and setup was also used for Experiments 2 and 4. In this experiment, the placement procedure was hidden from the subjects' view by a blue plastic occluder (100 cm × 50 cm). Different sizes of cloth pieces (15 cm × 20 cm, 15 cm × 12

Table 1
Species, Age, Sex, Rearing History, and the Experiments in Which Each Subject Participated

Name	Species	Age (years)	Sex	Rearing history	Experiment participation
Robert	Chimpanzee	28	Male	Nursery	1, 2, 4
Fraukje	Chimpanzee	28	Female	Nursery	1, 2, 4
Corry	Chimpanzee	27	Female	Nursery	1, 2
Ulla	Chimpanzee	27	Female	Nursery	1, 2, 4
Riet	Chimpanzee	26	Female	Nursery	1, 2, 4
Dorien	Chimpanzee	24	Female	Nursery	1, 2, 4
Natascha	Chimpanzee	24	Female	Nursery	1, 2, 4
Jahaga	Chimpanzee	11	Female	Mother	1, 2
Gertruida	Chimpanzee	11	Female	Mother	1, 2
Fifi	Chimpanzee	11	Female	Mother	1, 2
Sandra	Chimpanzee	11	Female	Mother	1, 2, 4
Frodo	Chimpanzee	10	Male	Mother	1, 2, 4
Patrick	Chimpanzee	7	Male	Mother	1, 2, 4
Brent	Chimpanzee	5	Male	Mother	1, 2, 4
Pia	Chimpanzee	5	Female	Mother	1, 2, 4
Alexandra	Chimpanzee	5	Female	Nursery	1, 2, 4
Annett	Chimpanzee	5	Female	Nursery	1, 2, 4
Alex	Chimpanzee	3	Male	Nursery	1, 2, 4
Dunja	Orangutan	31	Female	Mother	1, 2, 4
Bimbo	Orangutan	24	Male	Nursery	1, 2
Dokana	Orangutan	15	Female	Mother	1, 2, 4
Pini	Orangutan	16	Female	Mother	1, 2, 4
Padana	Orangutan	6	Female	Mother	1, 2, 4
N'diki	Gorilla	26	Female	Unknown	1, 2, 4
Bebe	Gorilla	25	Female	Unknown	1, 2, 4
Gorgo	Gorilla	23	Male	Nursery	1, 2
Viringika	Gorilla	9	Female	Mother	1, 2, 4
Ruby	Gorilla	6	Female	Mother	1, 2, 4
Joey	Bonobo	21	Male	Nursery	1, 2, 4
Ulindi	Bonobo	11	Female	Mother	1
Limbuko	Bonobo	9	Male	Nursery	1, 2, 4
Kuno	Bonobo	7	Male	Nursery	1, 2, 4
Yasa	Bonobo	7	Female	Unknown	1, 2, 4

cm, and 15 cm × 8 cm) were used as tools. The cloth for this experiment was a burlap material that the apes were familiar with in the form of blankets. Thus, the apes knew the material but had not used it in this sort of food-manipulation situation. Two Plexiglas bridges (21 cm × 3 cm × 6 cm) were also used. Banana slices served as food rewards in Experiments 1, 2, and 4.

Procedure and Design

The experimenter sat facing the subject behind the platform. The experimenter waited until the subject approached the platform to start a trial. The experimenter attracted the subject's attention by calling her name and then placed the occluder in front of the Plexiglas panel to hide the placement of the tools. The experimenter set up two tools, each with a banana slice as a possible reward. After this, the experimenter removed the screen and pushed the sliding platform forward to let the subject choose. The subject was only allowed to make one choice. All subjects were familiar with the sliding Plexiglas (which prevented them from choosing both sides simultaneously) from a previous study (Herrmann, Melis, & Tomasello, 2006). Subjects were able to move the sliding Plexiglas and pull one cloth piece through the Plexiglas panel to retrieve the food. It was only possible to obtain the food by choosing the correct tool because the food was always placed far enough back on the platform that it was out of reach. There were three different conditions used, similar to those used in previous articles in which cloth was presented to subjects (Hauser et al., 1999; Povinelli, 2000).

Side

Two cloth pieces (15 cm × 20 cm) were positioned on the two sides of the platform (see Figure 1 for illustrations of each condition). One banana slice was placed at the far end of one cloth piece, and the other slice was placed on the platform directly next to the far end of the other cloth piece. The subject could only retrieve the food by pulling the piece of cloth with the banana on top of it. Pulling the incorrect piece did not move the food, as the banana was sitting on the platform.

Ripped

One large cloth piece (15 cm × 20 cm) was positioned on one side and two small cloth pieces (15 cm × 12 cm and 15 cm × 8 cm) were put on the other side so that the small piece was closer to the subject. There was a 1-cm gap between these two pieces, so they were visibly disconnected. The bananas were placed the same distance from the subject on each side, at the far ends of the 20-cm and 12-cm cloth pieces, respectively. The subject was able to get the food only by pulling the large cloth piece. If the subject pulled on the ripped side, only the small cloth piece came toward it. The larger (12-cm) piece with the food on it remained still. The larger of the ripped cloth pieces was out of reach of the subject, so the only possible option on this side was to pull the small disconnected piece.

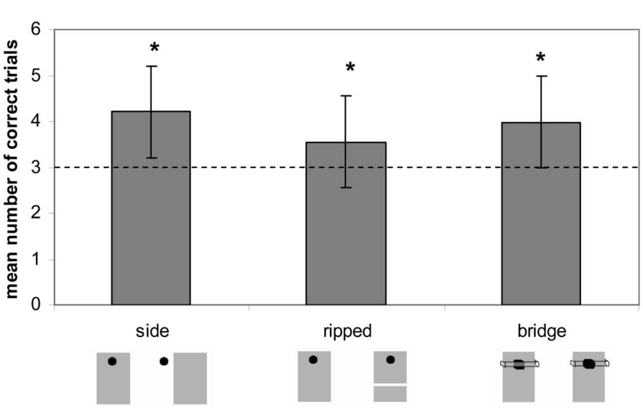

Figure 1. Mean number of correct trials (±95% confidence interval) across the three conditions in Experiment 1. * $p < .05$.

Bridge

Two cloth pieces (15 cm × 20 cm) were again positioned on the two sides of the platform. Two Plexiglas bridges were placed at the far ends of the two cloth pieces, equidistant from the subject. One banana piece was placed on top of one bridge. The other banana piece was placed on the cloth under the other bridge. The subject could obtain the food by pulling the cloth with the food on it. If the subject chose the side with the food on the bridge, the cloth would move but the food and the bridge would remain stagnant.

Each session consisted of 18 trials, 6 of each condition. The order of the conditions was randomized between trials, with the constraint that one condition was not presented more than two times in a row. The position (left vs. right) of the correct tool was counterbalanced so that it appeared an equal number of times on both sides and was not placed on the same side for more than two trials in a row. This session design was the same for Experiments 2 and 4.

Scoring and Analysis

Subjects' choices were coded live. A correct choice was scored if the subject pulled the correct tool first. Once a subject touched one of the tools, attempts to switch to the other tool were not allowed. All trials were videotaped, and a second observer independently scored 20% of the trials. Interobserver reliability with the main observer was 100%. We used nonparametric statistics throughout, comparing performance on each condition to chance using Wilcoxon tests, comparing performance across conditions using Friedman tests, and comparing performance on each condition across species using Kruskal-Wallis tests. The scoring and analysis were the same for all experiments.

Results

Figure 1 presents the mean number of correct trials across conditions. Subjects were above chance in all conditions (Wilcoxon test: side, $z = 4.48$, $p < .001$; ripped, $z = 3.0$, $p = .003$; bridge, $z = 3.27$, $p = .001$). There were significant differences between conditions, Friedman test: $\chi^2(2, N = 33) = 9.64$, $p = .008$. Pairwise comparisons revealed that subjects performed better in the side than the ripped condition (Wilcoxon test: $z = 2.96$, $p = .003$). There were no significant differences between species for any of the three conditions (Kruskal-Wallis test): side, $\chi^2(3, N = 33) = 1.10$, $p = .77$; ripped, $\chi^2(3, N = 33) = 7.29$, $p = .063$; and bridge, $\chi^2(3, N = 33) = 7.04$, $p = .071$.

Discussion

Apes were able to discriminate functional pieces of familiar cloth material from nonfunctional ones, with some variation in success between conditions. The four great ape species did not differ in their performance in any of the three conditions. Apes as a whole were more successful in the side condition, in which one food piece was visibly not in contact with the cloth, than they were in the ripped condition, in which they needed to understand the connectivity of the cloth material. Overall, the great apes tested here were able to successfully choose the functional tool in every condition.

This result was not particularly surprising, as even cotton-top tamarins, which do not commonly use tools, were shown to understand the properties of cloth being ripped versus whole after having been trained on a condition similar to our own "side" condition (Hauser et al., 1999). Japanese and crab-eating macaques, a gorilla, and capuchins have also been shown to understand properties of cloth after training (Spinozzi & Poti, 1989), and common marmosets were able to discriminate between food being on or off a piece of cloth without training or even familiarity with the test material (Spaulding & Hauser, 2005). Chimpanzees have been shown to be successful in a similar paradigm as well (Povinelli, 2000), thus the general success of all four species in this experiment confirmed that our particular subjects were able to understand the tool functionality paradigm and could discriminate successful tools with familiar materials, at least in this particular experiment, which manipulated only simple functional properties.

Experiment 2: Unfamiliar Material, Complex Properties

Given subjects' success in the previous experiment, in this experiment we used materials with which the apes had little or no familiarity and presented the apes with conditions that were more complex than those used in Experiment 1. These more difficult conditions simultaneously manipulated properties of both connectivity and contact between the tool and reward. Half of these connectivity conditions consisted of the food being in contact with the reward, a situation in which chimpanzees have shown prior success with experience (ropes; Povinelli, 2000). The other half of the conditions presented subjects with canes to manipulate the rewards. Trained tamarins, vervets, and lemurs have been shown to succeed at pulling canes to obtain food and discriminating among them according to connectivity, but untrained tamarins have had more difficulty with such discriminations, perhaps because in this instance the tool is not in contact with the reward (Hauser, 1997; Santos, Mahajan, & Barnes, 2005; Santos et al., 2006; Spaulding & Hauser, 2005). If subjects succeeded in this experiment, this would suggest that among great apes, material familiarity is not required to understand functional properties, that instead, apes are able to infer even complex functionality from visual information alone. Alternatively, if apes failed to discriminate functionality in this experiment, this would require further investigation of whether the difficulty of the properties or the unfamiliarity of the materials was responsible for such a failure.

Method

Subjects

See Table 1 for each subject's experimental participation along with its species, sex, age, and rearing history.

Materials

Two different materials were used in this experiment: plastic canes and pieces of a wool-like rope material. One large gray plastic cane (25 cm long × 2 cm wide; horizontal part 10 cm long), one short gray plastic cane (15 cm × 2 cm wide; horizontal part 10 cm long), and two gray plastic pieces (10 cm × 2 cm and 8 cm × 2 cm) were used in the cane conditions. In the rope conditions, two long ropes (15 cm and 25 cm), each attached to a piece of banana, and two short ropes (10 cm and 8 cm) were used. The rope was a thin, beige-colored pliable material unfamiliar to the subjects.

Procedure and Design

The basic procedure was similar to Experiment 1. Subjects participated in three different conditions with the rope and three with the cane. In this experiment, there was no occlusion of the tool placement because certain conditions required subjects to view the placement of the tools to understand the functionality distinction (such as the touching condition, in which the tools appeared to be connected on final examination but were placed on the table as distinct pieces). The tools were placed in a constant order (left to right) on every trial, with the side of the correct tool counterbalanced within sessions so that it appeared an equal number of times on each side. The experimenter began the same way as in the previous experiment, by waiting for the subject to approach the Plexiglas window and calling her name to get her attention. The experimenter then showed the subject the tool pieces before placing them on the platform. Subjects had to remain in front of the testing window throughout the placement for the trial to continue; if the subject moved away, she was called back to the window and the trial was restarted. In the cane conditions, the experimenter finished the tool placement and then put banana slices on each side simultaneously. In the rope conditions, the banana pieces were already attached to the rope before the experimenter laid the rope pieces on the table. After both tools were placed on the platform, the experimenter pushed the platform forward to let the subject choose. The subjects participated in three conditions with the cane and three conditions with the rope.

Cane

Broken. One solid large cane was placed on one side on the platform, and on the other side a small cane was placed so that its hook was the same distance away from the subject as the hook of the large cane (see Figure 2 for illustrations of each condition). A small plastic segment (8 cm) was then placed in front of the small cane with a 1-cm gap left between the two pieces. The banana slices were placed inside the hook of each cane.

On top. The same large and small canes from the broken condition were used, but in this condition a small segment (10 cm) was placed in front and on top of the short cane. The small segment was placed partially on top of the cane so that there was approx-

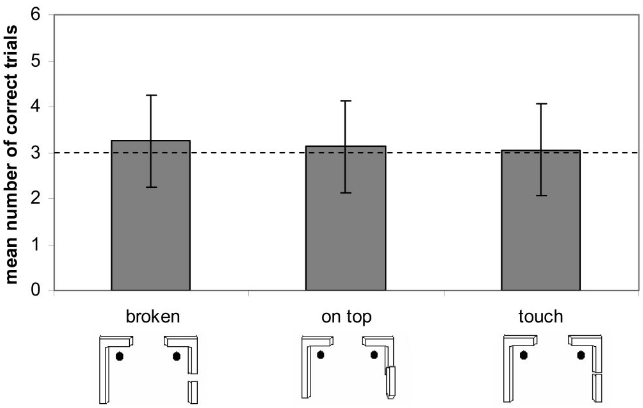

Figure 2. Mean number of correct trials (±95% confidence interval) across the three cane conditions in Experiment 2.

imately 1 cm of overlap. The banana slices were put in the same places as in the broken condition.

Touch. Again, the same large and small canes were used, and in this condition the small plastic segment (10 cm) was placed directly in front of the small cane but without any gap between the two pieces. The bananas were in the same place inside the hook of each cane.

In all three conditions, the subject could obtain the food by pulling the large cane and raking the banana within reach. Pulling on the small plastic piece did not move the food because the small cane was not connected to this piece in any way.

Rope

The rope conditions were similar to the cane conditions with the difference that in the rope conditions, the banana was attached to the rope.

Broken. A long rope (25 cm) tied around a banana slice at one end was placed on one side of the platform, and a shorter rope (15 cm) also tied to a banana slice was placed on the other side (see Figure 3 for illustrations of each condition). A small piece of rope (8 cm) was placed in front of this short rope so that there was a 1-cm gap between the two.

On top. The same long rope and shorter rope tied to banana slices were used. A small piece of rope (10 cm) was placed in front and slightly on top of (approximately 1 cm) the short rope so that there was visible overlap between the two.

Touch. Again, the same long and shorter ropes were placed, both tied to banana slices. The small piece of rope (10 cm) was placed directly in front of the short rope so that the two pieces were touching.

In all three conditions, subjects were able to retrieve the food by pulling the longer piece of rope. If the subject pulled one of the small pieces, the short rope tied to the banana slice remained on the platform, and the subject obtained only the small rope.

The basic session design was the same as in the previous experiment, but the cane conditions were all given in one session and the rope conditions in another (6 trials of each condition, 18 total trials per session). Half the subjects received the cane session first, and the other half received the rope session first.

Scoring and Analysis

The analysis was conducted for the cane and the rope conditions separately.

Results

Cane

Figure 2 presents the mean number of correct trials across conditions. Subjects were not above chance in any of the conditions (Wilcoxon test: broken, $z = 1.12$, $p = .26$; on top, $z = 0.78$, $p = .44$; and touch, $z = 0.15$, $p = .88$). There were no significant differences between conditions (Friedman test): $\chi^2(2, N = 32) = 0.15$, $p = .93$. Likewise, there were no significant differences between species for any of the three conditions (Kruskal-Wallis test): broken, $\chi^2(3, N = 32) = 0.84$, $p = .84$; on top, $\chi^2(3, N = 32) = 4.68$, $p = .20$; and touch, $\chi^2(3, N = 32) = 3.28$, $p = .35$.

Rope

Figure 3 presents the mean number of correct trials across conditions. Subjects were above chance in the broken condition (Wilcoxon test: $z = 3.43$, $p = .001$) but not in the other two conditions (Wilcoxon test: on top, $z = 1.33$, $p = .19$; touch, $z = 1.22$, $p = .22$). There were significant differences between conditions (Friedman test): $\chi^2(2, N = 33) = 6.69$, $p = .035$. Pairwise comparisons revealed that subjects performed better in the broken than in the touch condition (Wilcoxon test: $z = 2.34$, $p = .019$). There were no significant differences between species for any of the three conditions (Kruskal-Wallis test): broken, $\chi^2(3, N = 33) = 0.04$, $p = 1.0$; on top, $\chi^2(3, N = 33) = 2.72$, $p = .44$; and touch, $\chi^2(3, N = 33) = 0.46$, $p = .93$.

Discussion

Apes chose the intact rope significantly more often than the broken rope in the broken condition, although they did not discriminate between the two choices in the on-top or touch conditions. In contrast, apes failed to choose the functional (intact) cane over the nonfunctional one in all three conditions.

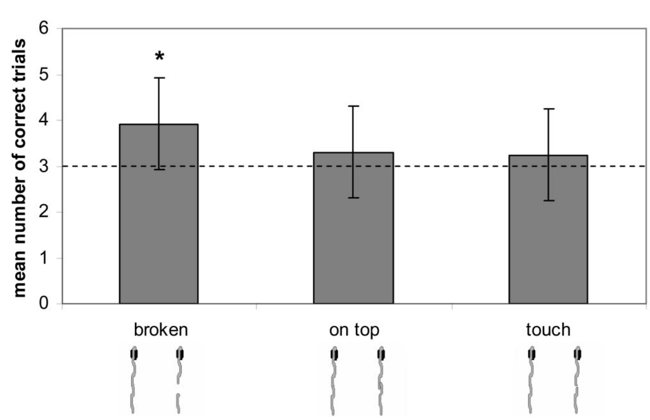

Figure 3. Mean number of correct trials (±95% confidence interval) across the three rope conditions in Experiment 2. $^{*}p < .05$.

These results suggest that apes perceived a distinction between the cane and rope conditions, with the rope conditions perhaps being simpler because the food was in contact with the tool. Although subjects failed at the on-top and touch conditions with both materials, it is likely that these conditions were too difficult because the division between the tools was not necessarily visually apparent at the time of choice, thus subjects had to pay fairly close attention to the placing of the tools to succeed. Performance on the broken condition was more informative in this instance, with subjects' failure on the cane-broken condition suggesting that apes have difficulty inferring connectivity in such materials in contrast to previous results that have shown that subjects with training can make such discriminations (Povinelli, 2000; Santos et al., 2006). Thus, these results support the notion that contact between the reward and the tool allows subjects to better perceive the properties of the tool itself, with lack of tool–reward contact introducing an extra element of difficulty. This would explain subjects' failure to use the functional tool in the cane-broken condition, as in this instance the cane was not in contact with the piece of banana.

One past experiment systematically investigated whether food contact does significantly affect subjects' success in discriminating functionality. This experiment tested chimpanzees' understanding of rope properties in a paradigm quite similar to the present experiment, determining whether physical connection or perceptual contact between ropes and food rewards influenced subjects' success. The results of this work suggested that perceptual contact was more influential than actual physical connection (Povinelli, 2000). For example, if subjects were presented with a choice between a rope tied to a banana reward versus a rope laying on top of a banana reward, they were not able to discriminate between the two, whereas they could distinguish a rope tied around a banana from a rope not touching a banana (Povinelli, 2000). Thus, it appears that the perceptual contact between the food and the cloth in Experiment 1 and the rope in this experiment may have enhanced subjects' performance beyond the level possible with the noncontacting cane situation. Past work with children also demonstrates that they are able to discriminate functionality in tools that are connected to the reward (strings) at an earlier age than with tools that are not connected to the reward (sticks) (Brown, 1990), supporting the idea that there may be some distinction between these two types of tasks.

It is possible that apes' failure may have represented a lack of motivation, or more interest in the rope material than in the plastic canes. Yet apes' continued participation in both conditions, with consistent taking of the food reward on retrieving it, suggested that they were motivated to obtain the food and not just to play with the objects (because if this were the case, they could have stopped participating after obtaining the object in the first trial). However, it is also possible that subjects' partial success in this experiment may have been due to greater familiarity with ropelike materials, rather than reward contact being the salient factor. These apes do have ropes in their enclosures, and although they have sticks, it might be that properties of their ropes were more easily generalizable to the test material used here than were the properties of the sticks to the cane materials. Thus, to further elucidate whether material familiarity or a property such as contact was more influential in determining performance, in the next experiment we tested a population of apes with limited experience with novel materials and limited cognitive test experience to determine whether their performance would differ from that of the Leipzig great apes.

Experiment 3: Unfamiliar Materials, Simple Properties

The results of Experiment 2 suggested that subjects should be able to infer functionality in novel materials if the properties manipulated are simple enough. In this experiment, we took the conditions in which subjects showed success in the first two experiments—the cloth conditions and the rope-broken condition—and presented these to a population of subjects completely unfamiliar with either material. If these individuals were successful, this would suggest that failure in Experiment 2 was because the principles used were too difficult for subjects to discern in novel materials, rather than increased familiarity with ropes leading to success on the rope condition. If subjects in this experiment failed to discriminate these simpler properties, this would suggest that apes' success in the previous experiments was solely because of their familiarity with either the exact material being used in the test or similar materials, implying that regardless of the difficulty of the property being tested, apes have difficulty discriminating functionality with novel materials.

Method

Subjects

One hundred six chimpanzees (*Pan troglodytes*) and 32 orangutans (*Pongo pygmaeus*) participated in this experiment. Thirty-six chimpanzees lived at the Ngamba Island chimpanzee sanctuary, Lake Victoria, Uganda, and 70 chimpanzees lived at Tchimpounga chimpanzee sanctuary, Republic of Congo. All orangutans lived at the Orangutan Care Center and Quarantine in Pasir Panjang, Kalimantan, Indonesia (see Herrmann, Hernandez-Lloreda, Hare, & Tomasello, 2007, for a detailed description of these sanctuaries). The chimpanzees ranged in age from 3 to 21 years with equal numbers of male and female chimpanzees. There were 15 female and 17 male orangutans, ranging in age from 3 to 10 years. All chimpanzees and orangutans came to the sanctuaries as orphans as a result of the trade in apes for pets and bushmeat. They were all raised by humans together with peers until they were old enough to join a social group.

At the time of testing, all chimpanzees and orangutans lived in social groups. The housing facilities for the vast majority of chimpanzees and orangutans consisted of outdoor forest areas where they were released during the day. In addition, all individuals had access to dormitories where they slept at night. Subjects were individually tested either in a familiar room in these dormitories or in a new room to which they were introduced before testing. Subjects were not food deprived before testing and could stop participating at any time. All apes had never participated in a tool functionality study before this test. Subjects were not afraid of the tools and did not have difficulty in manipulating them, despite being naïve to the test situation.

Materials

A wooden table (80 cm × 39 cm) with a sliding platform (78 cm × 35 cm) was used for the experiment. This table was placed in front of a Plexiglas testing window (69 cm × 48 cm) with three hand holes (6 cm in diameter) or a mesh panel. Subjects could reach their fingers through the holes or the mesh wire to make a choice. The material used for the tools was the same as for the three conditions in Experiment 1 and the rope-broken condition in Experiment 2. This material was totally unfamiliar to subjects. Banana slices served as food rewards for the chimpanzees and mainly mango pieces for the orangutans.

Procedure and Design

Subjects participated in all three cloth conditions (side, bridge, and ripped) of Experiment 1 and the rope-broken condition of Experiment 2. The procedure of the four conditions was the same as for the Leipzig apes in Experiments 1 and 2, except that apes received only three trials per condition and the order of the conditions was the following: cloth side, cloth bridge, cloth ripped, and rope broken.

Results

Figure 4 presents the mean number of correct trials across conditions. Subjects were above chance in all conditions (Wilcoxon test: side, $z = 7.59$, $p < .001$; ripped, $z = 5.14$, $p < .001$; bridge, $z = 5.49$, $p < .001$; and broken, $z = 3.42$, $p = .001$). There were significant differences between conditions (Friedman test): $\chi^2(3, N = 138) = 10.62$, $p = .014$. Pairwise comparisons revealed that subjects performed better in the side condition than in the all the other conditions (Wilcoxon test: ripped, $z = 2.63$, $p = .009$; bridge, $z = 1.98$, $p = .048$; and broken, $z = 3.26$, $p = .001$). There were no significant differences between species for any of the four conditions (Mann–Whitney test: side, $z = 0.23$, $p = .82$; ripped, $z = 0.26$, $p = .79$; bridge, $z = 1.52$, $p = .13$; and broken, $z = 0.34$, $p = .73$).

In addition, to ensure that the differing numbers of trials did not influence performance, we compared performance on the first three trials of each condition of the Leipzig chimpanzees and orangutans to the sanctuary apes. There were no significant differences in the number of correct trials between the Leipzig apes and the sanctuary apes for any of the four conditions (Mann–Whitney test: side, $z = 0.38$, $p = .71$; ripped, $z = 1.67$, $p = .09$; bridge, $z = 1.44$, $p = .15$; and broken, $z = 0.51$, $p = .61$).

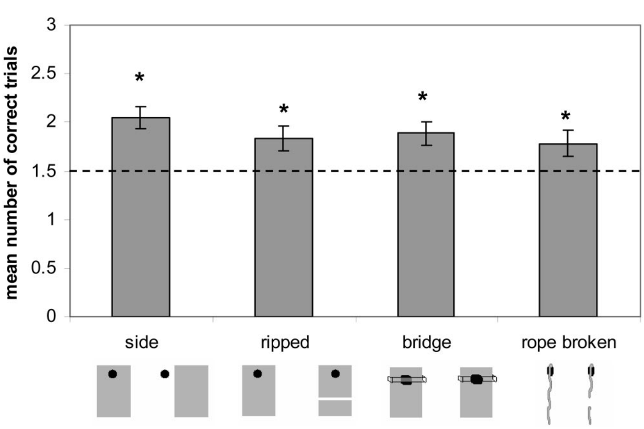

Figure 4. Mean number of correct trials (±95% confidence interval) out of three total trials across the four conditions given to sanctuary apes in Experiment 3. $^*p < .05$.

Discussion

Sanctuary apes who had no prior experience with the cloth or rope material successfully chose the functional tool over the nonfunctional tool in all four conditions presented here. As in the previous experiments, no significant differences between species were found in any conditions, which is notable given the large sample size for each species. Most of the ape tool-use literature is based on chimpanzee studies, and even though it is known that orangutans show a great variety of tool use in the wild (van Schaik et al., 2003), it had not previously been demonstrated that they would perform similarly to chimpanzees in a tool functionality study.

A further finding of this experiment was that the completely inexperienced sanctuary apes did not differ in their spontaneous performance from the Leipzig chimpanzees and orangutans, who have participated in numerous cognitive tests. In addition, this experiment confirmed the results from Experiment 1 that the side condition was the easiest for subjects.

These results suggest that material familiarity is not necessary for chimpanzees and orangutans to discriminate functional tools. Even apes with limited cognitive test experience were able to infer functionality in novel materials in a simpler set of tasks. The results from these three experiments suggest that failure with the plastic cane in Experiment 2 was probably not because of the novel material but was a result of the degree of difficulty of the presented problem. As mentioned in Experiment 2, apes understood tool functionality better for problems in which the food was in contact with the tool, as was the case in the four conditions in which the Leipzig and sanctuary apes succeeded. In the following experiment, we investigated whether contact between the food reward and the cane could increase performance with this material and whether experience would have an effect on performance.

Experiment 4: Familiar Materials, Complex Properties

While Experiment 3 demonstrated that great apes were able to infer functionality with no experience with the test materials, the results of Experiment 2 suggested that such inferences were not possible for more difficult functional distinctions. In the present experiment, we wished to investigate whether increased material familiarity would make these more difficult principles discernable, presenting subjects with cane conditions similar to those in Experiment 2. In addition, we investigated whether contact between the food reward and the tool could augment apes' performance on this difficult condition even further than added material familiarity. Thus, we presented subjects with conditions identical to those presented in Experiment 2 alongside conditions in which the reward was put in contact with the cane. If subjects succeeded at both conditions, this would suggest that individuals are able to understand more difficult functional properties with only a limited amount of experience—although having difficulty with absolutely no experience. If subjects succeeded at the contact conditions but not the original Experiment 2 conditions, this would suggest that the properties here were the most important factor, whereas experience did not allow subjects to succeed at the more difficult cane conditions. Finally, if subjects failed in both conditions here, this would suggest that there is some inherently simpler principle about the rope that allowed success in those conditions, rather than contact being the most important factor, and that only extensive experience allows subjects to discriminate more difficult functional distinctions, implying that the elements of connectivity presented in these conditions are particularly complex for even proficient tool users such as captive apes.

Method

Subjects

Subjects were a subset of those tested in Experiments 1 and 2 (see Table 1 for exact individual participation). These subjects had received experience with the cane plastic material by the time this experiment was carried out by participating in other tool-use experiments; subjects had received approximately 50 trials of experience with the gray plastic material, although never in the exact form used in Experiment 2 or the present experiment. Thus, by the time this test was carried out, subjects had a general familiarity with the plastic material, but did not have explicit training in understanding the connective properties of this material.

Materials

The same platform from Experiments 1 and 2 was used, but it was covered in blue plastic to create more contrast between the gray tools and the platform itself. The materials were the same as in Experiment 2's cane conditions.

Procedure and Design

Subjects received two versions of the cane conditions used in Experiment 2 (see Figure 5a and 5b). In the cane-contact version, the reward was placed on top of the corner of the canes, and in the cane version, the reward was placed on the platform inside the hook (as in Experiment 2). Thus, subjects received a total of six conditions: three in which the reward had physical contact with the tool (cane contact) and three in which there was no physical contact (cane). Each version of the task was given in a separate session. Half of the subjects received the cane session first, and the other half received the cane-contact session first. There were six trials per condition. We used the same scoring and analyses as in previous experiments.

Results

Figure 5a presents the mean number of correct trials across those conditions without contact between the reward and the tool. Subjects were above chance in the broken condition (Wilcoxon's test: $z = 2.83$, $p = .005$), but not in the other two conditions (Wilcoxon's test: on top, $z = 1.27$, $p = .20$, and touch, $z = 0.23$, $p = .82$). There were significant differences between conditions (Friedman test): $\chi^2(2, N = 26) = 8.61$, $p = .014$. Pairwise comparisons revealed that subjects performed better in the broken condition than in the touch condition (Wilcoxon's test: $z = 2.63$, $p = .008$).

Figure 5b presents the mean number of correct trials across those conditions with contact between the reward and the tool.

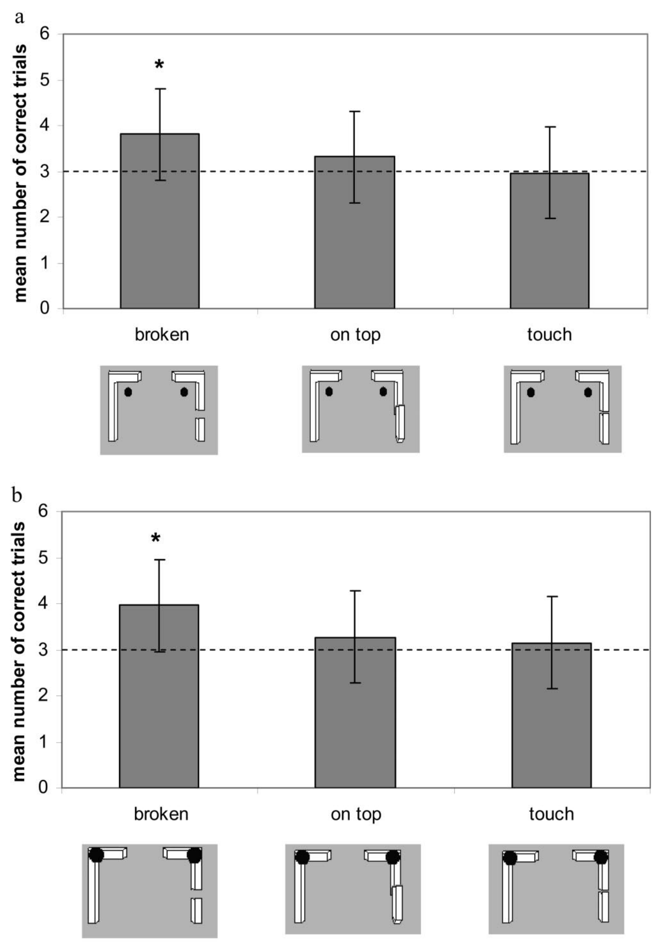

Figure 5. a: Mean number of correct trials (±95% confidence interval) across the three cane (no-contact) conditions in Experiment 4; $*p < 0 .05$. b: Mean number of correct trials (±95% confidence interval) across the three cane (contact) conditions in Experiment 4; $^*p < .05$.

Subjects were above chance in the broken condition (Wilcoxon's test: $z = 3.0$, $p = .003$) but not in the other two conditions (Wilcoxon's test: on top, $z = 1.22$, $p = .22$, and touch, $z = 0.59$, $p = .56$). However, there were no significant differences between conditions (Friedman test): $\chi^2(2, N = 26) = 4.63$, $p = .099$.

There were no significant differences between contact–no contact for any of the conditions (Wilcoxon's test: broken, $z = 0.56$, $p = .58$; on top, $z = 0.32$, $p = .75$; and touch, $z = 0.50$, $p = .61$). Therefore, we collapsed the conditions across reward contact and analyzed the effect of species for each condition separately. There were no significant differences across species for any of the conditions (Kruskal-Wallis test): broken, $\chi^2(3, N = 26) = 6.43$, $p = .093$; on top, $\chi^2(3, N = 26) = 4.10$, $p = .25$; and touch, $\chi^2(3, N = 26) = 0.89$, $p = .83$.

Discussion

Subjects' performance with the cane overall improved relative to Experiment 2, yet they were no better when the reward was in contact with the tool than when it was not in contact with the tool. Apes were successful in the broken conditions, both with reward contact and without, and still they did not prefer the functional tool in either version of the on-top and touch conditions. This success was in contrast to subjects' indifference between the two options in the cane-broken condition in Experiment 2. It is possible that the blue table alone increased subjects' level of success because the differences between tools could be seen more easily. However, other experiments we performed in the interim between Experiment 2 and the present experiment (Herrmann et al., 2004–2005) demonstrated that these color distinctions did not always augment performance, suggesting that although the blue table may have been a factor in subjects' performance, it was not the sole explanation for their success.

A more likely explanation is that subjects' increased amount of experience with the plastic material enhanced their abilities to discern its functionality. Through participation in other experiments with this plastic material, even without gaining familiarity with connectivity and canes per se, subjects were able to improve their understanding of this material's properties well enough to succeed at tasks at which they initially failed. This suggests that moderate experience, not even direct training, is required for subjects to infer more complex functional relationships, like the noncontact cane conditions.

General Discussion

The current four experiments suggested that both material familiarity and the property being tested are important in discerning tool functionality, with differing roles of each factor. Apes solved various versions of the support problem by discriminating between the reward when it was in contact with the cloth versus not in contact with the cloth (Experiments 1 and 3), whether this cloth material was familiar or unfamiliar. Subjects were also able to infer principles of connectivity when food was in contact with the reward, doing so with a familiar material in Experiment 1 and unfamiliar materials in Experiments 2 and 3. When the reward was not in contact with the tool, subjects had more difficulty, initially failing to discriminate connectivity with novel canes. However, after only a small amount of contact with this plastic material, subjects were able to succeed at making such distinctions, suggesting that experience is important for discriminating functionality when the distinctions presented are more difficult to perceive.

These results offer some insights into how apes perceive the relation between tools and rewards. It appears that the relation of support between the reward and the tool is an important component of their knowledge about tools, something that confirms previous studies (e.g., Natale, 1989). However, it is unclear whether support is perceived differently from mere contact or proximity. Shown a broken tool that perceptually appeared intact by joining its parts (touching condition, Experiments 2 and 4), subjects treated these two parts as if they were intact and did not discriminate between this and an intact cane. This confirms other studies showing that subjects treated contact relations as if they were support relations as when subjects pull strings that are in contact with but not tied to the reward (Köhler, 1925; Povinelli, 2000).

Despite this strong reliance on support (or contact), apes were able to solve the cane task (Experiment 4) in which the reward was not in contact with the tool. Thus, subjects successfully pulled various tools whose displacement made the reward move within their reach. Yet one could still argue that perceptual factors such as proximity play an important role in the decisions that the apes make. Recent studies have also reported similar results for capuchin monkeys and cotton-top tamarins (Fujita et al., 2003; Hauser et al., 1999). However, in these past studies, subjects had to be trained to pull the tools to obtain the reward. It took capuchin monkeys and cotton-top tamarins an average of 204 and more than 400 trials, respectively, to start selecting the correct tool above chance levels. In contrast, the apes performed this behavior spontaneously and performed above chance after only 12 trials (6 in Experiment 2 and 6 in Experiment 4). Thus, the effect that an intact tool can have on the reward is known by the apes in the absence of specific training and with solely increased familiarity with the material. This is also true for the species that use tools less often such as bonobos and gorillas.

As previously indicated, apes appeared more proficient than monkeys when initially given certain tool-use problems. For other problems, monkeys performed better than apes, although monkeys had invariably received initial training. Monkeys were able to transfer the knowledge that they had acquired during the training phase into the test conditions, which varied factors such as color, size, and shape of the tool. It is hard to know whether apes would have performed better in the on top and touch conditions presented here with additional training on the initial problem. We observed that subjects improved with additional experience in Experiment 4, suggesting that further experience may have allowed success in these more difficult conditions. Chimpanzees in the wild require several years of practice before being able to use a tool most effectively (Matsuzawa, 1994). However, it is difficult at present to say which elements of familiarity allow increased performance—whether subjects require increased tactile experience or whether increased visual experience alone would enable discrimination of properties. Thus, the question still remains which areas of functional understanding in apes can be enhanced by prior experience and what type of experience is most effective at allowing further generalization of tool-using principles.

A final note of caution is necessary. Although our results show that apes succeeded in some problems spontaneously, their group performance never exceeded 70% in the initial six trials. It is true that with additional trials performance increased, but it still remained quite low in most conditions. One possible explanation for this outcome is that their performance is not based on causal knowledge about the task. Another possibility is that they possess some causal knowledge, but that certain task features make it hard to express it consistently. For instance, motor or attentional biases present in the two-choice situation may have introduced some noise into the data. Alternatively, it is conceivable that subjects were not able to visually discriminate between options (this may have explained their failure to select gray canes seen initially) and might not attend to the properties being tested while still having some basic knowledge that we have not yet captured. Providing subjects with choices that are more visually distinct and that have to be more deliberate (such as a subject having to move to choose one object over another) may improve their performance. Presenting other paradigms that are not based on a forced-choice setup should be used as well, as has been performed in past tool research (e.g., Visalberghi et al., 1995).

In summary, we found that all four great ape species were able to spontaneously discriminate functional from nonfunctional tools in a variety of situations in the absence of material experience and training. They were best able to do so when the tool was in contact with the reward. All four ape species had difficulty when the tool was not in contact with the reward, but were able to discriminate such functional distinctions after only a small amount of experience.

Future research could help to pinpoint what sorts of experience, if any, are necessary to develop an understanding of tool properties. Some properties may require specific experiences, and others may be part of the individuals' "core" knowledge. Moreover, research about the understanding of functional properties needs to be conducted in different settings, such as more naturalistic tasks or more open-ended situations outside the forced-choice paradigm. It is only by combining these varied approaches that we can advance our knowledge in this area.

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